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20 Hz rhythm of activity in visual system of perceiving cat

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Abstract. Cats attended to either visual or acoustic moving stimuli in order to perceive the location of their disappearance, which signaled reward in left or right foodwell. The analysis of concomitant electroencephalograms revealed an elevation of the 20 Hz band in the Fourier spectra of activity of respective visual and auditory projection cortices. These oscillations appeared only on the trials that ended with a successful response. With use of directed transfer functions we were able to show that during the visual task, the 20 Hz frequency was propagated from the spot of appearance along the visual cortex, as well as towards the lateral geniculate nucleus.

Key words: modality differentiation task, 20 Hz oscillations, coherence of EEG, lateral geniculate nucleus, perigeniculate nucleus, visual cortex

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INTRODUCTION

The idea that the rich cortico-thalamic projection subserves the control function of the lateral geniculate nucleus (LGN) was put forward long ago (see Frigyesi et al. 1972, for a review) but still lacks good experimental support. The difficulty of studying this system arises from the fact that it is not operative during acute experiments on the anesthetized animals with synchronized electrocorticogram -ECoG, (Livingstone and Hubel 1981). It has been proposed that the descending system might be activated during the state of attention (see HernandezPeon 1966, Ahlsen et al. *1985)* and that this activation correlates with ECoG desynchronization observed in vigilant animals (see Lindsley 1960 and Steriade and Llinas 1988, for reviews). Recent investigations suggest that the "desynchronized" ECoG consists of fast oscillations of smaller amplitudes and different frequencies, serving as a carrier for coordination between cortical areas (see Bressler 1990). Whether these oscillation influence the thalamic cells activity is still not known (Steriade et al. 1991) mainly for the reasons mentioned above. During recording from the visual cortex of the vigilant dog it was found that a band of about 20 Hz appears when the animal focuses his attention on a target (Lopes da Silva et al. 1970) but even than the LGN activity seemed to be completely independent.

The present experiment was designed 10 see if careful examination of the electroencephalograms (EEGs) can reveal the activity of the cortico-thalamic circuit in behaving cats.

METHODS

Four cats were trained to perceive visual or acoustic stimuli during the same session. The animals were placed in a small *(20x45x45* cm) experimental wooden cage facing two translucent doors situated *5* cm from each other. The cat and the doors were separated by a transparent removable screen. The visual stimulus was a small (0.5x2 deg) slit of light, of *5* cd/m^2 intensity, moving sinusoidally with about 1-2 Hz frequency, left and right, behind the doors, on the level of the cat's eyes. After about 16 seconds the slit was stopped while projecting on one of the doors, indicating that a piece of meat was hidden behind it, and switched off. After a 1-3 second delay a transparent screen was raised and by pressing the correct door the cat could reach for the reward. The incorrect door was locked and the animal could not open it. It was not allowed to correct an error.

The acoustic stimulus was produced by a pocket-radio loudspeaker as a noise (with fundamental frequency of *5* kHz) of modulated intensity *(50-55* dB, with 2.5 Hz frequency) switched on behind the part of wall in between the doors, and consecutively moved around the corner of the cage, behind the left or right of the side-walls. After an average of 16 seconds the stimulus was switched off, and there was again a 1-3 s delay before the cat was allowed to press one of the doors. The rewarded door was the one on the side on which the stimulus vanished. Both visual and acoustic stimuli were used during the same session, ten times each, in random order.

The learning procedure started with the visual task and the acoustic stimulus was introduced after stabilization of the first response. For one cat, the visual stimulus also oscillated in the vertical plane between the doors (neutral position) during acoustic task to assure similar light-flux input in both the visual and auditory modality tasks. The recordings obtained from this cat did not differ from those of other animals. Training was considered complete when animals reached 90% performance accuracy. Following completion of training, surgery was performed under Nembutal anesthesia. Tungsten in lacquer recording electrodes were inserted under electrophysiological control: two in lateral geniculate and/or perigeniculate nucleus of the left hemisphere, and one in the contralateral hippocampus. A row of three chromonickel electrodes, about *1.5* mm apart, was placed in the primary visual cortex (VCx) of all animals and one electrode was inserted into the auditory cortex in only two cats. The electrodes and a plug were mounted on the animal's head by means of dental cement. The recordings started 5 to

7 days after surgery with one session a day, four sessions a week. The EEG signals (1 *Hz-5* kHz) were amplified and stored on DC magnetic tape recorder (Racal V-store). The data analysis was performed off-line with IBM-386 compatible, personal computer. For analysis we choose EEG recorded during presentation of discriminative stimuli, filtered up to 100 Hz and digitized with 200 Hz probing frequency. After the experiment the cats were anesthetized and perfused for histological verification of the recording sites.

