NeuroReport 10, 3589–3594 (1999)

Coupling of beta and gamma activity in cortico-thalamic system of cats attending to visual stimuli

Marek Bekisz and Andrzej Wróbel[CA]

Department of Neurophysiology, Nencki Institute of Experimental Biology, 3 Pasteur St., 02-093 Warsaw, Poland

We have previously shown that local field potentials (LFPs) recorded in the lateral geniculate nucleus (LGN) and primary visual cortex (VCx) of the cat contain significantly more beta frequency activity when the animal attends to visual than to auditory stimuli. In the present study we utilised data from the same experiments to calculate the cross-correlation between envelopes of filtered beta (16–24 Hz) and gamma (30–45 Hz) oscillatory signals recorded at the same sites. Correlation values obtained from visual trials were significantly higher than those calculated for the auditory task. This observation was typical in those LGN and VCx recording sites which corresponded to the central representation of the visual field. The cross-correlation function peaked within a 20 ms time window from the centre of the cross-correlogram. These findings support the hypothesis that beta activity provides an excitatory background for the appearance of oscillations in the gamma band. *NeuroReport* **10:3589–3594 © 1999 Lippincott Williams & Wilkins.**

Key words: Attention; Beta-gamma synchronization; Cat; Oscillations; 16–24 Hz, beta frequency; 30–45 Hz, gamma frequency

[CA]Corresponding Author

Introduction

It is well established that different behavioural conditions are accompanied by synchronous activity of neurones in numerous brain areas, which is consequently recorded as electrical field oscillations. Rhythmic activities at frequencies below 14 Hz characterize the functional state of thalamic and cortical networks during sleep and arousal [1–3]. The synchronization of higher frequencies in the so-called gamma band (> 30 Hz) has been postulated to serve as a feature-linking mechanism at different levels of cortical sensory processing [4,5]. We have shown previously that the local field potential (LFP) activity recorded in the lateral geniculate nucleus (LGN) and primary visual cortex (VCx) of cats attending to visual stimuli contained more power in the beta (16–24 Hz) frequency range than in the auditory attentive situation [6]. We have, therefore, proposed that such enhanced beta activity is an electrophysiological correlate of shifting the visual system to the attentive state. Support for this notion comes mainly from the observation that the beta activity appeared predominantly during correct performance of a visual discrimination task [6,7]. Such activity was rarely found at the same recording sites when an animal made an error or during auditory trials. We have further shown that the enhanced beta activity observed during the visual trials consists of 0.1–1 s long oscillatory events, appearing coincidentally in the retinotopically matching LGN and VCx recording sites [7,8]. Consequently, we have postulated that this type of activity is propagated from the cortical site by descending cortico-thalamic pathway [6] which, by means of a potentiation mechanism at the cortico-thalamic synapse [9–11], enhances the gain of thalamic relay during visual perception. By such a mechanism the amount of visual information reaching the cortex would increase in the visual attention state. The visual task in our experiment required from the cat to notice the visual cue stimulus and correspondingly we often saw an enhanced bursting activity in the gamma (30–45 Hz) frequency range. In this study we attempted to find the possible time correlation between the observed fluctuations in beta and gamma activities.

Materials and Methods

The experiments described below were approved by the Ethics Commission at the Nencki Institute.

Behavioural paradigm: Details of the methods have been published previously [6–8] and are reviewed briefly below. Three cats were trained to perform two differentiation tasks (involving visual and acoustic stimuli) during the same session. The

animals were placed in a small ($20 \times 45 \times 45$ cm) wooden cage and faced two translucent doors separated by 5 cm. The cat was separated from the doors by a transparent removable screen. The visual stimulus was a small (0.5°/2°) rectangle of light, of 3 cd/m^2 intensity, which was projected on the front wall at the level of the cat's eyes. It moved horizontally back and forth across both doors (a linear speed of about 10 cm/s) and simultaneously oscillated in the vertical plane (frequency 1 Hz, amplitude 4 cm). After 10–20 s (trial duration changed randomly) the stimulus was stopped on one of the doors, indicating that a piece of meat was hidden behind that door. After 1 s the stimulus was switched off.

The acoustic stimulus was a noise produced by a pocket-radio loudspeaker, with a fundamental frequency of 5 kHz and intensity modulated with a 2.5 Hz frequency between 50 and 55 dB. The stimulus was switched on behind the wall separating the doors, and consecutively moved around the corner of the cage, behind the left or right wall. After 10–20 s the stimulus was switched off. The reward was hidden behind the door to the side on which the auditory stimulus had been turned off.

