Evoked EEG alpha oscillations in the cat brain – a correlate of primary sensory processing?

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Abstract

Event-related alpha (10 Hz) oscillations in the EEG were measured in cats by means of intracranial electrodes. Simultaneous recordings were made from auditory and visual cortex while auditory and visual stimuli were applied (in separate sessions). Frequency domain analysis of the EEG responses showed marked alpha components only for adequate stimulation (e.g. visual cortex-visual stimulus). This hints at a functional relationship between alpha responses and primary sensory processing.

Keywords: Alpha oscillations; Frequency domain analysis; Auditory cortex; Visual cortex

For a long time, alpha (10 Hz) rhythms (or oscillations) in the EEG have been regarded as correlates of ‘idling’. Recently, however, it has been suggested that alpha oscillations might have ‘closer relationships to ‘events’ than one might have thought earlier’ [15], possibly being related to ‘cortical work’ [13]. This view has been summarized in the expression ‘functional alpha’ [1,5]. Since stimulus-dependent 10 Hz oscillations have also been observed at the cellular level [7], alpha oscillations may soon attract as much interest as the widely discussed gamma oscillations.

One of the functional correlates of alpha oscillations has become clear in cross-modality experiments, e.g. in visual cortex recordings of auditory and visual evoked potentials (EPs). The ‘alpha response’, obtained by digital filtering of the EP, was particularly dependent on whether the stimulus was adequate (in this case: visual) or not, suggesting a relationship between alpha response and primary sensory processing (in human scalp measurements [4] and in cat intracranial measurements [3]). In order to extend these results, we investigated frequency properties of EPs by means of a simple, yet effective quantitative evaluation of amplitude frequency characteristics [2].

Measurements were performed in six cats. Electrodes were implanted, under Nembutal anesthesia, in several structures, among them the auditory cortex ( gyrus ectosylvianus anterior, GEA) and the visual cortex (occipital cortex, OC; area 17) [6]. Three stainless steel screws in different regions of the skull served as a reference. Experiments started approximately two weeks after implantation, with cats freely moving or resting in a cage in a soundproof, dimly illuminated room.

Auditory EPs (2000 Hz tones, 1 s duration, 0.5 ms rise time) and visual EPs (intense step-function stimuli delivered via a fluorescent bulb) were recorded (N = 100 stimuli each with pseudo-random intervals of 2.5–3.5 s in separate sessions). One-second pre- and post-stimulus EEGs (filter limits 0.5–70 Hz) were sampled at 500 points/s and digitized.

EP frequency domain analysis [2], based on principles of systems analysis, aims at characterizing the ‘system’ brain by its input/output relation. The ‘classical’ approach to determine this relation is to stimulate the system with sinusoidal inputs of different frequencies. The plot of output amplitude as a function of input frequency is called amplitude frequency characteristics (AFC), where large output amplitudes indicate resonance responses. Observation periods can be shortened when the AFC is computed via the Fourier transform $G(j\omega)$ of the ‘impulse response’ $\lambda(t)$ eli-
cited by a brief stimulus containing all possible input frequencies:

$$G(j\omega) = \left( \frac{1}{\sqrt{2\pi}} \right) \int_{-\infty}^{\infty} \lambda(t) \exp(-j\omega t) dt$$

where $\omega = 2\pi f$ and AFC = $|G(j\omega)|$. The impulse response, in turn, is computed from the ‘step response’ $c(t)$, i.e. from the EP, by means of differentiation: $\lambda(t) = d[c(t)]/dt$.

Numerically, an FFT algorithm is used to evaluate the $N$ data points of a digitized time series $X_n$ ($X_n = X(t_n)$, $n = 0, ..., N - 1$) of duration $T = (N - 1)\Delta t$ as follows:

Computation of Fourier coefficients:

$$Y_k = Y(\omega_k) = \sum_{n=0}^{N-1} X_n \exp(-j2\pi N^{-1}nk); \quad \omega_k = 2\pi kT^{-1}$$

Computation of the AFC from the complex coefficients $Y_k = a_k + jb_k$:

$$\text{AFC}(\omega_k) = (a_k^2 + b_k^2)^{1/2}$$

For statistical evaluation, the values AFC($\omega_k$) were read and averaged within the frequency band of interest (e.g. 8–15 Hz range), giving the average amplitude

$$\left( \sum_{k=m}^{n} \text{AFC}(\omega_k) \right)^{1/(n-m)}$$

such that $\omega_m$ relates to $f = 8$ Hz ($\omega = 2\pi f$) and $\omega_n$ relates to $f = 15$ Hz (see [18] for an alternative procedure of quantitative AFC evaluation).

Fig. 1 shows AFCs computed from auditory EPs. For GEA (left), consistent maxima in the alpha (8–15 Hz) frequency range with some inter-individual variation are observed. Correspondingly, the spectral grand average for GEA (bottom; computed by averaging individual AFCs in the frequency domain) shows a peak extending from approximately 7–15 Hz. In contrast, no consistent maxima are visible for OC recordings (right). No clearly dominant peaks are seen in the spectral grand average for OC (bottom).

Fig. 2 shows AFCs computed from visual EPs. AFCs computed from GEA recordings (left) lack consistent maxima. Correspondingly, in the spectral grand average peaks in the 4–7 Hz range and in the 8–15 Hz co-exist, barely differing in amplitude. In contrast, high-amplitude peaks in the upper alpha range are visible in all but one of the AFCs for OC (right). In the spectral grand average, a maximum in the 8–16 Hz range is clearly dominant.

A common feature of Figs. 1 and 2 may be put as follows: inadequate stimulation was related to AFCs without domi-
Our results are consistent with previous studies in humans using EEG (high-amplitude alpha responses in occipital sites only with visual stimuli whereas theta responses were less stimulus-dependent [4]) and MEG [21]. (Note that alpha responses and alpha blocking may occur in the same subject depending on the amplitude of the pre-stimulus EEG [2,16] and that the spontaneous alpha rhythm in cats is less distinct than in humans.)

Our results are related to the concept of event-related oscillations which has recently become popular. This may be due to the fact that it served to link task-dependent gamma responses in the EEG to the widely discussed stimulus-dependent gamma oscillations at the cellular level [8,10].

For event-related alpha oscillations a similar development is under way [5]. Galambos [9] discerns the spontaneous alpha rhythm from several classes of event-related alpha oscillations with diverse functional correlates comprising memory and movement processes [12,17]. MEG studies permit a topographic differentiation of theta and alpha rhythms [11,14,19]. At the cellular level, stimulus-dependent 10 Hz patterns of action potentials [7] show intriguing parallels to EEG oscillations. Alpha rhythms have also been related to feature integration over long cortical distances [20].

In summary, we used a frequency domain approach based on the working hypothesis of the EP as a superposition of event-related oscillations in several frequency ranges [2]. A supplementary procedure (confirming and extending results of digital filtering [4] and wavelet analysis [3]) served to demonstrate stimulus-dependent evoked alpha oscillations in primary sensory cortices. This hints at a functional relationship between alpha responses and primary sensory processing.

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