

# SHORT COMMUNICATION

## Attention-dependent coupling between beta activities recorded in the cat's thalamic and cortical representations of the central visual field

Marek Bekisz and Andrzej Wróbel

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

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### Abstract

We have previously proposed that enhanced 16–24 Hz (beta) local field potential activity in the primary visual cortex and lateral geniculate nucleus may be an electrophysiological correlate of the attentional mechanism that increases the gain of afferent visual information flow to the cortex. In this study, we measured coupling between beta signals recorded in the thalamic (i.e. lateral geniculate or perigeniculate) and cortical representations of the central visual field (within 5° from *area centralis*), during visual and auditory attentive situations. Signal coupling was calculated in two ways: (i) by means of crosscorrelation between raw beta activities, which depends primarily on phase coherence, and (ii) by phase-independent crosscorrelation between amplitude envelopes of beta activities. Mean amplitudes of raw signal crosscorrelations obtained for thalamo-cortical recording pairs were not significantly different when calculated during behavioural demands for either visual or auditory attention. In contrast, amplitudes of envelope crosscorrelations obtained during behaviour requiring visual attention were, on average, two times higher than those calculated during the auditory task. This attention-related coupling emerged from synchronized amplitude modulation of beta oscillatory activity that occurs within the cortico-thalamic circuit involved in central vision.

### Introduction

In the mammalian visual system, the most numerous synapses on principal cells in the lateral geniculate nucleus (LGN) and on their recurrent inhibitory interneurons in the perigeniculate nucleus (PGN) are formed by corticofugal fibers of pyramidal cells in layer VI (Ide, 1982; Montero & Singer, 1984; Wilson *et al.*, 1984; Montero, 1991). Synapses formed by this rich cortico-thalamic projection show a prominent frequency potentiation mechanism, which was postulated to increase the gain of the retino-cortical flow of information during visual attention (Lindström & Wróbel, 1990). The attentional role of the cortico-thalamic pathway was supported by observations of attention-dependent increase of activity in the LGN of the cat (Bekisz & Wróbel, 1993; Wróbel *et al.*, 1994) and in the LGN and thalamic reticular nucleus of the rat (Montero, 1997; McAlonan *et al.*, 2000; Montero, 2000). Attention-related changes of activity were also found in the LGN of the monkey (Vanduffel *et al.*, 2000).

In our previous experiments, cats' attention was shifted between visual and auditory systems in a spatial differentiation task, which involved stimuli of either modality (Bekisz & Wróbel, 1993; Wróbel *et al.*, 1994). It appeared that local field potentials (LFPs), recorded in the LGN and primary visual cortex (VCx), contained more beta (16–24 Hz) activity when cats attentively expected visual rather than auditory cue stimuli. Moreover, such enhancements of beta power were not found prior to erroneous behavioural responses of the animal. We have therefore proposed that enhanced beta activity within the VCx

and LGN might be an electrophysiological correlate of the attentional mechanism that increases the gain of afferent visual information flow to the cortex.

The visual task in our experiments required a cat to react to the visual cue stimulus. This process should involve central vision. In order to investigate the functional relationship between the thalamus and visual cortex in visually and auditory attentive situations, we measured coupling between 16–24 Hz beta signals recorded in the representations of central visual space in both these structures.

### Materials and methods

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

#### *Behavioural paradigm*

Data presented in this paper were obtained from three cats with electrodes chronically implanted at various sites of the cortico-geniculate visual system. Cats were trained to solve a spatial differentiation test. They were placed in a small (20 × 45 × 45 cm) wooden cage facing two translucent doors 5 cm apart. The animal was kept away from the doors by a movable transparent screen.

The differentiation paradigm has been described in detail previously (Wróbel *et al.*, 1995; Bekisz & Wróbel, 1999). Two animals (Cats 4 and 5) had to notice the site of disappearance of either a visual or auditory stimulus (being a cue at the end of the presentation period), moving continuously back and forth in a horizontal direction during 10–25 s long trials. The trials of the third animal (Cat 6) started with a 1-s long preparatory visual or auditory stimulus: a diffuse light on the

Correspondence: Professor Andrzej Wróbel, as above.  
E-mail: wrobel@nencki.gov.pl

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doors or a white noise from a loudspeaker mounted behind the front wall above the doors. During the following delay period (8–10 s long), no stimulus was present until the cue stimulus (lasting 1 s) appeared at one of the doors. In both paradigms, the visual cue was a small ( $1 \times 0.5$  cm) rectangular light ( $5 \text{ cd/m}^2$  intensity) which was projected from behind the doors; the auditory cue was a noise from the loudspeaker ( $<50$  dB) switched off in the first paradigm or switched on in the second paradigm behind the left or right side wall of the cage. One second after the offset of the visual or auditory cue stimulus, the transparent screen was raised and the animal had to open the door on the side of the disappearance of the cue in order to reach the reward.