After the visual or acoustic stimulus had been switched off, the transparent screen was raised and the cat could reach for the reward by pressing the correct door. The animal could not open the incorrect door. It was not allowed to correct an error.

The learning procedure started with the visual task. The acoustic stimulus was introduced after the animal attained a 90% performance level on the visual task. For trained animals both visual and acoustic stimuli were repeated 12 times in each session during one experimental day. Training was considered complete when animals reached 90% performance accuracy during three successive experimental days.

Animal preparation: After the completion of training, surgery was performed under Nembutal anaesthesia (35 mg/kg with subsequent supplementary doses, premedication with combelen 0.2 mg/kg and 0.01 ml atropine (0.05% atropinum sulfuricum)). Two tungsten recording electrodes were inserted under electrophysiological control in the left LGN. A row of three or four chromonickel electrodes, about 1.5 mm apart, was placed in the left primary VCx. The electrodes and a plug were fastened to the skull using dental cement. The recordings started seven days after surgery. Ordinary Nissl procedure histology was used after each experiment to reveal the exact electrode locations.

Recordings and data analysis: The recorded local field potentials (LFPs; 1 Hz–0.5 kHz) were amplified and stored on FM magnetic type recorder (Racal V-store). For the computer off-line data analysis, LFPs frequencies >100 Hz were filtered out and the remaining signals were digitized with a 200 Hz sampling rate (Fig. 1A).

To show the frequency content of the investigated signal we applied the Fast Fourier Transform (FFT). FFT amplitude spectra were calculated for each trial for many consecutive time epochs. Each epoch was 256 samples (1.28 s) long. Before Fourier transformation the raw data within the epoch were multiplied by the Hanning window function. The time shift between the onset of two consecutive epochs from which the neighbouring spectra were calculated was 40 samples (0.2 s) for the running FFT and 128 samples (half of the epoch size) for mean FFT. The spectra were averaged separately for all epochs from error-free visual and auditory trials.

For further analysis the LFPs were digitally bandpass filtered (FIR filter with Kaiser window and no phase shift) into two bands with half amplitude cut-off frequencies 16–24 Hz and 30–45 Hz (Fig. 1B). The frequency borders were chosen to encompass the enhanced activity in beta and gamma bands in all three cats. The frequency bandwidth of the enhanced gamma activity was somewhat smaller for cat 1 (31–36 Hz, see Fig. 2) than for cats 2 and 3 (30–45 Hz). To obtain envelope type signals (Fig. 1C) the filtered LFPs were rectified, smoothed (five point box smoothing for 16–24 and three point for 30–45 Hz band) and their means were subtracted. Envelopes for both frequency bands were then normalised to have unitary variance and cross-correlated for signals recorded from each electrode separately. The cross-correlation window was one

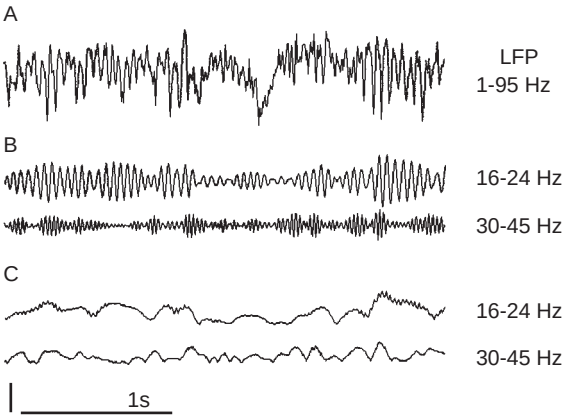

FIG. 1. (**A**) An example of 1–95 Hz local field potential (LFP) signal recorded during error-free visual trial (the signal shown comes from the 12.5–15.5 s period of the visual trial presented in Fig. 2A). (**B**) Beta (16–24 Hz) and gamma (30–45 Hz) frequency bands filtered from the signal in (A). (**C**) The same signals as in (B) after rectification and smoothing. The vertical calibration bar - 65 μV (A,B); 35 μV (C).

