SHORT COMMUNICATION

EEG theta synchronization conjoined with alpha desynchronization indicate intentional encoding

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Keywords: EEG power, faces, human, learning, words

Abstract

The involvement of different oscillating neuronal systems activated during intentional learning was investigated by measuring ongoing EEG activity. In 17 subjects, the EEG was recorded while learning pairs of words and faces. Subjective task difficulty was rated and a control condition of mental relaxation was also run. Spontaneous EEG activity during epochs which subsequently resulted in efficient encoding was associated with upper alpha desynchronization (10–12 Hz) and theta synchronization (4–8 Hz) when compared with spontaneous EEG activity during epochs of poor recall performance. The combined measure of theta desynchronization plus upper alpha desynchronization was enhanced selectively over left frontotemporal cortical regions during efficient learning of words and over right parietal cortical regions during efficient learning of faces (P < 0.001). This striking topographical dissociation between learning materials for the combined measure of theta and upper alpha EEG activity suggests that the mode of intentional learning relies essentially on an interdependent regulation of two neuronal circuits: the thalamo-cortical circuit and the hippocampo-cortical circuit.

Introduction

Encoding refers to a process that converts a perceived stimulus into an enduring neurophysiological trace. Thus, it represents the initial part of a memory process and is decisive for what is stored into memory (Tulving, 1983). Studies using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) revealed a network of brain regions activated selectively during encoding which included the left anterior frontal cortex and portions of the mid-temporal lobe (Kapur et al., 1996; Fernandez et al., 1998; Grady et al., 1998; Cabeza & Nyberg, 2000). Moreover, a left-hemispheric lateralization of activation for encoding words as compared to a more bilateral activation for pictorial stimuli was found (e.g. Haxby et al., 1996; Kapur et al., 1996; Wagner et al., 1999; Kirchhoff et al., 2000). Yet, how these metabolic changes translate to changes in electroencephalographic activity is unknown at present.

EEG activity reflects self-generated coherent activity within neuronal circuits that are assumed to be highly functional in that they organize and optimize ongoing information processing (Steriade, 2000; Nunez, 2000; Llinas & Ribary, 2001). Thus, ongoing rhythmic EEG activity may also be useful for distinguishing an internally generated mode of intentional encoding that is not strictly linked to external stimuli. Studies of event-related activity provided hints that two oscillatory processes contribute to encoding in a complementary way (Klimesch, 1995, 1999): (i) a desynchronization of the alpha rhythm (in particular in the upper range) which has been considered to reflect the selective activation of specific long-term memories residing in neocortical networks relevant for stimulus integration (Klimesch et al., 1997a), and (ii) an increase in theta activity considered to originate from increased activity in cortico-hippocampal feedback loops during intentional encoding (Buzsaki, 1996; Klimesch et al., 1997a; Kahana et al., 1999; Burgess & Gruzelier, 2000; Gevins & Smith, 2000). While the human studies on this issue focused on event-related EEG responses, it was of interest here whether the ongoing EEG activity, as a reflection of a mode of intentional encoding, is likewise characterized by upper alpha desynchronization and theta synchronization. As these two oscillations probably contribute jointly to successful encoding, the main analysis of spontaneous EEG activity was based on a combined measure of theta desynchronization plus upper alpha desynchronization.

Materials and methods

Subjects, and EEG, EOG and EMG recordings

Seventeen right-handed subjects (11 female, aged 20–31 years) participated in the study, which was approved by the local committee on research involving human subjects. EEG activity was recorded from Fp1, Fp2, Fz, F3, F4, F7, F8, T3, T4, T5, T6, Cz, C3, C4, Pz, P3, P4, O1, and O2 electrodes (International 10–20 system). Linked electrodes attached to the mastoids served as reference. Four electrodes were used to record vertical and horizontal eye movements (EOG). Muscle activity (EMG) was recorded from the left and right muscle temporalis, the forehead and neck. A single ground electrode

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Received 30 September 2001, revised 3 January 2002, accepted 16 January 2002
was attached at Fpz. EEG, EOG and EMG signals were recorded using a SynAmps EEG ampli®er (NeuroScan Inc., Sterling, VA, USA). Sample frequency was 500 Hz with 16-bit analogue-to-digital precision. EEG and EOG were ampli®ed within a band width of 0.15±70 Hz and EMG within 10±100 Hz. During the complete session, subjects sat comfortably in a reclining chair in a half supine position.