Two and a half second epochs of EEG activity recorded in one session, were selected for analysis from the last *5* seconds of EEG proceeding the learned responses. Fourier spectra were calculated from each of these epochs separately by fast Fourier transform (FFT) and directed transfer function (DTF, see below) procedures and averaged in sets obtained for the same stimuli and performance of the response.

RESULTS

The Fourier analysis of the EEG activity recorded from all electrodes was dominated by the low frequency (2-10 Hz) band in which two distinct peaks at about 2 and 6 Hz could be often distinguished (see Figs. 1,2). The analysis of this activity will be presented elsewhere. The present paper will focus on an additional, significant, elevation in 15-24 Hz (beta) range that was typically found either in visual or auditory cortical areas, during periods of presentation of relevant stimuli. These peaks were mainly due to the increased amplitude and frequency of appearance of short (usually less than 300 ins) bursts of oscillations (not illustrated). Increased beta activity was observed in the visual cortex recordings only during visual, and not during acoustic trials (Fig. *1A).* The difference between spectra was calculated separately at each, 0.5 Hz apart, frequency values by means of t-test. It was considered significant in the given frequency band when spectra appeared to be different $(P<0.05)$ in at least three consecutive frequency points.

Cat 1, for which the results are presented in Figs. 1A and *B,* was also allowed to see the same, but non-signalling visual stimulus in the neutral position in between the doors, during acoustic trials. The differences between the spectra obtained in both situations for this cat (Fig. *1A)* were similar to the remaining animals (e.g. Fig. 1 *C).* Consequently, we do not think that the observed increase of amplitude of 20 Hz oscillation during visual trials could be due simply to the stimulus induced activation of the visual system but results rather from setting the proper mechanism for its shift to the “attentive state”.

Further confirmation for the idea that the appearance of the 20 Hz peak coincides with the attentive state of the visual system came from its disappearance during trials on which animals made errors (Fig. *1B).* Also supporting our hypothesis was the finding of a mirror increase of the same frequency component in the spectrum obtained from EEG activity in the auditory cortex during attentive listening in one cat (out of two), which had an additional electrode implanted in ectosylvian gyrus (Fig. 1 *C, D).* However, we did not see such a component in the FFT spectrum of the auditory cortex activity of the other cat, nor did it appear in the spectra obtained from many recording sites in the visual cortex of different animals. It should be noticed that the increase of amplitude in the 20 Hz band, though observed in all cats, was usually recorded only from one of the electrodes implanted in the visual cortex (e.g. most posterior recording site in Fig. 2). In general, the magnitude of the observed 20 Hz peak varied with experimental days, although the analysis of this effect is not complete.

From trial to trial we often also observed higher frequency, significant peaks (more than 30 Hz, significance verified as above) in FFTs calculated for epochs encompassing presentation of visual stimulus (comp. Fig. 1 *C).* We have not analyzed them systematically in the present experiment.

It was difficult to trace differences in the beta range of the spectra obtained from noncortical recording sites. To better reveal such spectral components we differentiated the original EEG signal before applying Fourier analysis (Takigawa and Kidiyoor 1991). This procedure enhanced the amplitude of high frequency EEG components by a li-