The learning procedure started with the visual task. The auditory trials were introduced after the animal had reached 90% performance level in the visual task. Training was considered complete when the animals reached 90% performance in the task for each modality during three successive experimental days. For trained animals, both visual and auditory trials were repeated 12 times in each session (one session a day) in random order.

#### Electrode implantation

After completion of training, chronic electrodes (chromonickel wire for cortical, and tungsten wire for thalamic recordings, both  $100 \mu\text{m}$  in diameter,  $80\text{--}130 \mu\text{m}$  tip size and impedance between 50 and  $100 \text{ k}\Omega$  at  $1 \text{ kHz}$ ) were implanted within the left hemisphere under Nembutal anaesthesia. In this paper we have analysed signals recorded only from centrally placed electrodes (i.e. within  $5^\circ$  from *area centralis*) which were located as follows. Three (or two in Cat 6) electrodes, about  $1.5 \text{ mm}$  apart, were inserted into the primary VCx along the longitudinal fissure, according to maps provided by Tusa *et al.*, (1978). The recorded swish of multiunit activity (Sanderson, 1971) was used to determine the thalamic implantation sites. In Cat 4, one electrode was inserted into layer A and in Cat 6 into layer A1 of the LGN. In Cat 5, one thalamic electrode recorded from layer A in the LGN, and a second electrode from the PGN (binocular swish). Electrodes and a male connector were fastened to the skull using dental cement. After completion of the experiments, the animals were killed by an overdose of Nembutal. As verified histologically (Nissl staining) the displacement of retinotopic coordinates between thalamic and cortical electrodes varied from about 2 to 5 degrees.

#### Recordings and data analysis

Monopolar recordings of LFPs (amplification 1000 times with bandwidth  $1 \text{ Hz} - 5 \text{ kHz}$ ) started 1–2 weeks after surgery and all experimental sessions were stored on an FM magnetic tape recorder (Racal V-store). Low-pass filtered data (3dB amplitude attenuation at  $100 \text{ Hz}$ ,  $24 \text{ dB/octave}$ , Bessel filter) were digitized with  $400 \text{ Hz}$  sampling rate and then down-sampled to  $200 \text{ Hz}$ . For Cats 4 and 5, the signal analysis was performed on LFPs recorded during 10–25 s long periods of presentation of the moving stimuli. For Cat 6, the analysis period (8–10 s long) encompassed the time between the offset of the preparatory and the onset of the cue stimuli.

Fast Fourier Transform (FFT) amplitude spectra were calculated for successive signal epochs, each 256 samples long and shifted by 128 samples (50% overlap) from the previous one. Before Fourier transformation, raw data within each epoch were multiplied by the Hanning window function to reduce spectral leakage. Spectra from a number of epochs encompassing the whole trial or many trials were averaged. The significance of difference between mean visual and auditory amplitude values was checked for each frequency with Student's *t*-test.

For further analysis, LFPs were digitally band-pass filtered (FIR filter with Kaiser window and no phase shift) with half amplitude

cut-off frequencies 16 and  $24 \text{ Hz}$  (Fig. 1B). These frequency borders were chosen to encompass beta activity that was enhanced during the visual task in all three cats. This band matched the attention-elevated frequencies found in our previous experiments (Bekisz & Wróbel, 1993; Wróbel *et al.*, 1994). To obtain amplitude envelopes of beta activity (Fig. 1B), the filtered LFPs were rectified (absolute transform) and smoothed over a 20-ms long five-point window with equal weights.

Crosscorrelation between raw oscillatory signals or between their amplitude envelopes were calculated first for single trials (time lag varied from  $-1$  to  $1 \text{ s}$  in steps of  $5 \text{ ms}$ , correlated signals were always corrected for zero means) and then averaged over trials. Significant values of raw crosscorrelation require stable phase difference (i.e. phase coherence) between the analysed signals, during and over trials. On the other hand, phase-independent envelope crosscorrelation measures covariance (or simply the synchronisation) between amplitude fluctuations of these signals. Because both crosscorrelations were normalised with the geometric mean of autocorrelation coefficients, the results were independent of the mean amplitudes of thalamic and cortical beta activities. In addition, control crosscorrelations were obtained by using one of the signals time-inverted and taken from a different trial. This procedure approximated the uncorrelated signals very well. The significance of difference between mean visual and auditory correlation values was verified for each particular time lag

