MINUTE-scale fluctuations in the normalized EEG log spectrum, when correlated with concurrent changes in level of performance on a sustained auditory detection task, showed that a single principal component of EEG spectral variance is linearly related to minute-scale changes in detection performance. The particular EEG frequencies at which this coupling is expressed are similar for most subjects under a range of task conditions, and match those recently reported from analysis of verbal self-reports during drowsiness. The one-dimensional relationship between detection performance and the EEG spectrum confirms quantitatively the intuitive assumption that minute-scale changes in behavioral alertness during drowsiness are predominantly linked to changes in global brain dynamics along a single dimension of psychophysiological arousal.

Changes in alertness are a principal component of variance in the EEG spectrum

Scott Makeig[1,CA] and Tzyy-Ping Jung[1,2]

[1]Naval Health Research Center, PO Box 85122, San Diego, CA 92186-5122; [2]Computational Neurobiology Laboratory, The Salk Institute, LA Jolla, CA, USA

[CA]Corresponding Author

Introduction

One of the earliest observations of changes in the EEG spectrum correlated with behavior was that at transition to sleep, the EEG spectrum mostly shifts towards lower frequencies.[1] The link between changes in behavioral arousal and the EEG spectrum is strong enough to enable the appearance of the EEG spectrum to be used as a direct indicator of arousal level.[2] Here, arousal refers primarily to changes in behavior associated with transitions from slow-wave sleep to waking, and alertness to the waking end of this continuum. Although careful studies of human EEG records have revealed a range of normal and abnormal transitions between waking and sleeping EEG patterns,[3] physiological and behavioral arousal, if considered separately from attention,[4] are most often thought of as co-varying on a one-dimensional continuum (for example, when we say we feel 'half-asleep').

Recently, Makeig and Inlow[5] presented data from half-hour experiments in which subjects listened with eyes closed to sounds embedded in white noise, pressing a response button whenever they heard target sounds consisting of brief increases in noise amplitude. They showed that minute-scale fluctuations in local error rate, a moving-average measure of detection lapse probability, were coherent with minute-scale shifts in the EEG power spectrum in several discrete frequency bands, and that these EEG changes could be used to predict the time course of local error rate using individualized models constructed from EEG and performance data collected in previous task sessions. Changes in the EEG spectrum

could be used to estimate accurately the percentage of targets detected, i.e. not only to discriminate between alert and asleep conditions, but also to monitor the time course of performance during drowsy periods. Here we report, first, that a similar relation exists between changes in the EEG spectrum and auditory detection performance during eyes-open, dual-task performance, and second, that spectral changes linearly related to alertness form a single principal component of overall variance in the normalized EEG log spectrum.

Materials and Methods

Stimuli: A concurrent workstation recorded the EEG and delivered auditory stimuli to the subject in a constant 63 dB white-noise background. Stimuli consisted of targets (300 ms increases in noise amplitude; rise time 150 ms, fall 110 ms), presented 6 dB above each subject's detection threshold in the noise background. Mean target stimulus onset asynchrony (SOA) was 6 s. Non-target tones at two frequencies (568 Hz and 1098 Hz), were also presented in random order at 72 dB (normal hearing level) with SOAs randomly distributed between 2 s and 4 s. Visual targets consisting of 20 consecutive white squares forming a vertical line were produced by a 386 PC with a VGA color display (13 cm wide by 9 cm high) and presented over a video noise background ('snow') composed of 1 mm grey scale squares. Visual targets appeared at a mean rate of 1 per min, and were not correlated with auditory targets. Visual task data will be reported elsewhere.

Task conditions: Subjects sat in a comfortable chair, a two-button response box resting on a pillow in their lap, and were asked to press one button whenever they heard a target noise burst, and the other whenever they detected a visual target. Ambient light level was kept low in the small (5' × 5') subject chamber. Under these conditions, the white noise background and the monotony of subjects' tasks proved soporific for many subjects who found it difficult to remain alert throughout entire half-hour sessions. From a total of five sessions on each of 15 subjects, pairs of sessions from 10 subjects (9 male, age range 18–39 years) contained sufficient lapses in auditory detection (68 ± 32 lapses per session, 24 ± 11% of targets presented) and were used in the analysis.

EEG recordings: EEG data were collected at two scalp sites, Cz and Pz/Oz (midway between Pz and Oz), referenced to the right mastoid, and from horizontal and vertical bipolar EOG leads, at 12-bit resolution with a sampling rate of 312.5 Hz and a pass band of 0.1-100 Hz.

