Oscillations in the Alpha Band (9–12 Hz) Increase with Memory Load during Retention in a Short-term Memory Task

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To study the role of brain oscillations in working memory, we recorded the scalp electroencephalogram (EEG) during the retention interval of a modified Sternberg task. A power spectral analysis of the EEG during the retention interval revealed a clear peak at 9–12 Hz, a frequency in the alpha band (8–13 Hz). In apparent conflict with previous ideas according to which alpha band oscillations represent brain 'idling', we found that the alpha peak systematically increased with the number of items held in working memory. The enhancement was prominent over the posterior and bilateral central regions. The enhancement over posterior regions is most likely explained by the well known alpha rhythm produced close to the parietal-occipital fissure, whereas the lateral enhancement could be explained by sources in somato-motor cortex. A time-frequency analysis revealed that the enhancement was present throughout the last 2.5 s of the 2.8 s retention interval and that alpha power rapidly diminished following the probe. The load dependence and the tight temporal regulation of alpha provide strong evidence that the alpha generating system is directly or indirectly linked to the circuits responsible for working memory. Although a clear peak in the theta band (5–8 Hz) was only detectable in one subject, other lines of evidence indicate that theta occurs and also has a role in working memory. Hypotheses concerning the role of alpha band activity in working memory are discussed.

Introduction

Working memory is the process by which the brain sustains the activity of cells whose firing represents information derived either from brief sensory input or readout from long-term memory. Recent theoretical and experimental work has focused on the role of brain oscillations in working memory and there has been particular interest in oscillations in the theta and alpha frequency bands (Lisman and Idiart, 1995; Basar *et al.*, 2000; Kahana *et al.*, 2001; Nunez *et al.*, 2001). These oscillations can be recorded either by electroencephalographic (EEG) or magnetoencephalographic (MEG) methods (Hari and Salmelin, 1997; Nunez *et al.*, 2001). Gevins and colleagues investigated the EEG in the theta and alpha bands in an *n*-back task in which subjects were presented with a continuous stream of items and had to indicate whether the displayed item matches the one presented n positions back (Gevins *et al.*, 1997). They found that the frontal midline activity in the theta band increases with memory load (*n*), whereas posterior activity in the alpha band decreases. The decrease in alpha band activity with memory load is in apparent conflict with other EEG studies in which alpha band activity has been shown to increase with memory demands: Krause *et al.* (Krause *et al.*, 1996) showed that alpha band activity increased during auditory memory retention and Klimesch *et al.* (Klimesch *et al.*, 1999) reported that alpha band activity was stronger during retention of supraspan compared to subspan memory lists.

To find the cause of the discrepancies in the alpha band between these rather complex memory tasks we measured scalp EEG during a modified version of the classical short-term memory paradigm, the Sternberg task (Sternberg, 1966). The main advantage of this task over the *n*-back task is that the periods of encoding, retention and the recognition are all separated in time. Thus, this paradigm allows us to study both the temporal and spatial development in the alpha band during the different stages of short-term memory processing. Subjects were visually presented with short lists of letters (two, four or six). After a 2.8 s retention interval, a probe item was presented and the subject indicated by rapid button-press whether the probe item was on the list. We recorded the scalp EEG from 10 subjects during the retention and recognition interval of the task and analyzed the data using various forms of spectral and time-frequency analysis. We undertook this study hypothesizing that theta rhythm would be the most salient frequency, as in the *n*-back working memory task. To the contrary, our results revealed dominant oscillations in the alpha band. These oscillations had a clear spectral peak and their amplitude increased with memory load. Further analysis of the temporal properties of alpha showed that its power declined exactly at the end of the task. Topographical plots enabled hypotheses concerning the locations of the sources generating the alpha power. This load-dependent increase in the alpha band needs to be reconciled with the classic view of alpha, according to which it represents an 'idling' rhythm that occurs during disengagement (Pfurtscheller *et al.*, 1996). Various possible reconciliations are discussed.

Materials and Methods

Subjects

Ten subjects (ages 18–35, half male/half female) performed a modified Sternberg (Sternberg, 1966) task while the EEG was recorded. Informed consent was obtained from each subject prior to the study.

