

Beta activity: a carrier for visual attention

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ABSTRACT. The alpha (8-13 Hz), beta (15-25 Hz) and gamma (30-60 Hz) bands of the EEG have been long studied in clinical research because of their putative functional importance. Old experimental results indicated that repetitive stimulation of the visual pathway evoked synchronous responses at the cortical level with gain depending on frequency: oscillations within relevant bands were less damped at subsequent processing levels than others. Our current results show that in the cat, cortico-geniculate feedback has a build-in potentiation mechanism acting at around the beta frequency which activates thalamic cells and may thus lower the threshold for visual information transmission. We have also shown that enhanced beta activity is propagated along this feedback pathway solely during attentive visual behavior. This activity consists of 300 ms to 1 s long bursts which tend to correlate in time with gamma oscillatory events. Beta bursting activity spreads to all investigated visual centers, including the lateral posterior and pulvinar complex and higher cortical areas. Other supporting data on enhanced beta activity during attentive-like behavior of various species including man, are discussed. Finally, we put forward a general hypothesis which attributes the appearance of oscillations within the alpha, beta and gamma bands to different activation states of the visual system. According to this hypothesis, alpha activity characterizes idle arousal of the system, while beta bursts shift the system to an attention state that consequently allows for gamma synchronization and perception.

KEY WORDS. Animals' LFP, human EEG, resonance frequencies, cortico-thalamic loops, visual information flow: gain and organization, alpha beta and gamma frequency bands, activation states of the visual system

INTRODUCTION

The neuronal mechanisms underlying perception by the mammalian brain are poorly understood. Fast oscillatory (gamma) rhythms are believed to serve as a coactivation mechanism for populations of cells from different brain areas during the feature integration process (Eckhorn et al. 1988, Gray et al. 1989, Bressler 1990, Lopes da Silva 1991, Roskies 1999). Another hypothesized mechanism, attentional selection, posits that the same result is obtained by increasing the relative excitability of cells activated by attended objects or voluntary action (Treisman and Gelade 1980, Crick 1994). The possibility exists that both mechanisms cooperate; the attentional mechanism may activate populations of cells thereby allowing them to synchronize their activity. In a hierarchically organized system like the visual system, this hypothesis would require the harmonized activation of cell assemblies encompassing many processing levels via feedback pathways (Crick 1994, Zeki 1993). In our experiments we first approached the issue by analyzing the neuronal activity in the cortico-thalamic system of attending cats. These data are discussed together with scarce relevant observations from the literature and our own results obtained on human subjects. The paper

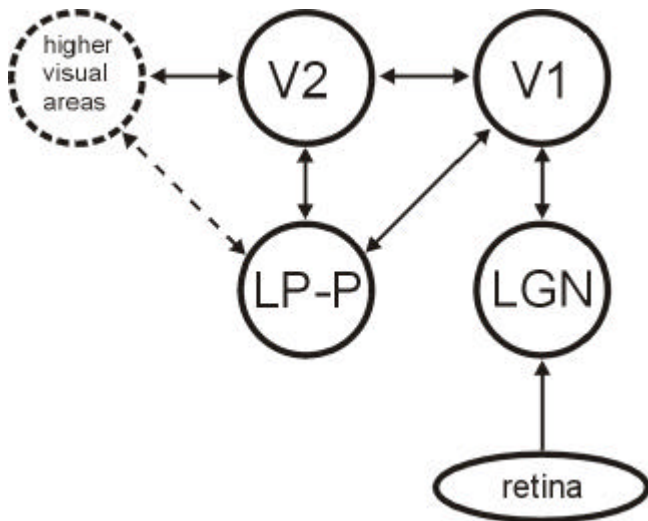


Fig. 1. Simplified scheme of the mammalian visual system. Consecutive processing levels are marked by circles. Notice the reciprocal connections between thalamic and cortical areas. LGN, lateral geniculate nucleus; LP-P, lateral posterior - pulvinar complex; V1 and V2, primary and secondary visual cortex.

focuses mostly on the analysis of local field potentials (LFPs) as these better mirror the modulation mechanisms (e.g. attention) and allow for more direct comparison with human EEG recordings.