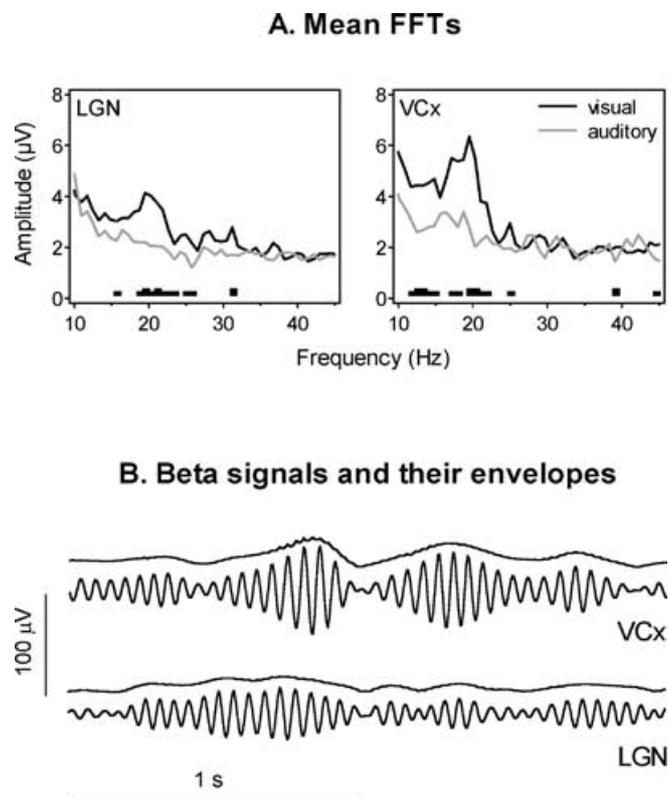


FIG. 1. (A) Mean FFT amplitude spectra of raw LFPs recorded in VCx and LGN during correctly performed visual and auditory trials in the same experimental session of Cat 5. The black lines above the horizontal axis denote frequencies at which significant differences were found (*t*-test; thick lines  $P < 0.01$ , thin lines  $P < 0.05$ ). Note the differences between visual and auditory spectra around  $20 \text{ Hz}$ . (B) Examples of beta ( $16\text{--}24 \text{ Hz}$ ) signals filtered from the raw LFPs recorded in VCx and LGN during a correct visual trial. These signals come from the visual trial from which the mean FFT spectrum presented in A was calculated. Above each filtered signal its amplitude envelope (obtained by rectification and smoothing) is shown.

with the Student's *t*-test. The *t*-test was also used to check at which time lags the averaged correlations differed significantly from zero (control correlation values did not differ from zero in this test).

Amplitude (i.e. the maximal absolute value of the crosscorrelation function) quantified the strength of correlation. Time shift (i.e. the time lag at the amplitude) described asymmetry of a crosscorrelation. Widths of crosscorrelation functions were measured at half amplitude. Raw crosscorrelation was substituted for calculation of this parameter by their envelope.

The analysed data samples did not differ from normal distribution (Kolmogorov-Smirnov test) and therefore differences between means could be compared with grouped or paired Student's *t*-test. All averaged data were expressed as means  $\pm$  SEM. For all statistical evaluations the significance level was set to  $P < 0.05$ .

## Results

The analysed beta (16–24 Hz) signal consisted of oscillatory bursts lasting typically from 100 to 350 ms (Fig. 1B). The power of beta activity recorded from VCx, LGN and PGN sites during correctly performed visual trials was consistently enhanced as compared to correctly performed auditory trials (Fig. 1A). The FFT peaks within 16–24 Hz range were also observed during auditory trials but in such cases they were of significantly lower amplitudes (comp. Bekisz & Wróbel, 1993; Wróbel *et al.*, 1994). Some visual and auditory spectra also differed outside the 16–24 Hz band (see Fig. 1A), but such findings were less consistent across trials and different animals.

Representative crosscorrelations calculated between raw thalamic and cortical beta signals and between their amplitude envelopes are presented in Fig. 2. The most striking result of this study emerges from the comparison of amplitudes of both types of crosscorrelations in visual and auditory trials. Typically, amplitudes of crosscorrelation obtained between raw beta signals in visual trials were similar to those calculated during the auditory task (Fig. 2A). For the whole group of electrode pairs (Fig. 3A), the mean amplitudes obtained for visual ( $0.136 \pm 0.029$ ) and auditory ( $0.146 \pm 0.027$ ) trials were not different ( $P = 0.56$ ). In contrast, all crosscorrelations calculated between envelopes of thalamic and cortical beta signals during visual trials had significantly larger amplitudes than those calculated during the auditory task (Fig. 2B). For the whole group of electrode pairs (Fig. 3B), the mean amplitude of envelope crosscorrelation for visual trials ( $0.265 \pm 0.022$ ) was about two times higher than that obtained during the auditory task ( $0.128 \pm 0.019$ ;  $P < 0.0001$ ) and than mean amplitudes of either visual or auditory raw correlations ( $P < 0.023$ ). Thus, attention-modulated coupling between thalamic and cortical beta signals was revealed only by phase-independent envelope crosscorrelation and was not shown by conventional crosscorrelation calculated between raw oscillatory activities, which requires phase coherence.