Task

One second after a warning tone, a horizontally arranged list of six consonants was presented simultaneously at the center of a computer monitor (with one blank space between adjacent characters) for 0.2 s. The memory set (*S*) consisted of the middle two, four, or six letters, with each unused position (i.e. in the *S* = 2 or 4 conditions) filled with an 'X' (which was never a member of the memory set), except for the middle position which contained a fixation cross throughout the retention interval. Thus, the display was always of the same physical size and the visual content was the same, irrespective of the size of the memory set. After a 2.8 s retention interval (blank screen), the probe replaced the fixation cross and was displayed for the duration of the recognition interval (1 s). Subjects were instructed to press a mouse button as quickly as possible without making errors to indicate when the probe was a member of the memory set. Hand of response was counterbalanced across subjects. Following the recognition interval, subjects were allowed 3000 ms to relax and blink. There were 25 positive trials (probe on the list) and 25 negative trials (probe not on the list) for each set size, making a total of 150 trials per subject. The trials were presented in random order with respect to set size. The task differed from the original Sternberg

paradigm mainly in that: (i) the items were presented all at once rather than sequentially; (ii) button presses were required only for positive trials; and (iii) no performance feedback was given.

Data Acquisition

EEG epochs were recorded during the encoding, retention and recognition interval (6 s per trial) using 32 electrodes located according to the International 10–20 System. See Figure 2 for approximate locations of the electrodes. The signals were sampled at 250 Hz and bandpass filtered at 0.01–100 Hz. The reference electrode was placed over the left mastoid. The electrooculogram (EOG) was recorded in order to monitor horizontal (hEOG) and vertical (vEOG) eye movements.

Data Processing

Traces >45 µV in electrodes vEOG, hEOG, F7, F8, Fp1 or Fp2 were considered artefacts due to eye blinks, eye movements or muscle activity. Horizontal eye movements typically give rise to opposite-going voltage traces in F7 and F8. Hence, when the correlation coefficient of the signals in F7 and F8 was <–0.2, the trace was also rejected as artefact. Using these criteria, 29% of the traces were considered artefacts and removed from the data set. Power spectra of the linearly detrended traces recorded during the 2800 ms retention interval were calculated for the individual trails using fast-Fourier transforms (256 points) applying a 50% overlapping Hanning window (256 points). The detrending served to remove DC offsets and slow drifts (<1 Hz) (Press *et al.*, 1997). The level of power in a broad frequency range varied substantially between subjects. Since our analysis aimed at detecting changes in alpha power with memory load, the power spectra for each set size were normalized by the power integrated from 5 to 20 Hz for $S = 2$ for each subject. This allowed comparison and averaging over subjects.

A Student t-test was applied to establish if the increase in power with memory load in each electrode was statistically significant by comparing $S = 4$ with $S = 2$, $S = 4$ with $S = 2$ and $S = 6$ with $S = 2$ ($n = 10$ subjects). The increase in alpha power (P) with respect to set size (S) was fitted to $P(S) = bS + a$. A one-tailed Student's t-test was applied to test if regression coefficient b, calculated from the 10 data sets, was significantly greater than zero (Kanji, 1999) To characterize the relative increase in alpha power per memory item we applied the measure

$$P_{inc} = 100\frac{1}{4}\frac{P(6) - P(2)}{P(2)} = 100\frac{b}{2b + a}$$

Time-frequency representations were calculated by Morlet wavelets as described previously (Tallon-Baudry *et al.*, 1997). The energy $E(t,f_0)$ at given time t and frequency f_0 is given by the squared value of the convolution of the signal $s(t)$ to a Morlet's wavelet,

$$w(t,f_0) = A\exp(-t^2/2\sigma_t^2)\exp(2i\pi f_0 t), \text{ where } \sigma_f = 1/2\pi\sigma_t \text{ and } A = (\sigma_t\sqrt{\pi})^{-1/2}$$

We have chosen the 'width' of the wavelet $m = f_0/\sigma_f$ to 7. As for the power spectral analysis, the time-frequency representations were calculated for the linearly detrended individual trials prior to averaging.