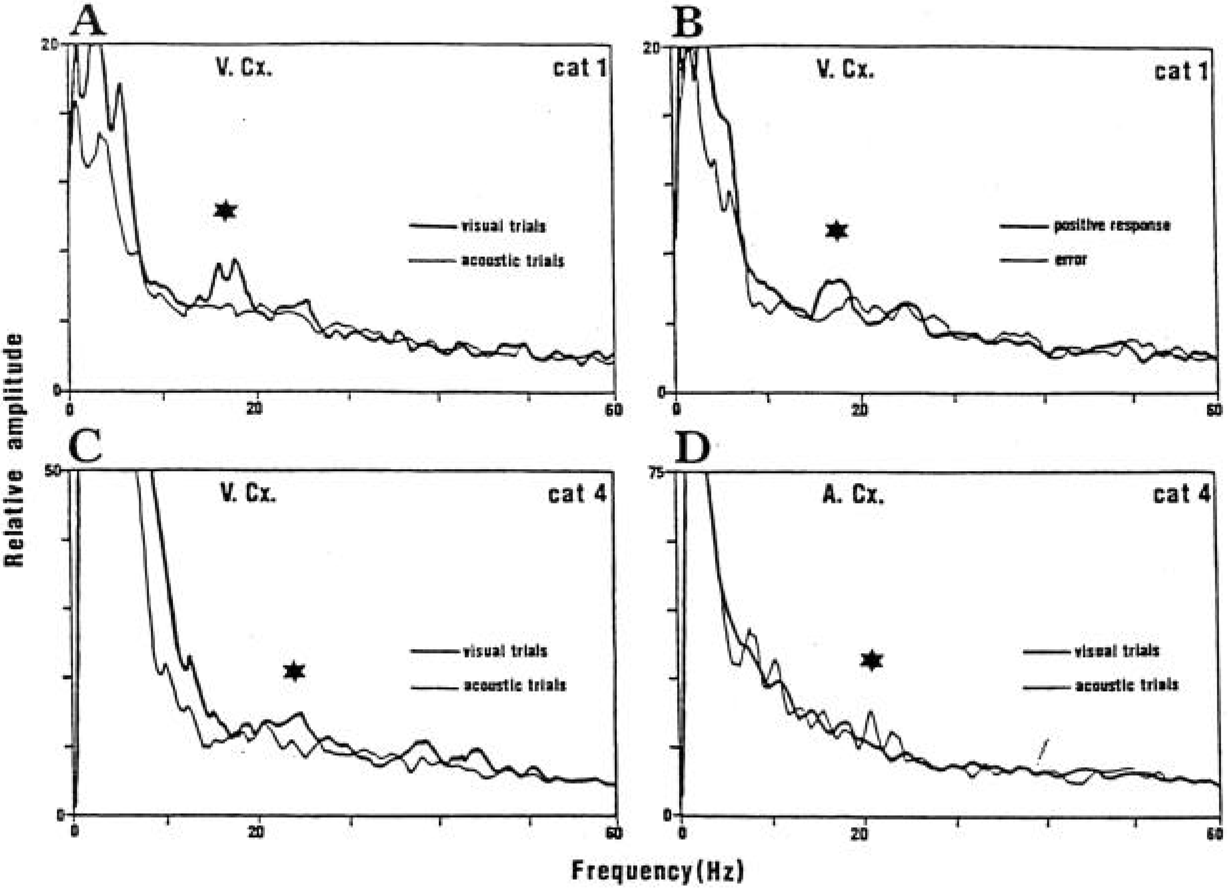

Fig. 1. Fast Fourier transforms (FFTs) obtained by averaging *2.5* s epochs of electrocoiticograms (ECoGs); A, B and C, D data from cat 1 and cat 4, respectively; *A,* Averaged FFTs calculated from 14 ECoGs epochs recorded at one session, from the same electrode placed in the primary visual cortex, during seven positive trials with visual (thick line) and ten with acoustic (thin line) cues. Nonsignalling visual stimulus accompanied the acoustic trials; *B,* Averaged FFTs obtained from epochs recorded during the same session, with the same electrode as in A. The ECoG epochs were chosen for averaging from five erroneous (thin line, five epochs) and six, consecutive, positive (thick line, eight epochs) trials; *C,* Averaged FFTs obtained from recordings registered at the same site of the visual cortex during seven acoustic (14 epochs) and six visual trials (12 epochs); *D,* Similar spectra obtained from simultaneously recorded epochs from acoustic cortex of the same cat. The statistically significant differences in the 20 Hz band have been marked by stars. The amplitudes were normalized by eye to the same value at 60Hz. See text for details.

near factor. FFJs of signals prepared this way are presented on the diagonals of the matrices in Fig. 2, left and right. After differentiation, it was more easy to follow the modality specific enhancement of 20 Hz band in recordings from lateral geniculate nucleus (LGN, compare upper left diagonal boxes in Fig. 2, left and right parts). The significance of this difference was confirmed as previously by t-test, at the 0.05 level. Interestingly, the peak in this band appeared only in parallel with the increase of the amplitude of the same frequency component in recording obtained from the aligned cortical site. The lowering of the cortical peak in consecutive days of experiment was reflected by similar change of the LGN 20 Hz band amplitude. We have never observed modality dependent differences in beta frequencies, in recordings obtained from perigeniculate nucleus (PGN) or hippocampus (Hipp., compare appropriate diagonal boxes on left and right parts of Fig. 2).

