Electroencephalogram alpha (8–15 Hz) responses to visual stimuli in cat cortex, thalamus, and hippocampus: a distributed alpha network?

Martin Schürmann, Tamer Demiralp, Erol Başar, Canan Başar Eroğlu

Abstract

To investigate possible functional correlates of alpha (8–15 Hz) oscillations in the electroencephalogram (EEG) intracranial recordings in cats (from thalamus, occipital cortex, and hippocampus) were performed. In response to visual stimuli, event-related alpha oscillations were observed. Such alpha responses were found not only in a specific sensory (visual) pathway but also in the hippocampus, hinting at a possible distributed alpha response system.

Keywords: Evoked 10 Hz oscillations; Alpha response; Visual evoked potential; Thalamus; Hippocampus

Numerous studies imply a functional relation between cerebral processes such as movement or memory and 8–15 Hz oscillations in the electroencephalogram (EEG), i.e. ‘alpha rhythms’ in humans [9,15,20] and ‘alpha-like’ oscillations in intracranial recordings, e.g. in cats [13]. Particular examples of such oscillations being far more than ‘idling activity’ are alpha responses to sensory stimuli (this term denotes damped 8–15 Hz oscillations returning to baseline 200–300 ms after stimulus [3–5], including alpha-like responses in cats). Intracranial recordings in cats are consistent with a theory of ‘hippocampo-cortical alpha networks’ [4,5]. Alpha responses to auditory and visual stimuli from primary sensory areas were found to be highly dependent on whether or not the stimulus was adequate for the area under study [22]. In contrast, hippocampal alpha responses were observed to both auditory and visual stimuli [8]. The present study is focussed on alpha responses to visual stimuli and their functional topography (slower frequency ranges will be evaluated for comparison only; for details, see, e.g. [12,16]). This approach aims at reconciling these earlier results with a theory established since the days of Adrian [1], namely that alpha oscillations are particular properties of thalamo- or cortico-cortical circuits [2,17]. Our data suggest that the hippocampus acts as an element of a ‘selectively distributed alpha system’ [4,5,7].

Measurements were performed in eight cats with chronically implanted electrodes (implantation under Nembutal anesthesia). Electrode locations were occipital cortex (area 17, ‘OC’), thalamus (‘TH’, close to the lateral geniculate nucleus), dorsal hippocampus (‘HI’: deep pyramidal layer CA3), and auditory cortex (gyrus ectosylvianus anterior, ‘GEA’) as described previously (details in [10]). Experimental sessions started approximately 2 weeks after implantation, with cats freely moving or resting in a cage in a soundproof, echo-free, and dimly illuminated room.

Evoked potentials (EPs) were elicited by means of intense visual step function-like stimuli (n = 100) delivered via a fluorescent bulb (pseudo-random interstimulus intervals, 2.5–3.5 s). One second pre- and 1 s post-stimulus EEGs were recorded (analogue filter: 0.5–70 Hz) and digitized at 500 points/s.

Taking into account the spectral properties of the EPs (‘EP frequency analysis’, [3]), digital filtering without phase shift was performed to visualize the time course of oscillatory signal components. Furthermore, for several pairs of electrodes we computed coherence functions.
where \( S_x(f) \) and \( S_y(f) \) are the power spectral density functions of the EEG data records \( x(t) \) and \( y(t) \), respectively, and \( S_{xy}(f) \) is the cross spectral density function. When \( COH_{xy}^2(f) = 0 \) at a particular frequency, \( x(t) \) and \( y(t) \) are said to be ‘incoherent’, (i.e. uncorrelated) at that frequency. If \( x(t) \) and \( y(t) \) are statistically independent, then \( COH_{xy}^2(f) = 0 \) for all frequencies. When \( COH_{xy}^2(f) = 1 \) for all \( f \), then \( x(t) \) and \( y(t) \) are said to be ‘fully coherent’ [11,23].

Fig. 1 shows evoked 10 Hz oscillations for various brain structures (for wide-band filtered curves see [8]). Fig. 1A presents averaged EPs for an individual cat (filtered 8–15 Hz). The response amplitude was highest in the occipital recording (OC) and marked in hippocampus and thalamus (HI, TH) as well. In the auditory cortex (GEA), an alpha response was barely visible. Fig. 1B shows the corresponding grand averages (\( n = 8 \) cats). Again, response amplitudes were highest in OC. Marked alpha responses were also visible in TH and HI (slightly higher amplitude in HI than in TH). No marked alpha response was observed in GEA. For these locations, alpha response amplitudes were significantly different (Friedman: \( P < 0.01 \); post-hoc: GEA vs. HI: \( P < 0.05 \); GEA vs. OC: \( P < 0.01 \)). The inset in Fig. 1B shows the cross-correlation for different pairings of the responses shown in Fig. 1B, the delays being markedly different from each other.