Results

In order to verify that the key behavioral findings of the Sternberg task were reproduced, we calculated mean reaction time as a function of memory load. As shown in Figure 1, reaction time increased systematically as a function of load, with a slope of 64 ms/item. This value is higher than the 38 ms/item reported previously (Sternberg, 1966), a discrepancy that may be due to differences in the experimental procedure (see Materials and Methods). The error rates were 1.2, 3.2 and 16% for memory load $S = 2$, 4 and 6, respectively.

To determine which frequency bands contained rhythmic activity during the retention interval, we measured the EEG during the interval beginning with the onset of the memory list and ending with the onset of the probe. Power spectra were calculated for each trial and then averaged. A grand average was

obtained from 10 subjects, each performing a total of 90 trials (after removal of artefacts). As seen in Figure 2, the power spectra revealed a peak in the 9–12 Hz alpha band. Over the central posterior areas (e.g. Pz and Cz), the peak frequency was
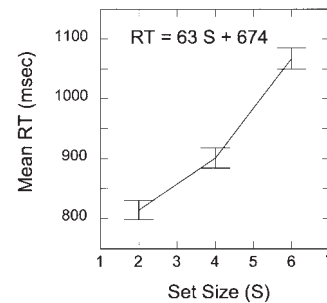
Figure 1. The reaction time (RT) as a function of memory load (S). The reaction time increases systematically with memory load.
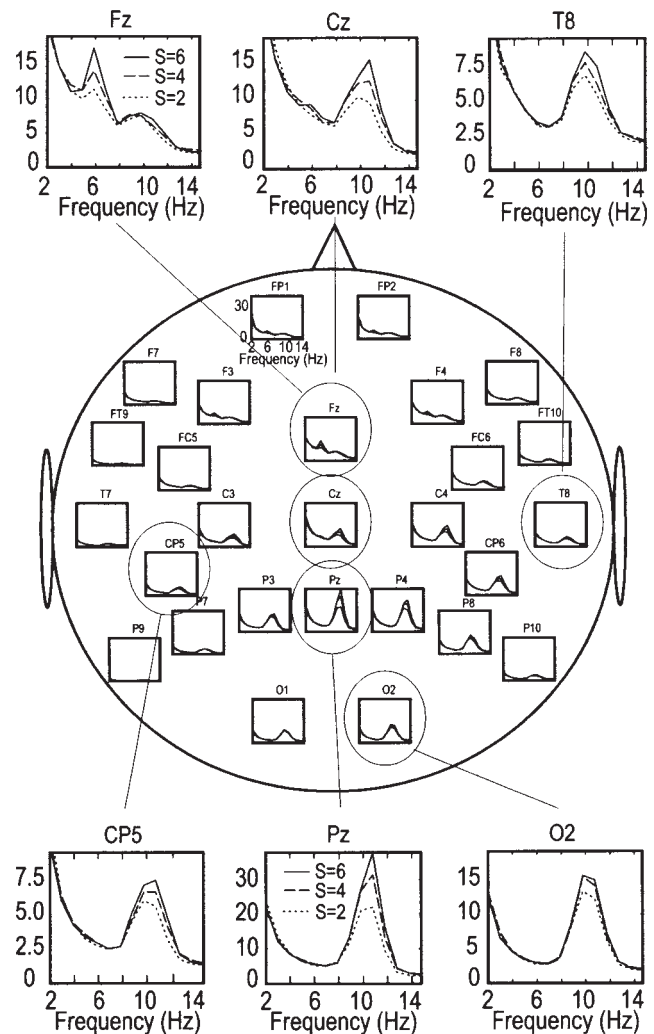
Figure 2. The averaged normalized power spectra calculated during the retention interval for all subjects and all trials. The graphs in the schematic head are organized topographically according to the approximate location of the electrodes on the scalp. The six enlarged graphs show the spectra for memory load $S = 2$ (dotted line), $S = 4$ (broken line) and $S = 6$ (solid line) for selected electrodes. Note that the scales of power are different in the enlarged graphs.

~11 Hz, whereas it was 9–10 Hz over bilateral central areas (e.g. FC5, T7, FT10, FC6, T8). This indicates that different sources produced the posterior and bilateral alpha band activity. There is also an indication of a ~6 Hz theta rhythm in the frontal areas (Fz, F3, F4, FP1 and FP2). However, further analysis revealed that the 6 Hz activity in the grand average was due to a large theta peak evident in one of the 10 subjects.