EEG spectra: Time-varying amplitude spectra for each channel were computed using 512-point fast-Fourier transforms (FFTs) of 50% overlapping (Hanning-windowed, zero-padded) 256-point data epochs, after rejecting epochs contaminated by eye movements or other artifacts producing excursions of $\geq 50 \mu V$ in any of the EEG or EOG channels. Spectra were then converted to a logarithmic scale and smoothed with a causal 95 s exponential window (90% down 95 s before its leading edge), yielding for each session 1024 smoothed log spectral estimates at 1.6384 s intervals. The log spectrum for each session was then normalized separately for each of 40 frequency bins between 0.61 and 24.4 Hz by subtracting the session mean and divided by the 25–75 percentile range of the resulting time series.

The normalized log spectra at Cz and Pz/Oz from the 20 sessions on 10 subjects selected for analysis were then submitted to principal component analysis (PCA)[6] producing 80 eigenvectors and 80 corresponding eigenvalues. PCA eigenvectors with largest eigenvalues represented directions of largest multi-dimensional variance in the log spectrum during the experiments.

Detection performance: Hits and lapses were defined as auditory targets responded to or not responded to within a 100–3000 ms window following target onset. Auditory task error rate was smoothed using the same 95 s moving exponential window used to smooth the EEG spectrum by multiplying a performance index (0 for each hit in the moving window, 1 for each lapse) by the appropriate window weight (determined by

the relative time of occurrence of each target within the window), summing the results, then normalizing the result by dividing by the sum of the window weights used in computing the sum. The performance smoothing window was moved through the performance index in 1.6384 s (512 point) steps, converting the irregularly spaced, discontinuous performance index into a regularly spaced, continuous local error rate measure representing the current probability that the subject will fail to respond to a presented target.
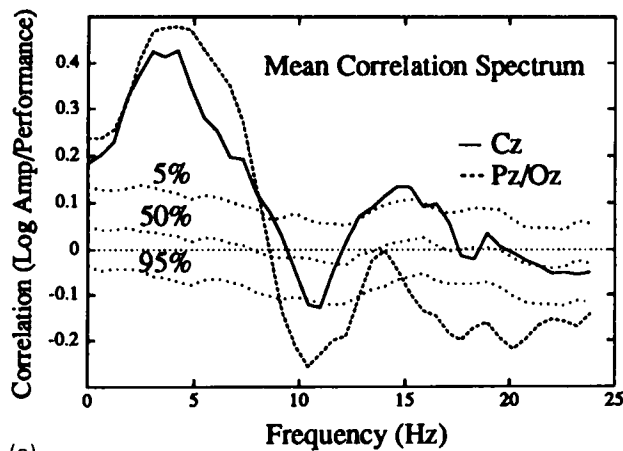
Correlation spectra: For each session, correlations between smoothed log spectral and error rate time series were then computed separately for each of 40 FFT frequency bins from 0.6 to 24.4 Hz. Results were said to form the 'correlation spectrum' of each experiment. A mean correlation spectrum was computed by averaging correlation spectra from the 20 sessions. Significance levels for the resulting mean correlation values were estimated using Monte Carlo methods. First, for each session the time course of log power at each of 40 frequency bins in the two channels was correlated with the time course of error rate in the other 19 sessions. Next, 500 surrogate mean correlation spectra were computed by averaging pseudo-randomly selected sets of 20 of these surrogate correlations. For each frequency bin, the 5th, 50th and 95th percentiles of the resulting correlation distribution were then identified. In addition, a grand correlation spectrum was computed for all 20 sessions simultaneously using the same normalized data used to compute the PCA.

Results

Mean and grand correlation spectra were nearly identical ($r = 0.995$, rms difference = 0.023). Figure 1a shows the mean correlation spectrum at the two sites, superimposed on traces showing significant levels from the surrogate correlation distribution (see Materials and Methods). Correlations between EEG power and performance were significant in four frequency bands: (1) at 4–5 Hz (θ) in both channels, (2) at 10–11 Hz (α) at Pz/Oz, (3) at 14–15 Hz (σ) at Cz, and (4) above 15 Hz (β) at Pz/Oz.

Figure 1b shows the eigenvectors corresponding to the two largest principal components of EEG variance in the sessions. The first component, accounting for 27% of the total variance, is uniformly positive (or negative). The second component, accounting for 16% of variance, strongly resembles the correlation spectrum shown in Figure 1a, with maximum near 4 Hz (in both channels) and 14 Hz (at Cz only), and minima near 10 Hz and above 20 Hz.