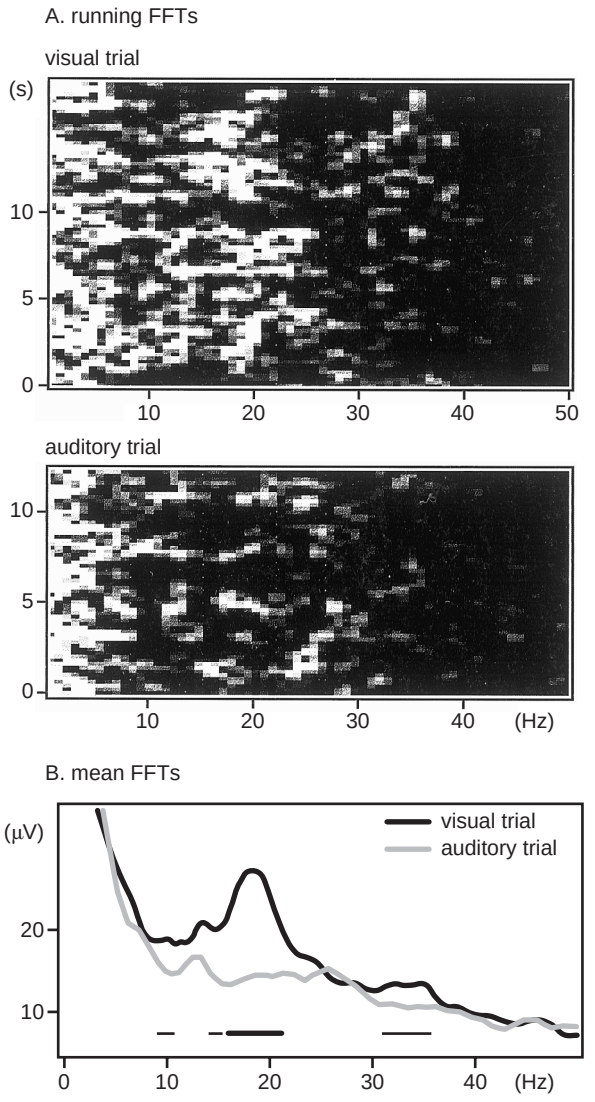

FIG. 2. (**A**) Representative running FFTs of LFPs recorded in primary visual cortex (VCx) during consecutive error-free visual and auditory trials of cat 1 (details of calculating running FFTs are described in Materials and Methods). FFT amplitudes $\geqslant 35\,\mu V$ are denoted in white; smaller amplitudes are represented in linear grey scale; amplitudes $\leqslant 15\,\mu V$ in black. Frequencies are along abscissa and time on the ordinate (the visual trial lasted longer than auditory according to randomization of the trial duration). (**B**) Averaged FFT spectra from both trials shown in (A). Spectrum from visual trial (black line) was obtained by averaging FFTs from 28 (1.28 s long) blocks of data, the spectrum from auditory trial (grey line) from 20 blocks. The black lines above the horizontal axis denote frequencies at which significant differences were found (Student's *t*-test; thick line $p < 0.01$, thin lines $p < 0.05$).

second. The cross-correlation functions were averaged separately for all error-free visual and auditory trials from three experimental days. Calculating cross-correlograms between beta and time-inverted gamma envelopes taken from different trials assessed the control, uncorrelated level.

Statistical significance was tested with the Wilcoxon matched pairs test and Student's *t*-test. A probability level of $\leqslant 0.05$ was considered as significant.

Results

Figure 2A presents running FFTs of representative LFP signal recorded from one electrode in primary visual cortex during consecutive, error-free visual (upper graph) and auditory (lower graph) trials. During the visual trial the LFP components concentrated within three frequency bands: low (8 Hz), beta (16–24 Hz) and gamma (31–36 Hz). During the auditory trial the eruptions of low frequency activity were of similar strength but the beta signal was weak. Much less activity was noticed also in the gamma band. The average amplitude spectra for each trial are shown in Fig. 2B. It is apparent that the main differences between these spectra are concentrated within beta and gamma bands, where FFT amplitudes calculated during the visual trial are higher. This was verified by Student's *t*-test using 28 (for visual trial) and 20 (for auditory trial) 1.28 s long pieces of data, with probability values $p < 0.01$ for beta and $p < 0.05$ for gamma frequencies.

Beta peaks were significantly more pronounced in averaged spectra calculated for error-free visual trials as compared to auditory ones, in all three animals. Gamma peaks of significantly higher amplitude during visual trials were found for two of three cats (i.e. for six recording sites in VCx and two in LGN).