Two observations indicate that larger envelope crosscorrelation amplitudes calculated during visual trials (Fig. 3B) cannot be related to the presence of sensory stimulation but result rather from an endogenous, centrally regulated process. The first argument came from a comparison between crosscorrelations obtained during correct and erroneously ended visual trials in Cats 4 and 5. During both correct and erroneously performed visual trials the animals stood or sat with their head directed towards the translucent doors on which the visual moving stimulus was projected, and pushed one of the doors (the wrong one in erroneous trials) immediately after it was allowed to do so. Despite similar behaviour and visual stimulation, the mean amplitude of envelope crosscorrelations calculated for correctly performed visual trials ( $0.258 \pm 0.029$ ) was significantly higher than the corresponding value obtained for visual trials ended with an erroneous

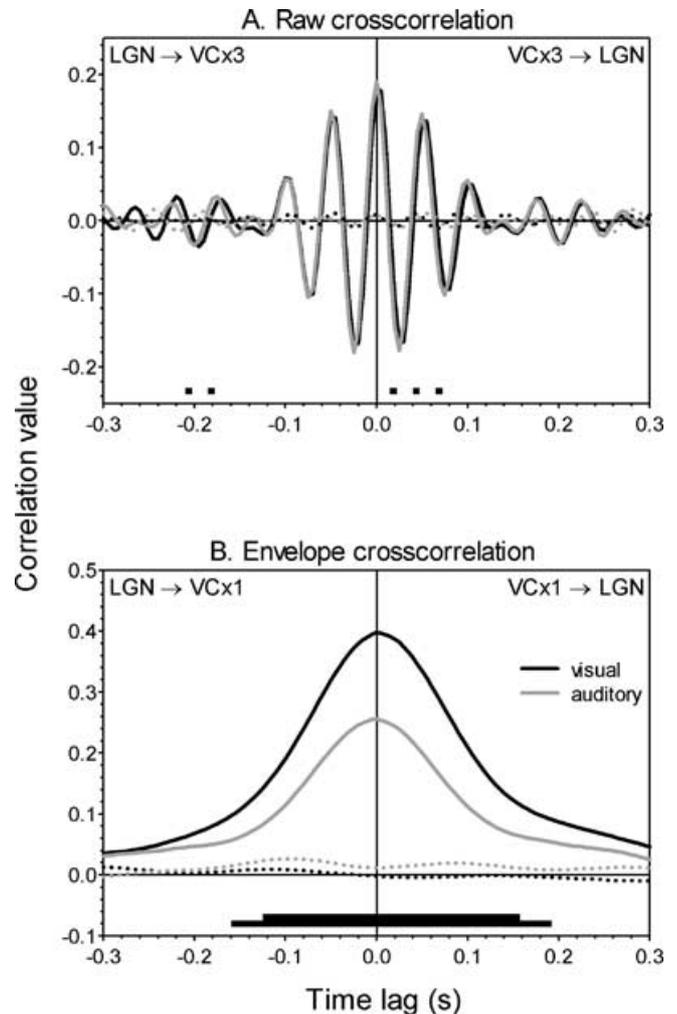


FIG. 2. Representative crosscorrelations calculated between thalamic and cortical beta signals (A) and between their amplitude envelopes (B). The graphs show mean crosscorrelograms averaged over 41 correct visual (black lines) and 45 auditory (grey lines) trials from seven experimental days in Cat 5. Dotted lines show control crosscorrelations for data of either modality (see Materials and methods). Black lines on the bottom of each graph indicate those time lags for which differences between mean visual and auditory correlation values are significant (*t*-test, thin lines  $P < 0.05$ , thick lines  $P < 0.01$ ). All electrodes recorded neuronal activity from representations of central vision (within  $5^\circ$  from *area centralis*). VCx1, VCx3 – most posterior and most anterior recording sites in the primary visual cortex. Both sides of the crosscorrelograms are labelled to indicate the crosscorrelation direction. Other explanation as in Fig. 1.

response ( $0.154 \pm 0.013$ ;  $P = 0.003$ ) which was also similar to the mean amplitude of crosscorrelation obtained for correct auditory trials ( $0.128 \pm 0.019$ ;  $P = 0.31$ ). Secondly, Cat 6 was not exposed to either visual or auditory stimuli during the analysed period of the trials, but the amplitudes of envelope correlation obtained for the visual task were also significantly higher than those calculated during the auditory situation.