Figure 2 shows a plot of the angles between each of the 80 PCA eigenvectors and the grand correlation spectrum. The second eigenvector is aligned within

(a)
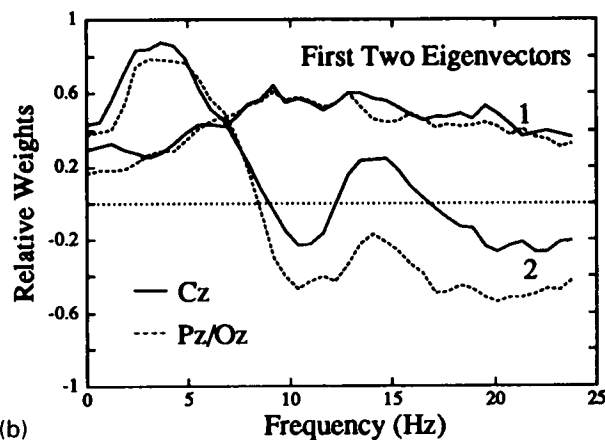
(b)

FIG. 1. (a) Grand mean correlation spectrum, showing mean correlations between EEG log power and local error rate (the probability of an auditory detection lapse) for 20 half-hour sessions on 10 subjects, both measures smoothed using a causal 95 s exponential window. Correlation spectra at two scalp channels, Cz and Pz/Oz, are superimposed on dotted traces showing the 5th, 50th, and 95th percentiles of the distribution of surrogate correlations computed by correlating EEG power and error-rate time series from separate sessions. (b) Plot of eigenvectors corresponding to the first two principal components of variance of the normalized EEG log spectrum in the 20 sessions. While the near-constant eigenvector 1 is (like eigenvectors 3–80) little related to performance, eigenvector 2 is highly related (see Fig. 2).

15° of the correlation spectrum vector, while all other eigenvectors are nearly orthogonal to it. Accordingly, the projection of the EEG spectral data on the second eigenvector correlated nearly as highly ($r = 0.58$) with the time course of error rate as multiple regression using projections on the first eight eigenvectors combined ($r = 0.60$). This result confirms that nearly all performance-related changes in the EEG spectrum are confined to one principal component (or eigenvector) of spectral variance.

Discussion

We now have found nearly identical linear relationships between normalized EEG log spectra and minute-scale changes in auditory detection probability during both single[5] and dual-task experiments.
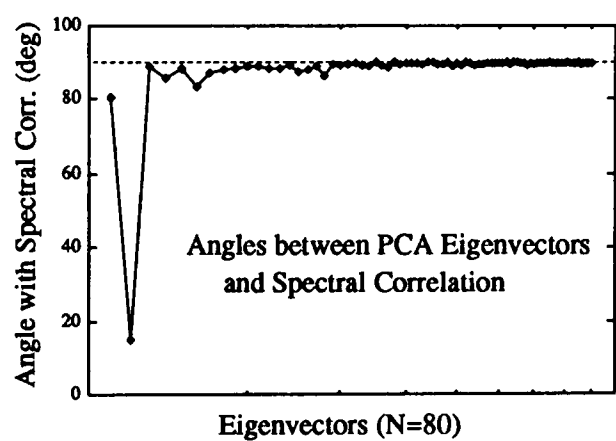

FIG. 2. Vector angles between the 80 PCA eigenvectors characterizing variance in the normalized EEG log spectrum, and the grand correlation spectrum vector consisting of correlations between performance and normalized EEG log power at 40 EEG frequencies and 2 scalp channels during all 20 sessions. Only the second PCA eigenvector is aligned with the performance correlation vector; all other principal components of EEG variance are nearly orthogonal to it.

Except near 10 Hz, the mean correlation spectrum in the current (dual-task, eyes-open) experiments (Fig. 1a) strongly resembles previous results obtained under single-task, eyes-closed conditions,[5] the stronger 10 Hz performance correlation during eyes-closed conditions reflecting the well-known decline in closed-eyes α during drowsiness.[1] Amplitude changes at θ, α, σ, and β frequencies have long been known to be associated with drowsiness and sleep onset.[1] Our results quantify the extent to which these changes co-vary linearly with performance changes on a continuous detection task.