The texture of the running FFT shown in Fig. 2A reveals the bursting oscillatory nature of activity within all three frequency bands. Specifically, a close inspection of the upper graph allows correlating the appearance of beta and gamma bursts. The beta frequency oscillations were often observed at the same time as gamma waves, for instance at 3, 12 and 14 s of the visual trial. There are however eruptions of gamma activity which are not accompanied by beta events (e.g. at 0 and 10 s; see also Fig. 1B). The frequency values of gamma bursts were typically not multiples of frequencies of concomitant beta activity (e.g. during visual trial presented in Fig. 2A, at 3 s 20 Hz *vs* 34 Hz, at 12 s 19 Hz *vs* 35 Hz, at 14 s 17 Hz *vs* 32 and 35 Hz). Both findings clearly prove that the gamma bursts are not harmonic correlates of beta events.

The 200 ms overlap between consecutive blocks in our running spectral analysis smeared the time of appearance and disappearance of relatively short beta and gamma activity epochs. The time resolution of this method was insufficient for accurate temporal correlation of beta and gamma events. For this purpose we filtered digitally LFPs into beta and gamma bands (Fig. 1B). The filtering revealed that both beta and gamma activity group in bursts of oscillations lasting from about 0.1 to 1 s. Two tendencies characterized these activities: beta bursts

lasted longer than gamma and some beta bursts correlated in time with gamma bursts, while others did not (see Fig. 1B). We verified the possible time correlation between oscillatory events in both frequency ranges by means of cross-correlation method. Beta and gamma envelope signals (see Fig. 1C) were cross-correlated for each error-free trial from three experimental days and averaged separately for all visual and acoustic trials. The resulting functions were called the beta/gamma cross-correlations and their plots beta/gamma cross-correlograms.

Figure 3 shows beta/gamma cross-correlograms obtained for all three sites in primary visual cortex and one LGN site of cat 3. All four electrodes recorded LFPs from regions representing visual scene within 3° from the area centralis. Black and grey lines denote correlograms obtained respectively for visual and auditory trials. Dashed lines show control (uncorrelated) cross-correlations for data of either modality. They were calculated between beta and time-inverted gamma envelopes chosen from different trials. The central peaks apparent in all cross-correlograms obtained for visual trials indicate that beta and gamma oscillatory bursts are closely correlated (coupled) in time. The central peaks were much smaller during auditory task, and often did not exceed the control level.

Maximal values for beta/gamma cross-correlograms for all VCx and LGN recording sites in all cats are summarized in the histogram of Fig. 4. Horizontal, dashed lines show control level, estimated as the mean of the maximum values of the corresponding control cross-correlograms. All VCx and two LGN electrodes were implanted in such a way that they recorded the neuronal activity elicited by visual stimulation from within 3° from the area centralis. The remaining two LGN electrodes recorded activity from representation of peripheral visual field. For all electrodes located in the visual cortex the maximal cross-correlation values calculated during visual trials were bigger than those calculated for the auditory task. This trend was statistically verified at the $p < 0.01$ level, using Wilcoxon matched pairs test. Similar trend was observed for cross-correlation values calculated from LGN data recorded from sites near representation of area centralis. The maximal correlation values obtained for peripheral LGN sites did not differ significantly between data recorded during visual and auditory trials. Although the variation of correlation values calculated in consecutive trials from one recording site was considerable, significant differences between maximal correlation amplitudes in visual and auditory trials were confirmed with