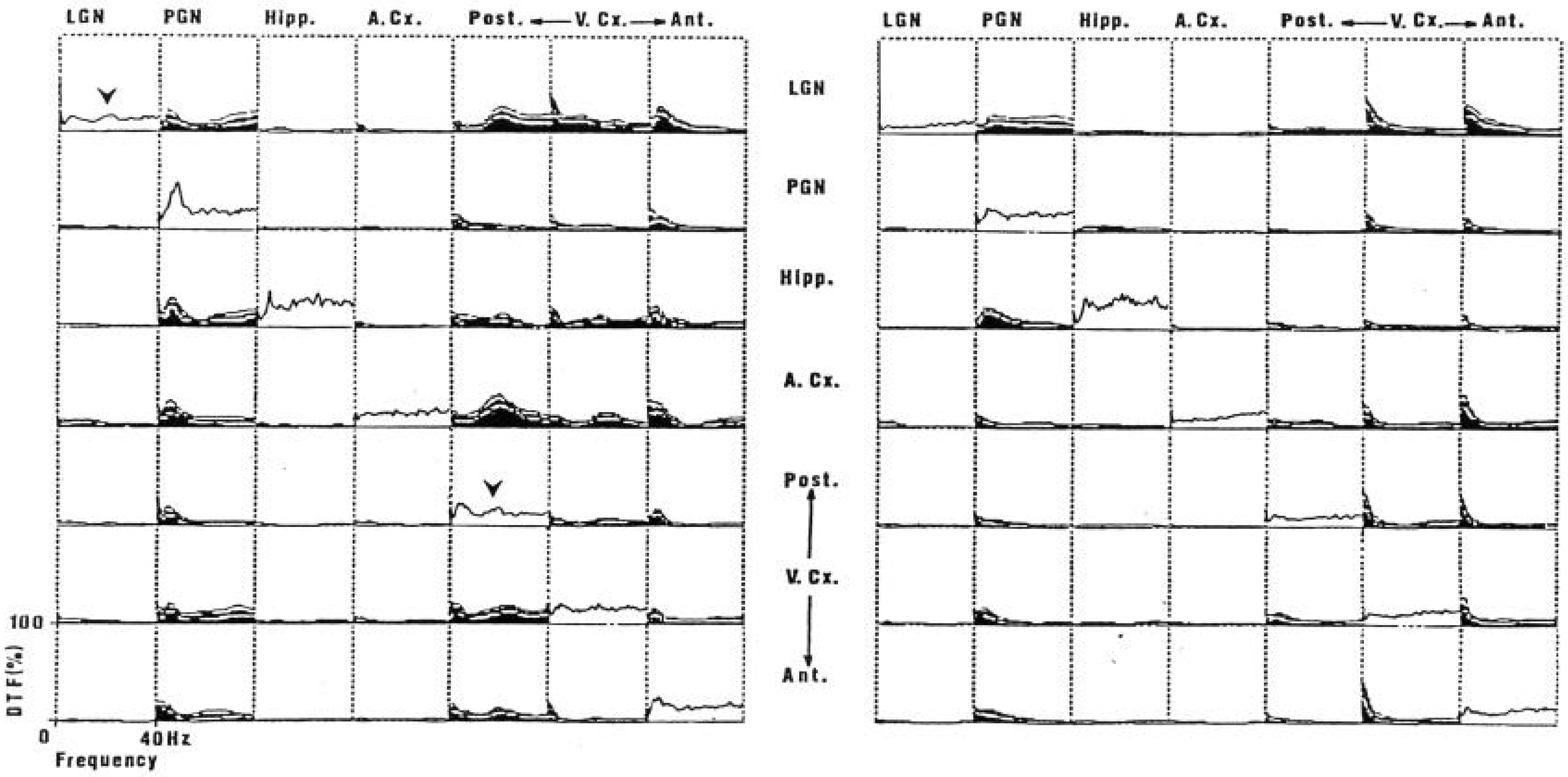

Fig. 2. Two matrices of directed transfer functions (DTFs) obtained between signals recorded from seven electrodes placed under physiological control as follows: LGN (azimuth 2^o/ elevation -2^o); PGN (5^o/ 0^o); V. Cx. (from posterior to anterior: 0^o/ 2^o, 2^o/ 0^o, -1^o/ -2^o). Hippocampal electrode was lowered stereotactically and confirmed to reach dentate gyrus; The remaining electrode (A. Cx.) was placed during surgery in posterior ectosylvian gyrus; Left matrix exhibits functions obtained from the signals recorded during visual trials ending with positive response. Right matrix - data from appropriate acoustic trials. Each small box on the diagonal contains averaged FFT of differentiated signals from the sites indicated above the matrix. Outside the diagonal directed transfer functions are presented. Values of the DTFs on the ordinate, frequency - on the abscissa (see text for details). The DTFs directed to LGN from other recording sites are shown in the uppermost row and those directed from the LGN towards other structures in the first, left column. Other source sites are listed in order, above the matrices and the target sites, to the side of them. Variability is shown by corridors of errors. All spectra normalized. The 20 Hz band in FFTs of the LGN and V. Cx. activities indicated by arrows in the left matrix. Note much higher DTF values between visual centers during performance of visual task.

The observation that the 20 Hz oscillatory component found in FFT of geniculate recordings follows the same frequency of cortical activity was confirmed by calculating directed transfer functions (DTFs), a recently developed method based on the multichannel AR (autoregression) model, invented to measure the direction and frequency content of the flow of the brain activity (Kamiñski and Blinowska 1991). In this model the DTF value at a given frequency is meant to describe the percent of the signal of this frequency recorded from one electrode, as appearing with some delay in the recording registered by a second electrode at the target point.

Outside the diagonals of the matrices of Fig. 2, the transfer functions are presented, which are calculated between the signals recorded from the seven points of the cat's brain during both auditory and visual experimental situations. Each box outside the diagonal contains the directed transfer function between the two EEG records as obtained from corresponding points indicated above and to the side of the matrix. As mentioned above the boxes on the diagonal consist of the FFTs of the differentiated signals as recorded from the appropriate points.