Further evidence for the generality of the EEG correlation spectrum shown in Figure 1a appears in a recent paper by Lehmann et al,[7] who put subjects to bed in a darkened room at their normal bedtimes, then prompted them, at 7 min intervals, to say whatever was on their mind at the moment the prompt sounded. After blind rating of the recorded verbal responses on 20 bipolar rating scales, the scaling data and EEG spectra just prior to the prompts were analyzed using canonical correlation. The largest correlation factor extracted by this procedure was most heavily weighted on verbal scale values associated with loss of recall and body awareness, with remoteness and indirectness — all qualities compatible with drowsiness and hypnagogy.

Although the (bipolar central-parietal) scalp derivations used by Lehman et al differ somewhat from ours, their first EEG factor closely resembles our correlation spectrum (Fig. 1a) and, even more strongly, the eyes-closed correlation spectra reported by Makeig and Inlow.[5] Note that Lehmann et al used quite a different task than we did, and that their subjects' failures to respond to the prompt were excluded from their data, while lapses in auditory detection were the subject of our analysis. Yet, both

experiments yield very similar frequency-weighted components relating changes in alertness and the EEG spectrum during drowsiness.

The significance of the performance correlation peaks in Figure 1a implies that the frequencies at which log power was correlated with detection performance are similar for most subjects. Examination of correlation spectra for individual subjects confirmed this conclusion, although stable between-subject differences also exist.[5,7] Note also that our finding of a significant long-linear component in the relation between EEG and performance does not preclude the possibility that this relationship also contains other non-linear terms, including performance floor effects, EEG saturation, or others. Such factors may make non-linear fitting algorithms or artificial neural networks more efficient than linear regression in estimating changes in alertness from EEG records.[8]

We also found that the mean correlation spectrum for these sessions nearly parallels a single principal component of variance in the normalized EEG log spectrum during the sessions, and is nearly orthogonal to all others (Fig. 2). Performance-related variations in this component of EEG spectral variance during these experiments are apparently produced by changes in brain arousal which are closely linked to changes in the probability of detecting (and/or responding to) above-threshold signals. These changes in detection probability may be caused by intermittent or noisy gating of the delivery of efferent auditory information to the cortex,[9] or possibly by drowsiness-related changes in other brain subsystems involved in performing the task. In our experiments, performance decrements appear as waves of (usually) intermittent detection lapses lasting ≥ 4 min and containing characteristic 15–20 s cycles.[10] The concentration of performance-related EEG spectral changes in a single eigenvector suggests a tight coordination of dynamic brain changes underlying minute-scale changes in arousal and sensory gating during drowsiness. During drowsiness as seen here under monotonous task conditions, brain and behavioral arousal do indeed co-vary on a one-dimensional continuum, as often assumed. It should be interesting to test whether similar results are obtained when links between EEG changes and behavioral alertness are examined using more complex or demanding tasks.

Conclusion

As has long been known, changes in brain arousal involve specific changes in oscillatory brain activity.[1–3,5,7–10] Our results show that correlations between minute-scale changes in the EEG log spectrum and performance on a sustained auditory detection task are similar for most subjects. At the two central scalp sites we have studied and except near 10 Hz, correlations between performance and EEG log amplitude are similar in eyes-open and eyes-closed conditions involving dual- or single-modality[5] detection tasks, and closely match those recently reported based on subjects' self-reports near sleep transitions.[7] During the current dual-task, eyes-open experiments, minute-scale changes in the frequency of auditory detection lapses were predominantly correlated with changes in the normalized EEG log power spectrum along a single principal component or eigenvector of EEG spectral variance. These EEG changes apparently index coordinated changes in activity of brain systems controlling central arousal (and/or auditory gating) which result in behavioral changes along a one-dimensional drowsy–alert continuum, as is commonly assumed. Elsewhere, we have shown that these EEG spectral correlates of loss of alertness can be used to monitor the time course of alertness in near real time, for scientific or applied purposes.[8]

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General Summary
We correlate minute-scale fluctuations in the normalized EEG log spectrum during drowsiness with concurrent changes in level of performance on a sustained auditory detection task, and show that a single principal component of EEG variance is linearly related to minute-scale changes in detection performance. The EEG frequencies at which this coupling is expressed are similar for most subjects during single- or dual-task and eyes-open or eyes-closed conditions. This pattern of performance correlations across EEG frequencies closely matches the profile of EEG frequency changes recently reported from analysis of cued verbal self-reports of thinking and awareness during drowsiness. These EEG changes apparently arise from simultaneous changes in brain mechanisms controlling central arousal and alertness, and in the levels of coherent neural activity at several characteristic neural oscillation frequencies. The unidimensional relationship between changes in performance and the EEG spectrum during drowsiness may make possible practical methods of EEG-based real-time alertness estimation.