It is important to stress that the magnitude of calculated crosscorrelation does not depend on the mean amplitude of the beta signal (see Materials and methods). Larger amplitudes of the thalamo-cortical envelope crosscorrelations, obtained during the visual trials, could not therefore directly result from larger FFT amplitudes within the beta range measured for thalamic and cortical sites. Envelope crosscorrelations were also calculated between beta signals recorded

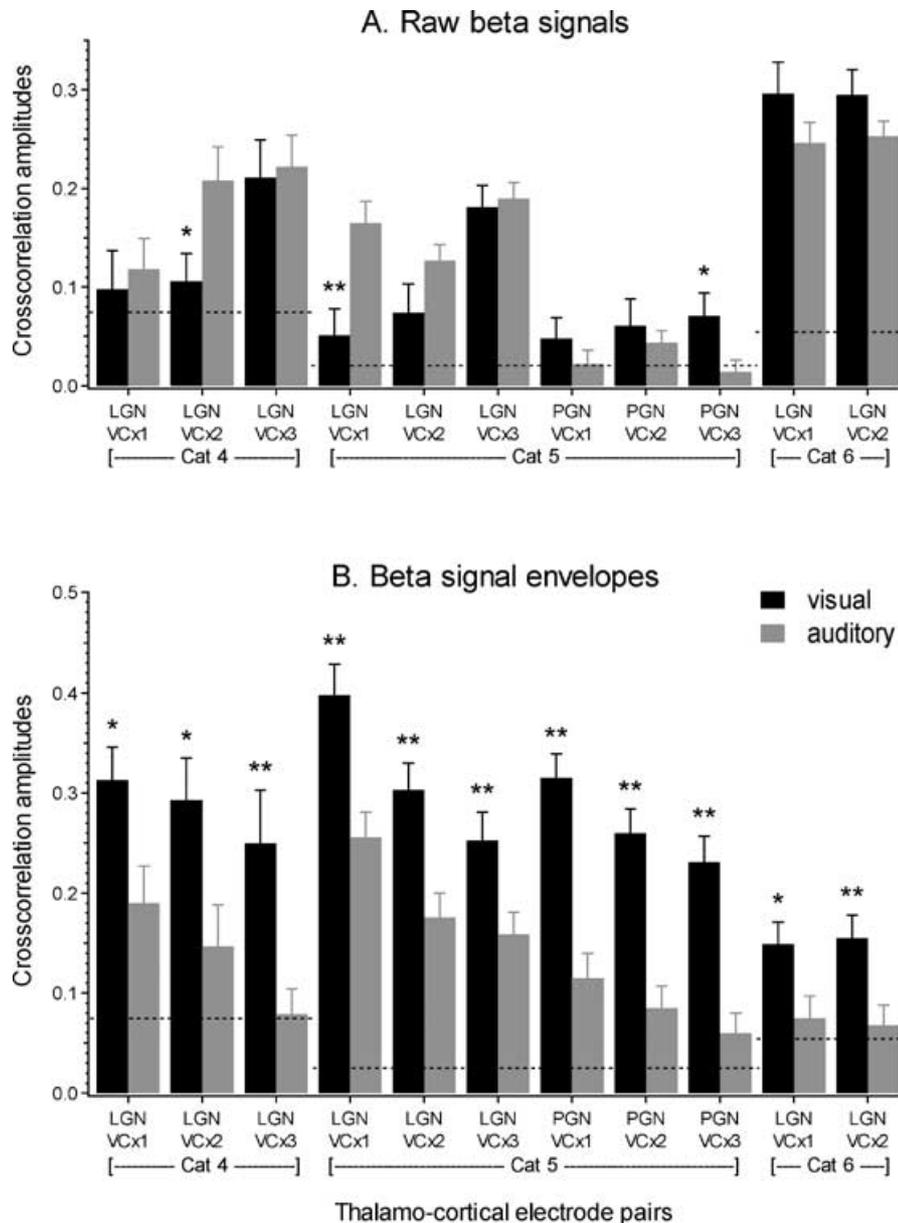


FIG. 3. Amplitudes (i.e. absolute maximal values) of averaged over trials crosscorrelations calculated between thalamic and cortical beta signals (A) and between their amplitude envelopes (B). This figure summarizes results obtained for all 11 pairs of recording sites from three animals which were aligned within the representation of central 5° of the visual field. Black bars, crosscorrelations averaged over visual trials; grey bars, over auditory trials. Error bars denote SEMs. Horizontal dotted lines indicate control levels, calculated as the mean amplitudes of corresponding control crosscorrelations. The consecutive indices for cortical electrodes denote their relative positions on the posterior gyrus along the longitudinal fissure, VCx3 being most anterior. Asterisks indicate those electrode pairs at which differences between visual and auditory crosscorrelation amplitudes were significant (*t*-test; \**P* < 0.05, \*\**P* < 0.01).

from seven different pairs of cortical electrodes. The average amplitude of such intracortical envelope crosscorrelations did not differ between visual ( $0.395 \pm 0.033$ ) and auditory trials ( $0.349 \pm 0.04$ ;  $P > 0.1$ ) however, despite a higher level of the cortical beta signal in the visual task.