RESONANCE FREQUENCIES IN THE VISUAL SYSTEM

The mammalian visual system is hierarchically organized (Fig. 1). Sensory activation is transmitted from retina through lateral geniculate nucleus (LGN) to the primary visual cortex (V1) and higher visual centers. Principal neurons at extraretinal levels of this system are under inhibitory influence of recurrent

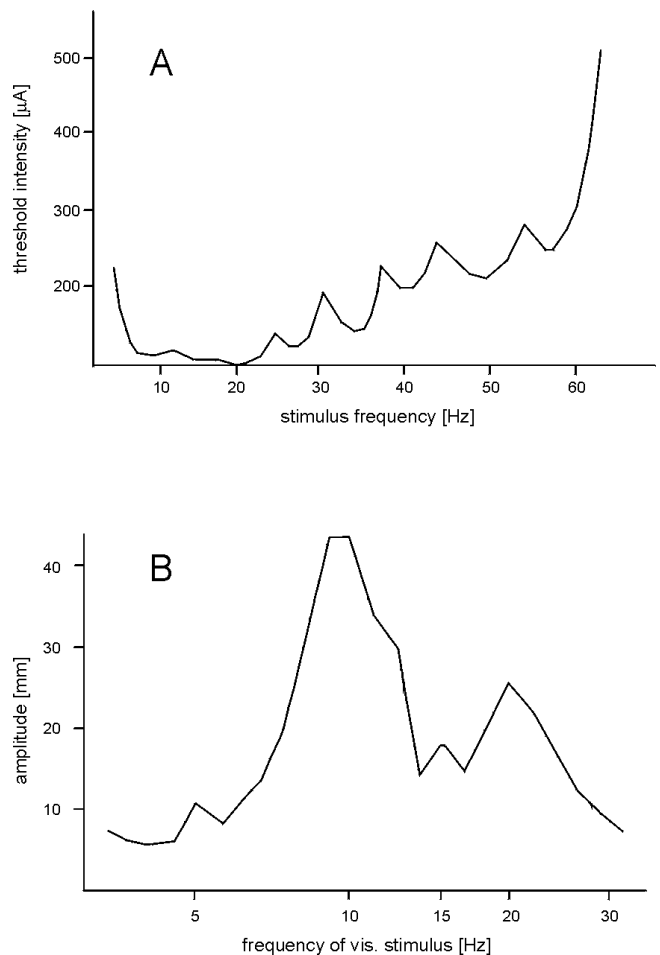


Fig. 2. A, Relative phosphene threshold intensity obtained with alternating electrical stimulation of the human eye (adapted from Motokawa and Ebe 1953); B, amplitude of occipital EEG signal evoked by visual stimulation of the human retina with sinusoidally modulated light of different frequencies (adapted from Utlett and Johnson 1958).

interneurones. Separate excitatory feedback pathways control the relay structures. Such a network of recurrent loops may exert various modulatory actions on cellular firing in the frequency domain.

For more than five decades researchers have known that repetitive stimulation of sensory pathways evokes synchronous responses at the cortical level with gain depending on frequency. For example electrical stimulation of the human optic nerve has shown that the phosphene threshold is lowest at 20 Hz and additional local minima are observed around 10 and between 30 and 65 Hz (Schwartz 1947, Motokawa and Ebe 1953, Fig. 2A). Relevant physiological measures were performed by stimulating the retina with sinusoidally modulated light intensity. It appeared that stimuli modulated with 10 and 20 Hz frequencies evoked a high amplitude oscillatory responses in occipital EEG recordings whereas other frequencies produced damped responses at the cortical level (Utlett and Johnson 1958 - Fig. 2B, Montagu 1967, Lopes da Silva 1970a). It has been further shown that such modulation can even

damping is necessary in order to secure stabilization. It is common to ascribe the damping mechanisms to feed-forward and recurrent inhibitory connections (Ahlsen et al. 1985). Disactivation of the inhibitory interactions or amplification of the excitatory loops leads to epileptic discharges within the system. Accordingly, we have shown that electrical stimulation of the cat's visual radiation provokes resonance oscillatory activity of about 20 Hz frequency in the retinotopically localized cortico-geniculate loop (Wróbel et al. 1998).