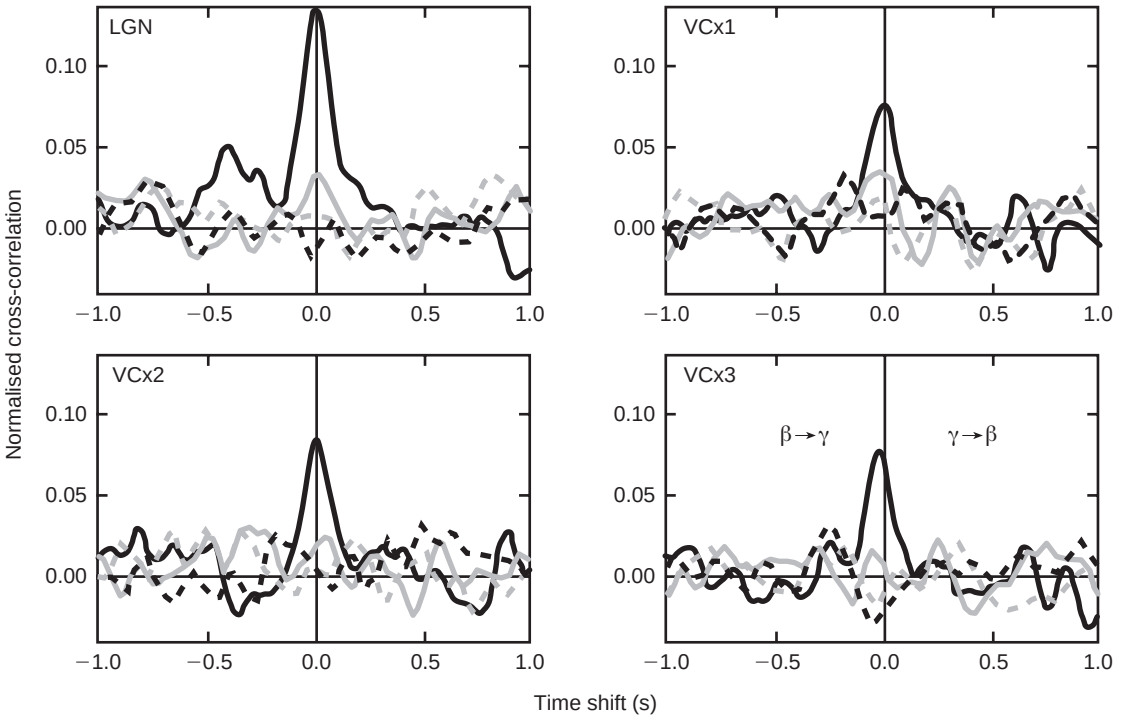

FIG. 3. Representative set of cross-correlation functions calculated between normalised (an unitary variance) envelopes of 16–24 Hz (beta) and 30–45 Hz (gamma) range signals, for one LGN and all VCx recording sites, from cat 3. All cortical electrodes were in striate cortex and recorded neuronal activity from central vision representation (within 3° from the area centralis). Black lines, visual trials; grey line, auditory trials. The graphs show cross-correlograms averaged for all error-free trials from three experimental days. Dashed lines represent control (uncorrelated) cross-correlograms. They were obtained using beta and time-inverted gamma envelopes chosen from different trials. The left half of each correlogram represents beta oscillations preceding gamma oscillatory events.