It should be noticed in Fig. 2 that in the situation requiring visual attention the 20 Hz oscillation appeared around the posterior cortical electrode (fifth column of the Fig. 2, left part); and it was propagated from there towards the LGN (first row box in the fifth column), other visual cortical sites (last two boxes in the same column) and the auditory cortex (fifth column - fourth row box). Notice that the ascending thalamo-cortical pathway seemed not to transfer any activity (first column of the Fig. 2, left part). There may be two explanations for this observation. Firstly, for the probing frequency of 200 Hz used by us, the DTF method shows time shifts between inputs only longer than five millisecond (Kamiñski and Blinowska 1991), a time probably long enough for transient (nonoscillatory) visual signals to be transmitted from LGN to the cortex. Secondly, the small peak of 20 Hz frequency observed in LGN Fourier spectrum (indicated by the arrow in upper-left diagonal box of the Fig. 2, left) probably represents too weak a source of activity to link the cortico-thalamo-cortical loop. The possibility of oscillation in this circuit, however, which might not be disclosed by the presented method, is now being checked in our laboratory.

We have not observed a trace of 20 Hz frequency oscillations during trials with the acoustic stimulus (Fig. 2, right part). The difference in this band, found between the two experimental situations, was significant as shown by errors in the appropriate boxes of the two matrices. Notice also that in general, much more activity is propagated among the different visual brain areas during the experimental situation requiring visual attention (Figs. 2, left) than during the acoustic task (Fig. 2, right).

In the 20 Hz frequency band only a dip was observed in the function directed from the PGN to the lateral geniculate (second column of the Fig. 2, left). The band of this frequency in the Fourier spectrum of PGN activity did not differ for the two experimental situations (second box on the diagonal of Figs. 2, left and right). This suggests that PGN might not be the source of the observed 20 Hz oscillations. However, the approximately 6 Hz frequency seemed to be propagated from this nucleus towards other brain structures, during the visually directed task. Interestingly, this frequency band also seemed to be propagated by the cortico-thalamic system from the anterior cortical site (the last column of Fig. 2, left part).

In the records presented in Fig. 2, neither the hippocampal nor the auditory cortical recording sites were found to be a source of the 20 Hz signal for other visual centers, in a similar way as described above for the site in primary visual cortex. This has also been confirmed in the other cat for which a significant 20Hz band was found during auditory trials (Fig. *1D)*.