With the hypothesis considering visual evoked potentials (EPs) as stimulus-induced LFP rhythmicities Basar (1980) found that amplitude-frequency characteristics of these potentials peaked

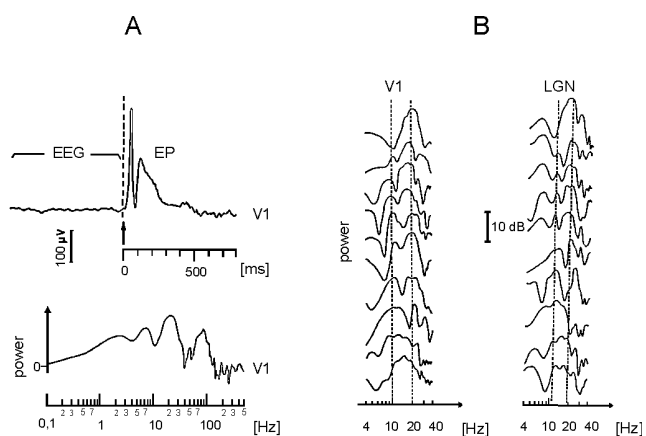


Fig. 3. Frequency characteristics of the evoked potentials (EPs) in the cat's visual system. A, Averaged EP recorded in the visual cortex and its power spectrum; B, power spectra calculated from consecutive EPs registered in the visual cortex (V1) and lateral geniculate nucleus (LGN). Dashed lines indicate frequencies of highest local power amplitude in spectrum averaged from all constitutives (adapted from Basar 1980).

be observed at the retinal level (Hughes and Maffei 1965) and the damping coefficients increase at subsequent processing levels in LGN and V1 (Spekreijse et al. 1971). It is obvious that in a system containing excitatory recurrent loops such

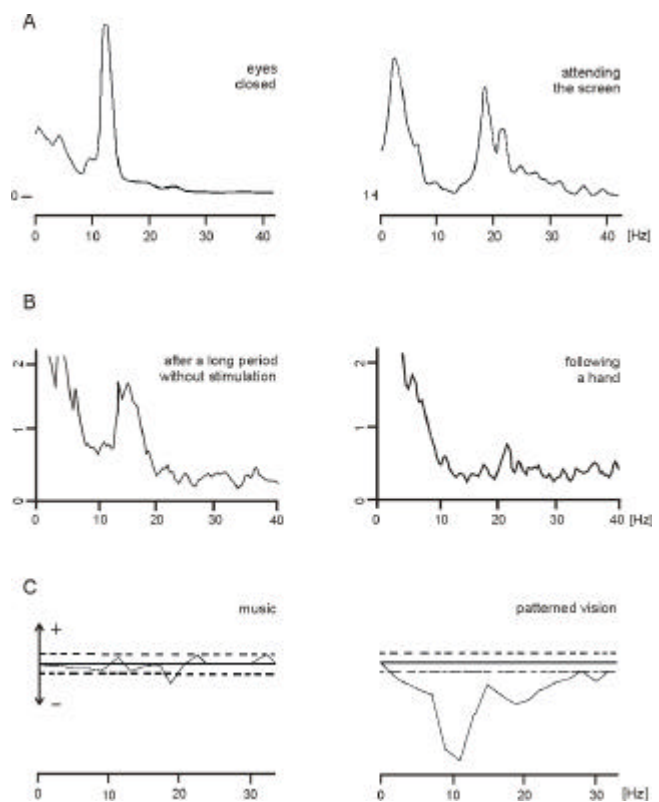


Fig. 4. A, Power spectra calculated from the LFP registered in dog visual cortex with eyes closed and during attentive observation of a hole in the screen in expectation of appearance of the reward (adopted from Lopes da Silva et al. 1970, 1991); B, Amplitude spectra of the LFPs registered from the visual cortex of the pretrigeminal preparation of the cat after habituation, and during a period in which eyes followed the hand of experimenter moving in vertical direction (Wróbel and Bekisz, unpublished); C, averaged difference of frequency spectra of the EEG registered from the occipital electrodes of the subjects when listening to music and observing the complicated posters (32 subjects of the 11-13 years age; adapted from Giannitrapani 1970).

for the same 10 and 20 Hz values with additional prominent peak developing above the 35 Hz (Fig. 3). All the above experiments support the notion that spike trains of distinct frequencies (about 10, 20, and above 35 Hz) pass through the mammalian visual system with the smallest decrement. These frequency bands may be therefore called resonance frequencies.