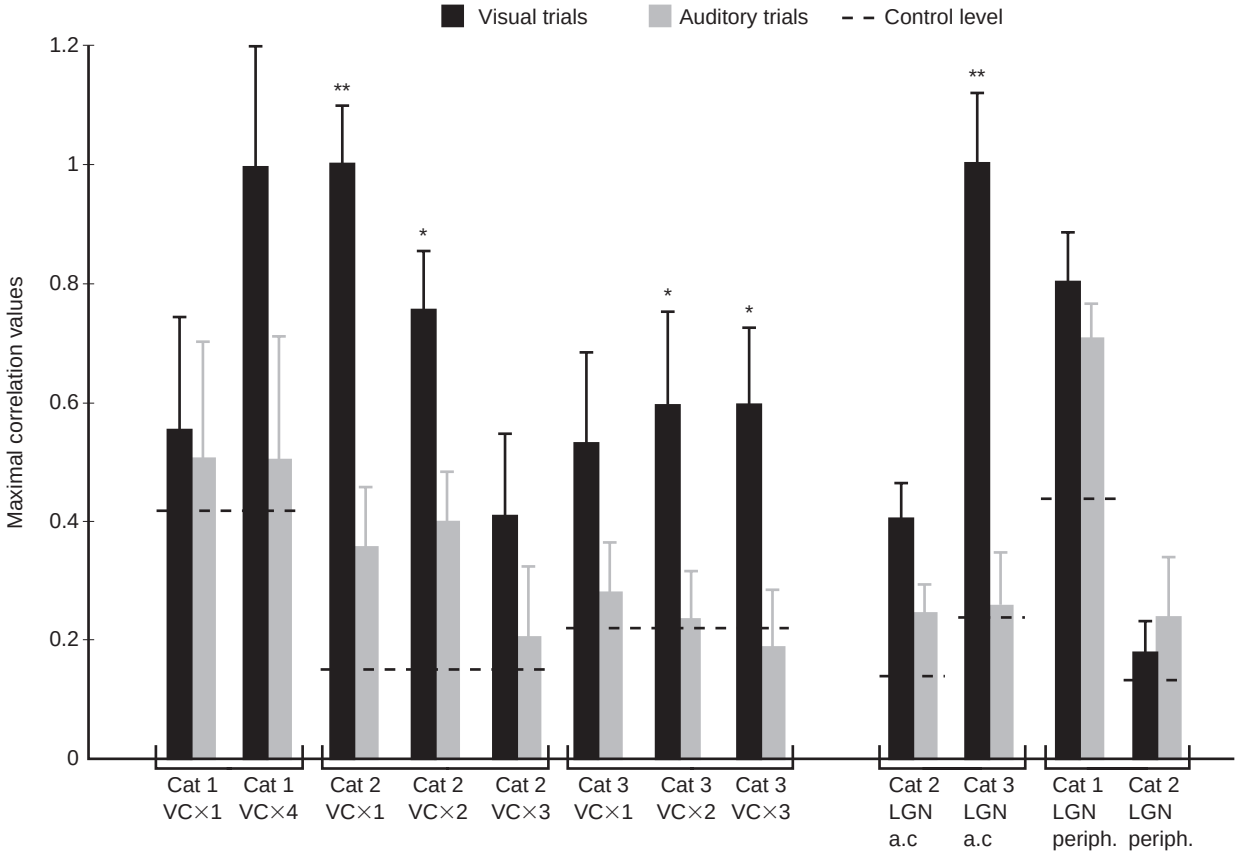

FIG. 4. Maximal values of mean beta/gamma cross-correlograms measured for all VCx and LGN recording sites, from all three animals. The values obtained for all recording sites in a given animal were normalised to the maximal. Black bars indicate maximal correlation values calculated from 23 (cat 1), 10 (cat 2) and 20 (cat 3) visual trials, grey bars: corresponding values obtained from 30 (cat 1), 11 (cat 2) and 22 (cat 3) auditory trials. Vertical line attached to the top of each bar show standard error of the mean. Horizontal dashed lines show control level, estimated as the mean of the maximum values of the corresponding control cross-correlograms. All VCx and two LGN recording sites were located within representation of three visual degrees of the area centralis (a.c.). The remaining two LGN electrodes recorded signals from the peripheral part of the nucleus (azimuth /elevation: 10°/−15°, cat 1; 7°/30°, cat 2). For data from all cortical sites the mean values for visual trials were larger than those obtained during the auditory task (Wilcoxon matched pairs test, $p < 0.01$). Asterisks indicate those separate electrode locations at which differences between visual and auditory values reached significance (Student's *t*-test; $^{*}\ p < 0.05$, $^{**}\ p < 0.01$). The consecutive indexes for cortical electrodes denote their relative position along the marginal gyrus in each cat. The higher number corresponds to the more anterior location of the electrode.

Student's *t*-test for four cortical sites and one centrally located LGN electrode (see Fig. 4 legend for details). Most of the correlation values obtained for auditory trials were close to the control level (Fig. 4), indicating that in this situation beta and gamma activities change independently.

The central peak of the beta/gamma correlograms was often shifted from the middle (zero) of the time axis. For instance, the peak of cross-correlogram from visual data presented at lower-right box of Fig. 2 is shifted to the left by 20 ms. All other correlation peaks obtained for visual trial data from the sites in VCx, were located within a 20 ms window around the middle of the correlogram, indicating strong temporal coupling of beta and gamma bursts during performance of visual discrimination task. In most cases (five of eight) these peaks were shifted to the left (with the median value −5 ms), one peak was located centrally and only two on the right side of the correlogram. These findings indicate that, in visual trials, beta oscillatory bursts tended to coincide with gamma events. In contrast, central extrema of cross-correogram calculated from auditory trials data seemed to be randomly distributed along the time axis (± 70 ms).

Discussion

In the present study we have shown that gross bursts of beta and gamma oscillations observed at the same sites of visual part of cortico-thalamic system were temporally correlated when cats attended to visual stimuli. Such coupling was found specifically in those locations of LGN and VCx, which represented the central vision. When animals directed attention to auditory modality the coupling was significantly weaker, and in most locations beta and gamma oscillation seemed to appear independently.