**Stimuli and procedure**

Subjects had to learn intentionally either pairs of words or pairs of faces. In the word pair condition they were shown six panels with nine word pairs per panel. In the face pair condition, six panels were presented with three pairs of faces per panel. The numbers of word and face pairs per panel differed; it was not the response to the single stimulus that was of importance here but to engage subjects in a constant mode with roughly comparable demands of encoding for a time period of 40 s. Pilot experiments had shown that subjects did not feel challenged enough by the task of encoding only three or even six word pairs. After the six panels had been presented, subjects were asked to recall the learned pairs in a cued recall situation. For the word pairs, this required subjects to retrieve from memory and report orally the second word of the pair upon presentation of the ®rst word. For recall testing of face pairs, subjects were presented subsequently with 18 panels each showing one face on the left side and 18 faces on the right side. For each panel, the subject had to decide which of the 18 faces on the right side belonged to the face on the left side. Three consecutive runs of learning (and subsequent recall) were performed. The subjects were instructed to engage in a rote rehearsal learning strategy during stimulus presentation involving repetitive silent reconsideration and imaging of the presented individual items.

Stimuli were presented to the subjects at a distance of 100 cm from their eyes. The word pairs had a width of 8–16 cm (4.6±9.2° visual angle) with the height of one letter about 1 cm. The face pictures had a width of 6.7 and a height of 9 cm (3.8 and 5.2° visual angle) and were printed in black and white (with grey scales). Each panel was presented for 40 s, and during this interval the EEG was recorded. During stimulus presentation, subjects were not allowed to speak and were to avoid large eye movements and blinks. At the end of each condition, subjects were asked to rate the task dif®culty on a seven-point rating scale (±3 to +3). The order of both conditions was balanced across subjects. A resting EEG, during which the subject performed a mental relaxation task, was recorded twice, once during a 40-s interval after the ®rst condition and the second time during a 40-s interval after both conditions. The subjects were instructed to ®xate with their eyes on a centrally located dot on the opposite wall,
Table 1. *F*-values from ANOVA for intentional learning with repeated measures for Material (words, faces), and Topography

<table>
<thead>
<tr>
<th>Components of EEG activity</th>
<th>Material (F-Values)†</th>
<th>Material × Topography (F-Values)‡</th>
<th>Significance at single electrodes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delta (1–4 Hz)</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Theta (4–8 Hz)</td>
<td>–</td>
<td>–</td>
<td>T5, ** F7*</td>
</tr>
<tr>
<td>Alpha-1 (8–10 Hz)</td>
<td>5.8*</td>
<td>–</td>
<td>C4, O2, T6,** Pz, P4, O1, T4*</td>
</tr>
<tr>
<td>Alpha-2 (10–12 Hz)</td>
<td>–</td>
<td>3.8**</td>
<td>C4, Pz, P4,** C2, O2, T6*</td>
</tr>
<tr>
<td>Beta (12–25 Hz)</td>
<td>9.0**</td>
<td>–</td>
<td>Cz, C4, Pz, P3, P4, O1, O2, T5, T6,** C3, T4*</td>
</tr>
</tbody>
</table>

†d.f., (1, 16); ‡d.f., (18, 288). Topography: Fp1, Fp2, Fz, F3, F4, Cz, C3, C4, Pz, P3, P4, O1, O2, F7, F8, T3, T4, T5 and T6. Only EEG epochs from good trials are included. Right columns indicate significant differences for pair-wise comparisons performed for each electrode site. Significant effects indicate greater power for words than faces in all cases. **P < 0.01, *P < 0.05.

and to imagine that ‘they were lying on a beach, the sun was shining and the waves were rolling softly’.