Fig. 2 shows responses to visual stimulation recorded from the cat hippocampus (wide-band vs. alpha range). Distinct alpha responses were present in the first 200 ms after stimulation, in the averaged EP as well as in the single trials. Remarkably, the alpha responses were visible even in the wide-band filtered single trials.

Fig. 3 shows coherence values for the electrode pairs HI–OC and TH–OC (spontaneous EEG vs. EP). Coherence values tended to increase after visual stimulation (significant for all frequency ranges except theta, see Table 1). In general, these stimulus-related increases were larger for HI–OC than for TH–OC (see interaction of factors experiment and channel in Table 1, significant for alpha). Coherence increased most consistently in the alpha range (Fig. 3).
where the mean post-stimulus coherence was 0.41 for HI-OC, but only 0.18 for TH-OC. (Coherences for electrode pairs not shown were at a noise level.)

It is widely believed that 10 Hz oscillations are generated in thalamo-cortical circuits. Consequently, previous analyses with intracranial electrodes covered structures such as thalamus and cortex (e.g. [2,17]), with some studies reporting task- or behaviour-related modulation of alpha rhythms [13,21].

Remarkably the present study demonstrates alpha responses in the hippocampus, i.e. outside of primary sensory pathways (for alpha responses in primary sensory areas, see Ref. [22]). A functional significance of this hippocampal involvement is suggested by the fact that stimulus-induced coherence increases were higher for the pairing hippocampus–visual cortex than for thalamus–visual cortex. Together with the differences in phase delays (Fig. 1B) this may indicate hippocampal processing of stimuli in parallel with the processing in the visual pathway (‘secondary alpha circuit’ [5]).

Auditory stimulus sequences with omissions showed that hippocampal theta responses in cats are more task-dependent than alpha responses [14]. Therefore alpha responses might be part of a system of ‘obligatory’ sensory processing occurring with every stimulus, e.g. related to hippocampal functions in motivation, emotion, and short-term memory [14]. Furthermore, in remarkable contrast with cortical alpha responses [22], hippocampal alpha responses occur with auditory as well as visual stimuli [5,6]. This is consistent with the view of the hippocampus as a supramodal centre [24].

Notably, alpha-like response patterns were observed in numerous single EP trials even without digital filtering (example in Fig. 2). The remarkable similarity between unfiltered and filtered recordings suggests that particular single trials are ‘pure alpha responses’ (or ‘real brain responses’ [4,5]). The results of digital filtering have been confirmed by wavelet analysis [8]. Volume conduction is an improbable cause of the hippocampal alpha responses (note the non-zero peaks in the cross-correlation in Fig. 1B and differences between closely spaced electrodes as reported in [3]). The marked inter-location differences in response amplitudes suggests local rather than global wave phenomena as an explanation of the results [19].

In conclusion, our data demonstrate that the hippocampus can react to sensory stimuli with a 10 Hz enhancement. The remarkable stimulus-induced increase in hippocampo–cortical coherence suggests a functional meaning of this response, such as, e.g. signal processing in structures parallel to the visual pathway, possibly with supramodal properties. Within the concept of ‘selectively distributed alpha systems’ [4] such alpha responses are interpreted as correlates of the ‘selectively distributed processing’ going on in neurocognitive networks [18].

Table 1 Two-way repeated measures ANOVA for coherence values (separate tests for each frequency band); factors: experiment (`EXP', spontaneous EEG vs. visual EP); channel (`CH', HI-OC vs. TH-OC) and the interaction term (`EXP' x `CH')

<table>
<thead>
<tr>
<th></th>
<th>Delta (0.5–3.5 Hz)</th>
<th>Theta (4–7 Hz)</th>
<th>Alpha (8–15 Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>EXP</td>
<td>F = 30.06; P &lt; 0.001</td>
<td>F = 2.54; P &lt; 0.068</td>
<td>F = 26.83; P &lt; 0.001</td>
</tr>
<tr>
<td>CH</td>
<td>F = 4.35; P &lt; 0.070</td>
<td>F = 4.66; P &lt; 0.155</td>
<td>F = 8.66; P &lt; 0.022</td>
</tr>
<tr>
<td>EXPxCH</td>
<td>F = 5.51; P &lt; 0.051</td>
<td>F = 5.36; P &lt; 0.054</td>
<td>F = 30.42; P &lt; 0.001</td>
</tr>
</tbody>
</table>

Fig. 3. Coherence values (dimensionless) for the electrode pairs thalamus–visual cortex (TH-OC, top) and hippocampus–visual cortex (HI-OC, bottom). Each pair of dots represents coherence for corresponding EEG (left) and EP (right) segments in an individual cat. Note the marked stimulus-induced increase in coherence for HI-OC. Statistics in Table 1.

[1] Adrian, E.D., Rhythmic discharges from the thalamus, J. Physiol. (Lond.), 113 (1951) 9–10.