To determine whether the alpha activity was affected by memory load (*S*), the power spectra were investigated with respect to *S* = 2, 4 and 6. As shown in the enlarged graphs in Figure 2, the power in the 9–12 Hz band increased systematically with memory load in both posterior (e.g. Pz and O2) and lateral electrodes (e.g. CP5 and T8). In Fz, a systematic increase with memory load was observed at 6 Hz (the theta band). As mentioned above, this effect was dominated by a single subject.

Over which areas was the alpha activity strongest? Figure 3*A* shows the topography of the power of the 9–12 Hz activity during the retention interval for the three memory loads. Little difference is observed between the three conditions. Power was strongest over posterior areas (maximum at Pz), suggesting that the measured 9–12 Hz activity is dominated by the well-known alpha sources in the parietal-occipital sulcus. Figure 3*B* shows the topographies of the relative increases in the 9–12 Hz band with memory load during the retention interval. When comparing *S* = 4 to *S* = 2 posterior electrodes show an enhancement, but lateral electrodes also contribute. As seen by the electrodes in which the increase was significant (denoted by white asterisks, *P* < 0.05), the enhancement is left-lateralized. The topography emerging when comparing *S* = 6 to *S* = 4 is more frontal and right-lateralized. The maximum increase (~8%) is less than when comparing *S* = 6 to *S* = 4; however, it is highly statistically significant as shown by the white asterisks. When comparing *S* = 6 to *S* = 2, the increase in 9–12 Hz activity was distributed over posterior and left and right central areas. The regression coefficient of the 9–12 Hz power on the three memory loads was calculated. The electrodes in which the regression coefficient was significantly greater than zero (*P* < 0.05) included all the electrodes in which the increase was significant when comparing *S* = 6 to *S* = 2 (white asterisks). Additional electrodes with positive regression coefficients are marked by the white circles (electrodes with a significant positive regression coefficient: CP5, C3, Cz, C4, P3, Pz, P4, CP6, P8, P10, O2, T9 and FT10). A tendency to right-lateralization was observed by this measure.

Is the enhancement in power with memory load due to a short-lasting increase in the 9–12 Hz activity, or is it explained by a sustained increase throughout the retention interval? To answer this question, we conducted a wavelet-based time–frequency analysis. Only electrodes with a significant increase in power with memory load were included in the time-frequency representation (asterisks and circles in Fig. 3*B*, panel 3). The 9–12 Hz activity was low during the first 300–400 ms following the onset of visual presentation. Then the 9–12 Hz activity increased for the remaining 2.5 s of the retention interval. Figure 3*D* shows the time-frequency representation of the increase in 9–12 Hz activity with memory load per item. This measure is derived from the regression coefficient of power on memory load (see Materials and Methods). The 9–12 Hz power increase with memory load was present during the last 2 s of the retention interval. The topography of the increase in the 9–12 Hz band with memory load over time was investigated by dividing the retention and recall interval into eight subsections. As seen in Figure 3*E* the load-dependent enhancement in the 9–12 Hz band was strong from 1.0 to 3.0 s (panels 2–5). The central parietal

electrode Pz continuously measured a load-dependent increase. Over central areas, the trend is an initial left-lateralization (0.6–1.4 s), which eventually becomes right-lateralized (1.8–3 s).

In subject 9 we observed strong activity in the theta band over frontal areas during the retention interval (Fig. 4*A*). The theta activity increased systematically with memory load (*P* < 0.05). A time-frequency analysis demonstrated that the theta activity reached a peak ~1–2 s after the onset of the retention interval and was temporarily suppressed at the time of memory scanning (Fig. 4*B*). Interestingly, posterior alpha activity was also observed in this subject (e.g. Pz, Fig. 4*C*). The alpha activity appeared to increase with memory load, but the increase was not statistically significant. The time-course of the posterior alpha activity as shown in Figure 4*D* was similar to the 9–12 Hz activity observed in the grand average (Fig. 3*C*).