Data analysis and statistical evaluation

For each recorded 40-s EEG interval, one 20.48-s long EEG period free of large eye movements or other artefacts was selected. If possible, these 20.48-s epochs for analysis were taken from the centre of the 40-s interval. Smaller ocular artefacts were corrected with the regression method using the vertical and horizontal EOG (Gratton et al., 1983). Using a Fast Fourier Transformation (FFT) the 20.48-s epochs of EEG-activity were transformed into log amplitudes of a power spectrum, and average values for the delta (1–4 Hz), theta (4–8 Hz), alpha-1 (8–10 Hz), alpha-2 (10–12 Hz) and beta (12–25 Hz) bands were obtained. The power spectrum was calculated by averaging the FFT of nine overlapping segments of 2048 points each after standard tapering of each data segment. For EMG signals, an FFT was used in the same way as for the EEG signals except that only power in the 70–100 Hz band was calculated. For EOG analysis, root mean square values were calculated after low pass filtering at 2.5 Hz.

Our analysis concentrated on a combined measure of ‘alpha-2 desynchronization plus theta synchronization’, accounting for the assumed reciprocal relationship between respective oscillatory networks. Taking reference to similar measures employed for analyses of event-related EEG desynchronization (Pfurtscheller & Aranibar, 1977; Klimesch et al., 1997b), percentage alpha-2 desynchronization (α-2DS) was expressed by the formula:

$$\alpha-2_{DS} = \left[\frac{(\text{α-2}_\text{MR} - \text{α-2}_L)}{\text{α-2}_\text{MR}}\right] \times 100$$

Where, α-2MR is alpha-2 power during mental relaxation and α-2L is alpha-2 power during learning. Correspondingly, percentage theta synchronization (θ3) was calculated by the formula:

$$\theta_3 = \left[\frac{(\text{θ}_\text{MR} - \text{θ}_L)}{\text{θ}_\text{MR}}\right] \times 100$$

For the combined measure of alpha-2 desynchronization plus theta synchronization, high values express pronounced alpha-2 desynchronization in conjunction with strong synchronization in the theta range and vice versa, low values relatively synchronized alpha activity and relatively desynchronized theta. For mental relaxation, the mean of the power values from the two 20.48-s epochs was calculated.

Statistical analyses relied on analysis of variance (ANOVA). The first analysis was on the data from the learning condition and included repeated measures factors for Stimulus Material (words, faces), and Topography (i.e. the electrode locations). A further factor for Learning Efficacy was introduced to differentiate trials with good vs. poor performance at later recall testing. On good trials the number of items correctly recalled (on subsequent recall testing) was ≥ 4 for word pairs and ≥ 1 for face pairs. Poor performance was defined as < 4 for word pairs and < 1 for face pairs.

A second analysis compared the EEG (and EMG) of intentional learning and mental relaxation. This analysis included repeated measures factors for Condition (learning, relaxation) and Topography. All analyses included trials from the first learning run, only. (The second and third runs were excluded because of ceiling effects in learning performance and also to avoid potential influences of retrieval testing.) Evaluation of self-rated task difficulty was also based on ANOVA. A P < 0.05 was considered significant. A Greenhouse–Geisser correction of degrees of freedom was applied where appropriate.

Results

Power spectral measures

Analysis of the EEG during learning revealed a distinct dependency for the combined measure of alpha-2 desynchronization plus theta synchronization on both the stimulus material and the learning efficacy, as confirmed by a significant Material × Efficacy × Topography interaction (F18,288 = 3.2, P < 0.01) in the overall ANOVA (Fig. 1, left). Subsequent analyses on only good trials, i.e., with efficient learning, showed that the combined measure of alpha-2 desynchronization plus theta synchronization for words was selectively enhanced over left frontal and temporal regions (F7, T3: P < 0.05) and for faces over right parietal cortical regions (Pz, P4: P < 0.01 and C4, T6: P < 0.05; F18,288 = 4.8, P < 0.001, for respective Material × Topography interaction term, Fig. 1, right). No similar effects were obtained in analyses on the poor trials, P > 0.3 for Material × Topography).