The other parameters (see Materials and methods) remained similar for raw and envelope crosscorrelations and also did not change between visual and auditory attentive situations. The crosscorrelation width varied between 130 and 310 ms for different recording pairs (mean  $179 \pm 6$  ms). Such width values correspond well with typical durations of beta oscillatory bursts (100–350 ms). Time shifts of crosscorrelation functions varied within  $\pm 35$  ms. The mean time shifts (for all pairs) obtained for either visual or auditory trials and both crosscorrelation types were within  $\pm 5$  ms with SEM of similar magnitude. Consequently, such values did not differ significantly from zero ( $P > 0.05$ ). This result implied that, on average, thalamic and cortical beta oscillatory bursts correlated with no consistent temporal shift and neither of the structures could therefore be considered as a leading site.

## Discussion

In this study, we demonstrated that correlation between amplitude envelopes of beta (16–24 Hz) signals, recorded in the thalamus (i.e. LGN or PGN) and primary visual cortex within representations of the central visual field, was approximately two times stronger during a visual than during an auditory attentive situation (for simplicity in the discussion we will use the term correlation instead of crosscorrelation amplitude). By contrast, the correlation measured between raw thalamic and cortical beta signals did not differ between visual and auditory attentive situations and was as weak as envelope correlations obtained in auditory trials. The larger envelope correlation during visual trials did not result from the presence of the visual stimulus. Moreover, envelope correlation values obtained during visual trials that ended with an erroneous response were lower than values calculated for correctly performed visual trials. These results suggest that the cortical and thalamic parts of the visual system involved in central vision are stronger coupled during the visually attentive task and that this coupling is due to more synchronized amplitude modulation of beta

activity between thalamus and visual cortex. It is worth emphasizing that the attention-related coupling revealed by envelope correlation was completely missed by calculation of correlation between raw beta signals, which primarily depends on phase coherence.

There might be different explanations for weak and attention-independent correlation between raw thalamic and cortical beta activities. Firstly, phase coherence between thalamic and cortical beta signals might simply not be important for coupling of the system during the visually attentive state. Although the involved cortico-thalamic synapses require beta activity for frequency potentiation to take place (see further in the Discussion), the cortical and thalamic beta signals do not need to be in phase. Simultaneous occurrence of thalamic and cortical oscillatory bursts could secure sufficient coupling on a longer time-scale (e.g. needed for attention supported feature integration). Secondly, weak phase coherence between beta signals recorded in both structures may also result from displacement of electrodes implanted in cortical and thalamic recording sites. Taking into account the retinotopic precision of the interconnection between the geniculate and cortical maps (Grieve & Sillito, 1995; Murphy & Sillito, 1996), it seems likely that the cortical electrodes could have gathered most of their signal from ocular dominance columns receiving inputs from different LGN layers than those in which were located thalamic electrodes. Moreover, since the retinotopic positions of our geniculate and cortical electrodes differed by 2–5°, the activity of corticofugal axons probably exerted compound effects on the target principal cells, with varying contributions of excitatory and inhibitory components (Tsumoto *et al.*, 1978).

Envelope correlation method appears to be very useful in search for functional relations within the visual system. It has been previously used by us to show that beta and gamma signals in the primary cortex are more strongly coupled during a visual than auditory attentive task (Bekisz & Wróbel, 1999) and by other authors (Bruns *et al.*, 2000) in order to reveal coupling between gamma signals, which was missed by coherence.

It is reasonable to propose that the coupling of beta activity observed between thalamic and cortical recording sites in the present experiment is mediated by reciprocal connections of the cortico-thalamic loop, with the two parts comprising ascending fibres from the geniculate principal cells, and descending axons from the pyramidal cells in cortical layer VI. It follows that difference in the strength of envelope correlation between the visual and auditory attentive states could rely on changes of either network or membrane properties of the thalamic and cortical neurons involved. Our correlation data do not allow us, however, to determine the site which might be the source of the recorded beta oscillations.