Discussion

We examined brain oscillations in the scalp EEG of 10 subjects performing a modified Sternberg task. During the retention interval, the power spectra showed a clear peak in the alpha band. The 9–12 Hz power increased parametrically with memory load and the load-dependent enhancement was present in at least the last 2 s of the 2800 ms retention interval. Judging from topographical plots, sources in both posterior and bilateral brain regions could be responsible for producing the enhancement in the 9–12 Hz band with memory load. We observed frontal theta activity in only one subject. The theta activity increased with memory load and persisted during the retention interval.

Our results show not only that 9–12 Hz activity is present during the retention interval of the modified Sternberg task, but that its amplitude increases with load. This is an important result because it indicates that activity in the alpha band does not simply reflect a unitary working memory state, but has a graded quality that depends on the number of items being stored. This gradedness could reflect the amplitude of the underlying oscillation, but it could also reflect the degree of synchronization across multiple brain regions or the number of regions involved. Our results provide evidence for gradedness within the framework of a Sternberg-type task, in which the list length is always taken to be less than memory span. Previous work (Klimesch *et al.*, 1999) has shown that alpha band activity can depend on the type of list (subspan versus supraspan).

We also found that the 9–12 Hz activity was temporally linked to the working memory task. Each trial ended when the subject made a response thus knowing that the memory set no longer needed to be retained. The 9–12 Hz activity decreased in power within a few hundred milliseconds of the response.