Separate analyses of the different frequency bands indicated generally higher power for words than faces for the low alpha and beta frequencies. Note, while overall ANOVA on this data set did not reveal significant effects for the theta band, contrasts at single electrodes indicated for good trials, significantly higher theta power over left frontal and temporal regions (T5: P < 0.01; F7: P < 0.05) for word pair than face pair learning (Table 1 summarizes ANOVA results). For the alpha bands the differences between words and faces, with lower power for faces clearly focused over right posterior cortical areas (Fig. 2). Contrasting trials with good vs. poor performance at later recall testing indicated a significant Material × Efficacy × Topography interaction for alpha-2 power (F18,288 = 2.8, P < 0.01). The effect reflected primarily a reduced alpha-2 power over parietal regions (Pz, P4: P < 0.01; P3, Cz and T4: P < 0.05) for efficient as compared to poor learning of faces.
Comparisons of effects of learning and mental relaxation showed that in the lower frequency bands (delta and theta) power was higher during learning than mental relaxation (respective main effects of condition: $F_{1,16} = 26.2$, $P < 0.001$ for delta and $F_{1,16} = 10.0$, $P < 0.01$ for theta). While the differences in delta power were wide spread and significant in all pair-wise comparisons at single electrode sites, the increase in theta power was particularly prominent over occipital and frontotemporal electrode sites ($F_{18,288} = 10.4$, $P < 0.001$ for Condition $\times$ Topography and for pair-wise comparisons at O1, O2, $P < 0.01$ at Fp2, F4, F8, T3, T4 and T6). Also, power in the upper alpha frequency band during learning was decreased as compared to mental relaxation over left parietotemporal areas ($P < 0.01$, for Condition $\times$ Topography interaction; $P < 0.05$ for pair-wise comparisons at P3 and T5). Power in the beta band appeared to be higher during learning than mental relaxation, but this effect was restricted to lateral prefrontal areas and may in part reflect muscular contamination (see below).

**Muscle and EOG activity**

No differences in EMG activity between learning of faces and words and between good and poor trials were observed. EMG activity was enhanced at the forehead lead during learning as compared to mental relaxation (Condition $\times$ Topography, $F_{3,48} = 11.8$, $P < 0.001$; $P < 0.001$ for pair-wise comparisons between the two conditions at the forehead lead). Vertical and horizontal EOG (VEOG and HEOG) activity did not differ between learning of faces and words or between good and poor trials, while an expected increase in EOG activity during learning in comparison with mental relaxation was revealed to be significant only for the HEOG ($P < 0.01$).

**Learning performance and self-rated task difficulty**

The number of correctly recalled items after the first learning run was (mean ± SEM): 28.0 ± 2.3 (51.9 ± 4.3%) for words and 3.8 ± 0.7 (20.9 ± 3.7%) for faces. Learning of words was rated less difficult than that of faces (1.00 ± 0.33 vs. 2.71 ± 0.11, $P < 0.001$). However, there was no significance for the task difficulty, if introduced as a covariate in the EEG analysis, for any frequency band.

**Discussion**

The combined measure of alpha-2 desynchronization plus theta synchronization revealed a most striking dissociation between trials with efficient vs. poor encoding and a distinct topographical differentiation between encoding of words vs. faces. Trials with efficient encoding were accompanied by a higher value of alpha-2 desynchronization plus theta synchronization and this effect was particularly pronounced over left frontal and temporal cortical areas during learning of words, which is known as a left hemispheric task. This pattern bears remarkable similarities with fMRI findings: Wagner et al. (1998) showed that the ability to remember memorized words at a later time can be predicted from the magnitude of blood oxygenation levels dependent (BOLD) signal activation in left prefrontal and temporal cortices during word encoding. For encoding of faces, typically involving the right rather than left hemispheric regions (e.g. Haxby et al., 1996), effects concentrated over right parietal areas (Fig. 1). The circumscribed changes in oscillatory EEG activity show a topography as would be expected from corresponding imaging studies of encoding of faces and words using fMRI and PET (Grady et al., 1998; Kelley et al., 1998; Smith & Jonides, 1998). However, it must be considered that at present, knowledge about the exact relationships between EEG oscillations and fMRI/PET activations is only limited (Logothetis et al. 2001).