The increase in the amount of beta frequency

signal in the LFP was previously found in our laboratory to correlate with the attentive state of the visual system. We proposed that beta activity transmitted via the cortico-thalamic pathway, could gain the excitability of geniculate relay cells and therefore increase the amount of visual information reaching the visual cortex [6–9]. This idea was in line with the 'searchlight hypothesis' described earlier by Crick [12]. He suggested that the attention control system may use the descending activity for transient enhancement of relay transmission. Such an hypothesis posits that perception is enhanced with more visual information reaching the cortex. If, on the other hand, perception would rely on the synchronisation of neuronal ensembles with gamma frequency oscillation [4,5], such an activity should increase in the attentive state of the visual system. The present finding, that beta and gamma oscillation are temporally correlated in cats attending to visual stimuli, is in good agreement with the proposed earlier hypothesis [6,9].

Traditionally, activities within different frequency bands have been assumed to appear independently. Our findings suggest that brain rhythms of different frequencies are functionally related in certain behavioural conditions. Recently, other reports seem to propose similar ideas. Shanze and Eckhorn [13] showed the phase correlation between low frequency activity (i.e. alpha and beta) and 30–90 Hz (gamma) oscillations in visual cortex of awake monkeys. Similarly Chrobak and Buzsaki [14] reported that gamma oscillation in the entorhinal cortex could be coupled to the negative phase of the theta rhythm in freely behaving rats. Finally, Roelfsema *et al*. found that about 20 Hz synchrony appears among different cortical areas when animals are engaged in an attention-requiring task [3]. On the other hand data from the same laboratory support the hypothesis that 40 Hz synchronization is related to a feature binding mechanism [5]. These observations taken together are in accordance with our notion that beta frequency signal increase in order to activate functionally related visual structures, providing the necessary background for gamma synchronization, which may then serve more detailed visual mechanism.

Conclusion

In LFPs recorded from LGN and VCx sites related to central vision we have observed that bursts of beta oscillations correlate in time with events of gamma waves. These findings support our previous notion, that beta activity provides the excitatory background for appearance of oscillations in the gamma band [6].

References

1. Steriade M, McCormick A and Sejnowski TJ. *Science* **262**, 679–685 (1993).
2. Chatila M, Milleret C, Buser P and Rougeul A. *Electroencephalogr Clin Neurophysiol* **83**, 217–222 (1992).
3. Roelfsema PR, Engel AK, König P and Singer W. *Nature* **385**, 157–161 (1997).
4. Eckhorn R, Bauer R, Jordan W *et al. Biol Cybern* **60**, 121-130 (1988).
5. Gray CM, König P, Engel AK and Singer W. *Nature* **338**, 334–337 (1989).
6. Bekisz M and Wróbel A. *Acta Neurobiol Exp* **53**, 175–182 (1993).
7. Wróbel A, Bekisz M and Waleszczyk W. 20 Hz bursts of activity in the cortico-thalamic pathway during attentive perception. In: Pantev C, Elbert Th and Lutkenhoner B, eds. *Oscillatory Event-Related Brain Dynamics.* New York: Plenum Press, 1994: 311–324.
8. Wróbel A, Bekisz M, Kublik E and Waleszczyk W. *Acta Neurobiol Exp* **54**, 95–107 (1995).
9. Lindström S and Wróbel A. *Exp Brain Res* **79**, 313–318 (1990).
10. Bekisz M, Eaton SA and Paulsen O. *Eur J Neurosci* **10 (Suppl. 10)**, 138 (1998).
11. Von Krosigk M, Monckton JE, Reiner PB and McCormick DA. *Neuroscience* **91**, 9–20 (1999).
12. Crick F. *Proc Natl Acad Sci USA* **81**, 4586–4590 (1984).
13. Schanze T and Eckhorn R. *Int J Psychophysiol* **26**, 171–189 (1997).
14. Chrobak JJ and Buzsaki G. *J Neurosci* **18**, 388–398 (1998).

ACKNOWLEDGEMENTS: Excellent technical help at each stage of this experiment was provided by Ms Dorota Krakowska and Mr Wojciech Borkowski. We would like to thank Dr Ole Paulsen for critical comments on the manuscript. This study was supported by a grant from the State Committee for Scientific Research (4.P05A.079.09).

Received 1 September 1999; accepted 23 September 1999