The presence of alpha band activity during the retention period of the Sternberg task appears to be a robust finding. Examination of the power spectrum shows a clear peak in the alpha band at 9–12 Hz. This point needs to be emphasized because many EEG studies integrate the overall power in a frequency band and study how this integral is affected by task conditions — e.g. the method of event related synchronization and desynchronization (Krause *et al.*, 1996; Pfurtscheller *et al.*, 1996). This leaves open the possibility that the power in a given frequency band does not actually occur because of an oscillation at that frequency (e.g. non-sinusoidal signals at a given frequency generate power in frequency ranges other than the repetition frequency). The direct demonstration of a peak in the power spectrum provides a much stronger indicator that the brain regions involved are actually producing rhythmic activity at that frequency. Our results in this respect are consistent with those of previous workers (Klimesch *et al.*, 1999), who also observed
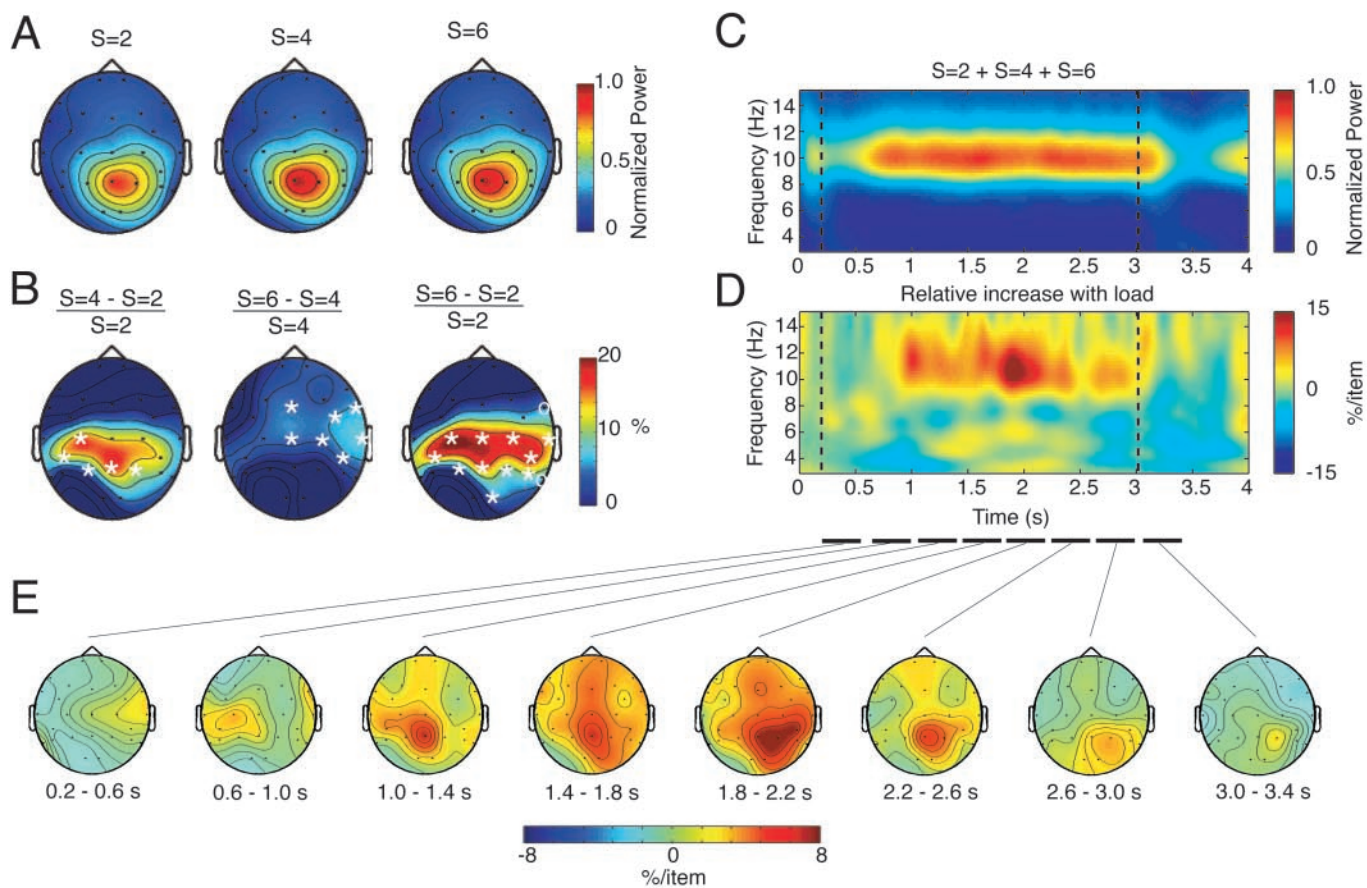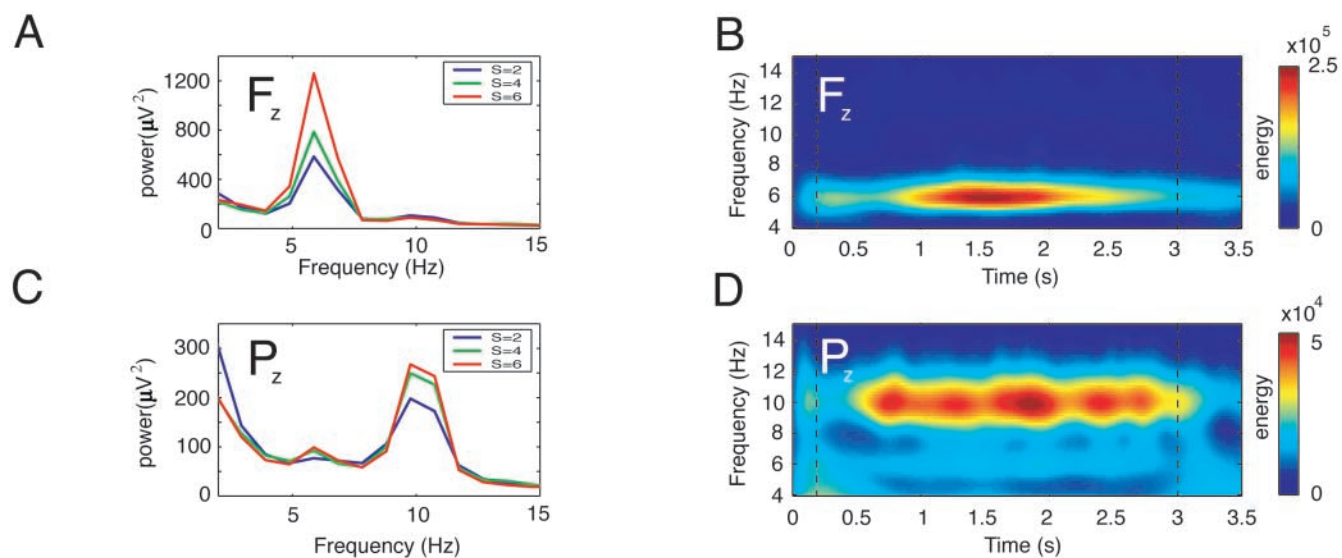
Figure 3

Figure 4

a prominent alpha band peak in the scalp EEG during a memory scanning task.