Our finding, that the combined measure of upper alpha desynchro-
between memory performance and learning material than changes in the separate bands, presumably reflects the focus of the present analysis on self-generated modes of neocortical rhythmic activity occurring during intentional encoding. Event-related synchronization and desynchronization have been previously used separately to measure demands on episodic (working) and semantic memory, respectively (see Klimesch, 1999 for a review). However, in contrast to the 1–2-s EEG epochs surrounding stimulus presentation in event-related desynchronization studies, the present experiments analysed 20.48 s of activity within a 40-s long learning interval. Thus, the conjoined activity of the two different oscillatory neural circuits involved in different aspects of encoding activity during this sustained learning epoch is not surprising. In this context, hippocampo-cortical and thalamo-cortical circuits have been suggested as possible sources for theta and upper alpha oscillations, respectively (Steriade, 1993; Fernandez et al., 1999; Klimesch, 1999), although the origins of the rhythms in humans remain debated (Lopes da Silva et al., 1997; Uchida et al., 2001).

Though less effective, separate analyses of activity in the upper alpha and theta frequency bands revealed evidence for a contribution of these oscillatory systems to memory encoding. Both an increase in theta power and a reduction of upper alpha power (particularly over left parietotemporal regions) discriminated EEG activity between learning and mental relaxation. Moreover, separate analysis of upper alpha power revealed a significant dissociation between trials of good vs. poor performance (at later recall), i.e., efficient encoding of faces was associated with reduced parietal upper alpha power. Furthermore, encoding of faces as compared to words showed a decrease of alpha activity, in particular, over the right parietal cortex. However, the left hemispheric reduction of alpha during encoding of words failed to reach significance, probably for two reasons: (i) encoding of faces also involves some left hemispheric activity (Grady et al., 1998). (ii) Memorizing faces was rated distinctly more difficult than memorizing words, thus increased effort spent in encoding faces, may have expressed itself in a more pronounced desynchronization of alpha activity. Results of both comparisons, efficient vs. poor intentional encoding and the topographical power distributions during encoding of faces vs. words, point to an association of upper alpha desynchronization with the process of encoding. Notably, these data are consistent with several studies of event-related alpha activity (Klimesch et al., 1997a, b). We therefore suppose that analysis of ongoing upper alpha activity accompanying a mode of learning can catch the same changes as analysis focusing on stimulus locked activity. This may, however, only account for tasks with considerably high demands of encoding, as required here by the face material. For the word material, being easier to encode and, thus, allowing also for more frequent lapses of intermittent mental relaxation, the respective desynchronization remained nonsignificant (see also Doppelmayr et al., 1998; Vogt et al., 1998).

Separate analyses of theta synchronization also provided hints at a contribution of this oscillatory system to the intentional encoding process. Theta activity was enhanced over left temporal areas during encoding of words as compared to faces corresponding with findings of increased event-related EEG theta synchronization during stimulus encoding (Klimesch et al., 1996; Klimesch, 1999). Moreover, the left temporal focus of theta synchronization during intentional encoding of words is consistent with the commonly held view of a left hemispheric processing of such materials (e.g. Kelley et al., 1998; Kirchhoff et al., 2000). However, theta activity per se did not appear to be very sensitive to the effects of encoding efficacy.

In conclusion, the ability of a combined measure accounting for upper alpha desynchronization and theta synchronization to clearly differentiate intentional encoding, i.e., trials of efficient from poor encoding and of words vs. faces, suggests a complementary contribution of the underlying two oscillatory systems to the processes of memory encoding. Based on the presumed psychological interpretation of alpha desynchronization and theta synchronization, this suggests that processes of encoding into working memory and exchange between short-term and long-term memory operate in parallel to integrate newly acquired information within an appropriate context (Baddeley, 1992).

Acknowledgements

This research was supported by a grant from the Deutsche Forschungsgemeinschaft to H.L.F. and J.B. We thank Jenny Wiebe for help in data acquisition.

Abbreviations

EEG, electroencephalogram; FFT, Fast Fourier Transformation; fMRI, functional magnetic resonance imaging; PET, positron emission tomography.

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