It has been previously shown that an electrically activated cortico-thalamic part of the cat's visual system possesses resonance properties since it spontaneously stabilizes its oscillation within 13–24 Hz frequency (Wróbel *et al.*, 1998). The beta activity in the descending arm of the circuit can depolarize geniculate cells by a frequency potentiation mechanism observed in the cortico-thalamic synapse (Lindström & Wróbel, 1990; Bekisz *et al.*, 1998). Such depolarization may lower the threshold in geniculate neurons and thus increase the gain of the retino-cortical flow of information during visual attention (Lindström & Wróbel, 1990; Bekisz & Wróbel, 1993; Wróbel *et al.*, 1995). On the other hand, the ascending part of the cortico-thalamic circuit also has a built-in nonlinear augmentation mechanism (Ferster & Lindström, 1985; Castro-Alamancos & Connors, 1996) operating at frequencies between 7 and 14 Hz. Augmenting responses are, however, abolished during arousal or stimulation of reticular midbrain (Steriade & Morin, 1981; Castro-Alamancos & Connors, 1996) whereas cortico-thalamic frequency facilitation (reaching its maximal value at beta range) is

enhanced by neuromodulatory projection from the brain stem (Castro-Alamancos & Calcagnotto, 2001). It is therefore reasonable to suggest that enhanced activity within the cortico-thalamic system during vigilant behaviour is mainly determined by frequency sensitivity of the cortico-thalamic synapse.

One possible source of enhancement of the cortico-thalamic envelope correlation might be related to inputs from the brain stem (Munk *et al.*, 1996). The general arousal produced by brain stem neuromodulatory pathways should not, however, differ during our experiment in which the attention is shifted between visual and auditory modalities. Moreover, the brain stem projections are widely distributed in the sensory structures but the enhancement of the envelope correlation observed in the present experiment was restricted to only retinotopically aligned central recording sites. When one of the electrodes recorded from a site representing peripheral visual field, the envelope correlations measured during visual and auditory attentive situations did not differ (Bekisz & Wróbel, 2002). With such electrode arrangement we have also previously noticed low coincidence of thalamic and cortical beta bursts during visually attentive trials (Wróbel *et al.*, 1994, 1995). All our data together seem to indicate that enhanced coupling between cortex and thalamus is caused by attentional influences from higher cortical areas.

The possible function of beta oscillations is still not understood, but many lines of evidence indicate a close relationship between such activity and visual attention (compare Wróbel, 2000; for a review). The increase of beta signal in the visual system was originally found in our laboratory as a correlate of visually attentive behaviour (Bekisz & Wróbel, 1993; Wróbel *et al.*, 1994, 1995). The beta signal of frequency around 18–25 Hz was later found in primary visual cortex of monkeys (Graille & Rougeul-Buser, 1996) and between different visual cortical areas of cats solving a behavioural task requiring visual attention (Roelfsema *et al.*, 1997). Recently, we have noticed stronger coupling between beta and gamma signals during a visually attentive task (Bekisz & Wróbel, 1999). Thus, attention-related beta activation might provide a necessary background for feature binding (Bekisz & Wróbel, 1999; Wróbel, 2000). Coupling between cortical and thalamic beta signals during attentive visual processing, as shown in this paper, is consistent with such a hypothesis.

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## Abbreviations

LGN, lateral geniculate nucleus; PGN, perigeniculate nucleus; VCx, primary visual cortex; LFPs, local field potentials; FFT, fast Fourier transform.

## References

- Bekisz, M., Eaton, S.A. & Paulsen, O. (1998) Frequency facilitation of cortical input to mouse ventrobasal thalamic relay neurones *in vitro*. *Eur. J. Neurosci. Suppl.*, **10**, 138.
- Bekisz, M. & Wróbel, A. (1993) 20 Hz rhythm of activity in visual system of perceiving cat. *Acta Neurobiol. Exp.*, **53**, 175–182.
- Bekisz, M. & Wróbel, A. (1999) Coupling of beta and gamma activity in cortico-thalamic system of cats attending to visual stimuli. *Neuroreport*, **10**, 3589–3594.
- Bekisz, M. & Wróbel, A. (2002) Attention-related coupling between thalamic and cortical beta signals. *FENS Abstracts*, **1**, A159.2.