We did not detect a peak in the theta band, except in one subject. Strong theta activity has been detected in the EEG recorded directly from the surface of the cortex of epileptic patients (Kahana *et al.*, 1999; Raghavachari *et al.*, 2001). A recent MEG study reports on a systematic increase in frontal theta activity with memory load (Jensen and Tesche, 2002). Thus, our failure to observe theta in scalp recordings in most subjects should in no way imply that it does not occur in the brain.

The increase in alpha band power with memory load appears at odds with a report that alpha power decreases with memory load during a different working memory task. Using the *n*-back task, previous workers (Gevins *et al.*, 1997) have demonstrated a decrease in the alpha band when *n* = 3 is compared to *n* = 1. We suspect that this difference might be related to the very different nature of the memory tasks. The *n*-back task is quite demanding: each time a new item is presented the subject must encode the item, perform memory scanning, give the answer and delete previous items from memory. In the Sternberg task, encoding, retention and recognition are temporally separated. In order to facilitate the many overlapping operations while performing the *n*-back task, it is possible that subjects are more prone to utilize a visual strategy than when performing the Sternberg task. Assuming that alpha activity reflects suppression of processing in visual areas, increased demands to the visual system with memory load would explain the posterior decrease in alpha activity.

It is of interest to compare the 9–12 Hz activity during retention to the 9–12 Hz activity that occurs during rest with eyes closed. By the use of MEG it has been possible to separate spontaneous rhythms in the 9–12 Hz band into at least two major components (Hari and Salmelin, 1997). Posterior brain areas whose sources have been localized close to the parietal-occipital fissure produce the first component, the alpha rhythm. Such sources most likely produce spectral peaks at ~11 Hz over central posterior areas (e.g. Cz, Pz, P3 and P4; Fig. 2). The second component identified during rest is a component of the Rolandic mu rhythm, which typically has spectral peaks simultaneously in the ~10 Hz, and ~20 Hz band. The main sources of the mu rhythm have been localized close to the hand area of the primary somato-motor cortex (Salmelin and Hari, 1994). Thus, sources in somato-motor cortex are likely to explain the lateral peaks at ~9–10 Hz (e.g. T7, FC5, FC6, T8 and P8; Fig. 2) and the topography of the alpha enhancement (Fig. 3*B*). Improved methods for identifying sources of ongoing oscillatory activity might help to resolve this issue (Jensen and Vanni, 2002). In conclusion, it is possible that the memory-dependent alpha 9–12 Hz is generated by the same parietal-occipital alpha sources and the somato-motor sources that generate 9–12 Hz activity during rest.

When inspecting the topographical plots in Fig. 3*B*, the 9–12 Hz enhancement appears left-lateralized when comparing *S* = 4 to *S* = 2, and right-lateralized when comparing *S* = 6 to *S* = 4. The temporal development of the memory-dependent topography (Fig. 3*E*) appears left-lateralized initially and shifts to a right-lateralization by the end of the retention interval. These lateralizations should be interpreted with caution, since they might partly be explained by statistical fluctuations. Furthermore, the use of a left mastoid electrode as reference might also bias the lateralization.

Our results, together with recent findings from several laboratories (Krause *et al.*, 1996; Klimesch *et al.*, 1999), suggest that the standard view of alpha as an 'idling' rhythm may need revision. The standard view arose from the observation mentioned above that alpha occurs during rest with eyes closed. The alpha activity can be blocked by mental activity or the sensory stimulation produced by opening the eyes (Berger, 1929; Pfurtscheller *et al.*, 1996). It was therefore thought that alpha represented a default mode of brain regions when they were not functioning. If this was the case, one must ask why alpha activity should increase during a working memory task and why this increase should be graded with task requirements. One interesting idea that could reconcile these results is the hypothesis of Klimesch *et al.*, which assumes that the generators of the memory-dependent alpha are similar to the generators producing spontaneous alpha during rest (Klimesch *et al.*, 1999). Klimesch *et al.* suggested that alpha activity signifies that these areas are not being used in processing and, in fact, are being inhibited by other active brain regions. In this inhibited state or state of disengagement, these regions would generate alpha in a manner similar to that which would occur when the brain regions were inactive during the relaxed state. Such inhibition might actually play a functional role in preventing the flow of information into areas which are retaining memory items. For instance, the inhibition or disengagement of occipital-parietal areas could serve to suppress input from the visual stream, which could disturb the maintenance of working memory in frontal areas. This idea of active inhibition is supported by recent EEG work exploring which occipital regions produced alpha activity in a visio-spatial attention task (Worden *et al.*, 2000). It was demonstrated that alpha activity increased in a given occipital area if a hemifield which was to be ignored projected to that area. Similarly, an increase in alpha activity produced by somato-motor areas could reflect inhibition or disengagement of the motor system during the retention