DISCUSSION

In this experiment we found that a 20 Hz frequency band (average of *15-25* Hz range) of the Fourier transform of EEG activity registered from the visual cortex and lateral geniculate nucleus of the cat, grew significantly in amplitude at the time when the animal was ready to solve the visual task. The amplitude of this peak was typically elevated in only one of the recording sites of the visual cortex. During the same visual trials we also observed an increase in the amplitudes of lower frequencies of the FFT spectrum (2- 10 Hz; with maxima at 2 and 5 Hz). Simultaneously, a broad peak of about 6 Hz dominated the Fourier spectrum of activity recorded from the perigeniculate nucleus, with no trace of an enhanced 20 Hz band.

Although electrophysiological correlates of behavior have been intensively studied for years, there are only a few findings in this area related to the analysis of beta frequency oscillations in the range discussed. In complex studies on visual and acoustic evoked potentials, Basar (1980) has shown a stimulus induced stabilization of certain frequency bands in the sensory systems of-the awake cat. Interestingly the 10 and 20 Hz bands were best represented in the frequency spectra of responses evoked from lateral/medial geniculates and visual/acoustic cortices. In his experimental situation no behavioral activity was required from the animal. This could be the reason why the EEG recorded between stimuli did not contain any specific frequencies.

A 10 Hz frequency was shown by Chatila et al. (1992) to dominate the EEG recorded from area 18 of cats quietly waiting for a hidden mouse to become visible. This frequency was not seen in recordings from area 17. They also found this rhythm vanished during attentive fixation. Since we recorded both 10 and 20 Hz oscillations from the. stiate cortex of attending animals the two observations might be based on different mechanisms. On the other hand, Lopes da Silva et al. (1970) have shown a 20 Hz rhythm occurring in the visual cortex of the dog “focusing his attention on a target”. At the same time they observed only an 11 Hz peak in the Fourier spectrum of the signal recorded from LGN. It should be stressed here that we were able to dissolve the 20 Hz peak in geniculate activity only after a differentiation procedure. In the experiment of Lopes da Silva, closing the dogs eyes’ stopped beta rhythm in the cortical EEG. Similarly we found that 20 Hz rhythm disappeared in the activity of the visual centers when the cat started to attend the acoustic stimulus.

Freeman and van Dijk (1987) reported oscillatory activity in the visual cortex of the behaving monkey with similar broad Fourier spectra and bursting oscillations following the appearance of a learned stimulus. According to the previous analysis of the olfactory system (Skarda and Freeman 1987), they associated the spatial activity patterns in striate cortex with the representation of the stimulus rather than attention. Their findings, however, are limited to higher frequencies since they filtered the data with a cut off frequency of 20 Hz. Similarly to Freeman and van Dijk (1987) we also found the foci of beta rhythm to be rather limited in space, but our analysis was not accurate enough to discuss spatial stability of any cortical patterns.

In one cat with the electrode in the auditory cortex we could also see the 20 Hz rhythm during perception of the acoustic stimulus. Thus this beta band might be similarly enhanced during activation of all sensory systems (comp. Basar 1980, for visual and auditory system resonance frequencies). Quite similar bursts of about 20 Hz frequency were recorded by Rougeul et al. (1979) in the Si area of baboon, directly proceeding a manipulatory movement. These authors connected such activity with the maintenance of immobility in the somaesthetic channel though the observed bursting might also have been due to increased sensitivity of the thalamic cells (comp. more recent discussion in Chatila et al. 1992). Notice also, that in the awake rat suppression of the cortical activity in area Si reduces the responsiveness of ventrobasal neurons most severely in the 20 Hz band (Yuan et a!. 1986).

We have recently demonstrated that cortico-geniculate EPSPs are frequency potentiated and with repetitive cortical activation reaching 20 Hz exceed by far the optic tract evoked EPSP (Lindström and Wróbel 1990). We proposed that the potentiation mechanism might be used according to the needs of the animal, e.g. during attentive perception. This hypothesis required frequent activation of layer 6, cortico-thalamic, pyramidal cells to increase the gain of retino-cortical transmission through the geniculate relay. In other experiments, we observed that the tonic phase of a focal seizure evoked in the cortico-thalamic loop has a resonance frequency of about 20 Hz (Lindström and Wróbel, unpublished). Subthreshold oscillations of similar and higher frequencies have been also reported in many thalamo-cortical cells of the sleeping cat, by Steriade et al. (1991). The present observation, that the 20 Hz rhythm, originated in the visual cortex during visual attention, reaches further the geniculate cells, agrees with our previously proposed hypothesis. Short synchronized bursts of beta frequency in cortico-thalamo-cortical loop may be thus used fcr gain changes during focused attention.

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