- Bruns, A., Eckhorn, R., Jokeit, H. & Ebner, A. (2000) Amplitude envelope correlation detects coupling among incoherent brain signals. *Neuroreport*, **11**, 1509–1514.
- Castro-Alamancos, M.A. & Calcagnotto, M.E. (2001) High-pass filtering of corticothalamic activity by neuromodulators released in the thalamus during arousal: *in vitro* and *in vivo*. *J. Neurophysiol.*, **85**, 1489–1497.
- Castro-Alamancos, M.A. & Connors, B.W. (1996) Short-term plasticity of a thalamocortical pathway dynamically modulated by behavioral state. *Science*, **272**, 274–277.
- Ferster, D. & Lindström, S. (1985) Augmenting responses evoked in area 17 of the cat by intracortical axon collaterals of cortico-geniculate cells. *J. Physiol. (Lond.)*, **367**, 217–232.
- Graille, C. & Rougeul-Buser, A. (1996) Posterior parietal electrocortical (ECoG) 'attention rhythms' in macaque during a visually guided manual task. *Eur. J. Neurosci. Suppl.*, **9**, 122.
- Grieve, K.L. & Sillito, A.M. (1995) Differential properties of cells in the feline primary visual cortex providing the corticofugal feedback to the lateral geniculate nucleus and visual claustrum. *J. Neurosci.*, **15**, 4868–4874.
- Ide, L.S. (1982) The fine structure of the perigeniculate nucleus in the cat. *J. Comp. Neurol.*, **210**, 317–334.
- Lindström, S. & Wróbel, A. (1990) Frequency dependent corticofugal excitation of principal cells in the cat's dorsal lateral geniculate nucleus. *Exp. Brain Res.*, **79**, 313–318.
- McAlonan, K., Brown, V.J. & Bowman, E.M. (2000) Thalamic reticular nucleus activation reflects attentional gating during classical conditioning. *J. Neurosci.*, **20**, 8897–8901.
- Montero, V.M. (1991) A quantitative study of synaptic contacts on interneurons and relay cells of the cat lateral geniculate nucleus. *Exp. Brain Res.*, **86**, 257–270.
- Montero, V.M. (1997) C-fos induction in sensory pathways of rats exploring a novel complex environment: shifts of active thalamic reticular sectors by predominant sensory cues. *Neuroscience*, **76**, 1069–1081.
- Montero, V.M. (2000) Attentional activation of the visual thalamic reticular nucleus depends on 'top-down' inputs from the primary visual cortex via corticogeniculate pathway. *Brain Res.*, **864**, 95–104.
- Montero, V.M. & Singer, W. (1984) Ultrastructure and synaptic relations of neural elements containing glutamic acid decarboxylase (GAD) in the perigeniculate nucleus of the cat. *Exp. Brain Res.*, **56**, 115–125.
- Munk, M.H.J., Roelfsema, P.R., König, P., Engel, A.K. & Singer, W. (1996) Role of reticular activation in the modulation of intracortical synchronization. *Science*, **272**, 271–274.
- Murphy, P.C. & Sillito, A.M. (1996) Functional morphology of the feedback pathway from area 17 of the cat visual cortex to the lateral geniculate nucleus. *J. Neurosci.*, **16**, 1180–1192.
- Roelfsema, P.R., Engel, A.K., König, P. & Singer, W. (1997) Visuomotor integration is associated with zero time-lag synchronization among cortical areas. *Nature*, **385**, 157–161.
- Sanderson, K.J.C. (1971) The projection of the visual field to the lateral geniculate and medial interlaminar nuclei in the cat. *J. Comp. Neurol.*, **143**, 101–118.
- Steriade, M. & Morin, D. (1981) Reticular influences on primary and augmenting responses in the somatosensory cortex. *Brain Res.*, **205**, 67–80.
- Tsumoto, T., Creutzfeldt, O.D. & Legendy, C.R. (1978) Functional organization of the corticofugal system from visual cortex to lateral geniculate nucleus in the cat. *Exp. Brain Res.*, **32**, 345–364.
- Tusa, R.J., Palmer, L.A. & Rosenquist, A.C. (1978) The retinotopic organization of area 17 (striate cortex) in the cat. *J. Comp. Neurol.*, **177**, 213–236.
- Vanduffel, W., Tootell, R.B.H. & Orban, G.A. (2000) Attention-dependent suppression of metabolic activity in the early stages of the macaque visual system. *Cereb. Cortex*, **10**, 109–126.
- Wilson, J.R., Friedlander, M.J. & Sherman, S.M. (1984) Fine structural morphology of identified X- and Y-cells in the cat's lateral geniculate nucleus. *Proc. R. Soc. Lond. B Biol. Sci.*, **221**, 411–436.
- Wróbel, A. (2000) Beta activity: a carrier for visual attention. *Acta Neurobiol. Exp.*, **60**, 247–260.
- Wróbel, A., Bekisz, M., Kublik, E. & Waleszczyk, W. (1995) 20 Hz bursting beta activity in the cortico-thalamic system of visually attending cats. *Acta Neurobiol. Exp.*, **54**, 95–107.
- Wróbel, A., Bekisz, M. & Waleszczyk, W. (1994) 20 Hz bursts of activity in the cortico-thalamic pathway during attentive perception. In: Pantev, C., Elbert, Th & Lutkenhoner, B., Eds. *Oscillatory Event-Related Brain Dynamics*. Plenum Press, New York, pp. 311–324.
- Wróbel, A., Hedström, A. & Lindström, S. (1998) Synaptic excitation of principal cells in the cat's lateral geniculate nucleus during focal epileptic seizures in the visual cortex. *Acta Neurobiol. Exp.*, **58**, 271–276.