Figure 3. A spatio-temporal characterization of the 9–12 Hz activity during retention and recall. (*A*) The topography of the 9–12 Hz power for memory load *S* = 2, 4 and 6, calculated during the retention interval and averaged over the 10 subjects. (*B*) The topography of the relative increase in power during the retention interval. The three plots show the respective comparisons of *S* = 4 with *S* = 2, *S* = 6 with *S* = 4 and *S* = 6 with *S* = 2. The white asterisks indicate electrodes in which the increase was statistically significant (*t*-test, *P* < 0.05). The regression coefficient was calculated for the increase in power on memory load (*S* = 2, 4 and 6). The electrodes which had a regression coefficient significantly greater than zero (*t*-test, *P* < 0.05) overlapped with those calculated when comparing *S* = 6 with *S* = 2. In addition, two electrodes (marked by white circles) were found to have a positive regression coefficient. (*C*) A time-frequency representation of power ('energy') during the retention and recall periods. At *t* = 0 s, the memory list is presented for 0.2 s and at *t* = 3 s the probe arrives. The time-frequency representations were averaged over the electrodes which had a significant increase in alpha power with memory (white asterisks and circles in the last panel of *B*). (*D*) A time-frequency representation of the change in energy with memory load per item, derived from the regression coefficient of power on memory load (see Materials and Methods). The time-frequency representations were averaged over the same electrodes as applied in *C*). (*E*) The temporal development of the topography of the alpha enhancement with memory load during retention and recall.

Figure 4. The spectral properties of the frontal (Fz) and posterior (Pz) EEG recorded from subject 9. (*A*) The power spectra for Fz calculated during the retention interval reveal a systematic increase in the theta band at 6 Hz with memory load (*P* < 0.05). (*B*) A time-frequency analysis (right) of the frontal EEG during retention and recall. Theta becomes particularly strong 0.8 s following presentation of the items (*t* = 0–0.2 s) and is sustained throughout the retention interval (*C*) The power spectra from Pz indicate an increase in the 9–12 Hz at 10 Hz with memory load, but it is not statistically significant. (*D*) The time-course of the activity in the 9–12 Hz band resembles the grand-average in Figure 3*C*.

interval. This hypothesis is consistent with the 'freezing' observed in humans when strong concentration is required.

Yet another possibility is that the alpha activity during the retention interval is explained by a rebound following the suppression of the alpha activity by the visual presentation of the memory items: the more items presented, the greater the alpha rebound. This hypothesis is not very likely, since the display of memory items was controlled such that the visual content across all three conditions was the same (as described in the Materials and Methods section).

An alternative to the inhibition hypothesis is that alpha band activity is directly involved in the neuronal mechanisms responsible for maintenance of working memory. A physiological model has been developed in which 5–10 Hz cortical oscillations are responsible for the active maintenance of working memory representations (Lisman and Idiart, 1995; Jensen and Lisman, 1998), However, there are several arguments against load-dependent alpha band activity being directly involved in the maintenance of STM. First, alpha band activity emerges in conditions not involving memory. Second, the location of working memory functions based on brain imaging (D'Esposito *et al.*, 1995; Cohen *et al.*, 1997; Smith and Jonides, 1997; Rympa *et al.*, 1999) and lesion studies (Shallice and Vallar, 1990) does not directly involve brain areas in which the sources of the alpha band activity have been identified.

In conclusion, the increase in alpha band activity with memory load appears either to be a consequence of active inhibition of alpha-producing brain areas or it is explained by a mechanism in which alpha band oscillations are directly involved in memory maintenance. Further research is required to distinguish between these two hypotheses.

Notes

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