FUNCTIONAL MEANING OF THE RESONANCE FREQUENCIES

Long clinical experience has ascertained that the spectral power of the specific EEG signal bands changes with different functional states of the brain. Much interest has been recently focused on the alpha (8-13 Hz), beta (15-25 Hz) and gamma (30-60 Hz) bands. First observations indicated that general arousal is accompanied by decreased power in the low frequency, alpha band (Berger 1930) which was described as EEG desynchronization. With better quality recordings it turned out that more characteristic for cortical arousal was decrease of amplitude of slow 1-4 Hz oscillations (delta) and the accompanying alpha power could even increase at the same time (Childers and Perry 1970, Bekisz and Wróbel 1993, 1999, Herculano-Houzel et al. 1999). Interesting from this point of view are observations of increased beta activity in subjects habitually using vivid visual imagery as compared to negligible beta activity recorded in subjects with relatively inadequate visual imagery ability (Mundy-Castle 1951, v. Stein et al. 1993). Beta activity in both groups was highly correlated with the observed power in the alpha band (Mundy-castle 1951).

It is generally assumed now that alpha activity mirrors idle arousal of the visual network (Childers and Perry 1970, Lopes da Silva 1990, Steriade et al. 1990, Steriade 1993, Vanni et al. 1997, Castro-Alamancos and Connors 1997) and gamma oscillations serve as a mechanism for feature binding (Roskies 1999). Functional role of beta band reminds, however, still obscure (Steriade 1993).

Prominent beta band activity was registered from the occipital cortex of dog which expected a rewarding piece of meat to appear visually (Lopes da Silva 1970b, Fig. 4A) and from occipital electrodes of subjects performing emotional and

cognitive tasks (Ray and Cole 1985). Recording cortical LFPs from the vigilant cat pretigeminal preparation we have observed the appearance of beta activity during the following reflex, when the eyes tracked the hand of the experimenter. This activity ceased after a long habituation period without any visual stimuli presented (Wróbel and Bekisz, unpublished data, Fig. 4B). Preliminary data show enhanced beta activity in monkey visual cortex during behavior based on attentional tasks (Graille and Rougell-Buser 1996). On the other hand decrease of beta spectral power was detected in EEG signals recorded from occipital electrodes of subjects perceiving patterned visual stimuli (Giannitrapani 1971, Fig. 4B, V. Stein et al. 1993). Such confusing results can be explained by the assumption that visual processing organizes cortical activity into specific spatial pattern replacing the global synchronization present during idle state. This hypothesis will be discussed below together with supporting data from our cat experiments. The increased beta activity in the cortical EEG of human subjects has, however, recently been observed during a delay time preceding visual differentiation response. This activity was associated with mechanism of short-term memory (Tallon-Baudry and Bertrand 1999). Our intensive investigations which are reviewed below suggest that all the described results can be consistently understood by assuming that beta band activity reflects an arousal of the visual system during increased visual attention (Wróbel 1997a).

THE ROLE OF CORTICAL ACTIVATION IN GAIN OF THE RETINO-CORTICAL FLOW OF INFORMATION

Neuronal circuits located in higher levels of the mammalian visual system project feedback pathways terminating on principal cells of the preceding level (Felleman and Van Essen 1991, Zeki 1993). The idea that the descending systems might be used for control of the attention processes is not new (Adrian 1953, Hernandez-Peon 1966, Singer 1977, Sherman and Koch 1986) but it was only recently that the neural mechanisms underlying such control has been demonstrated (Lindström and Wróbel 1990, McCormick and van Krosigk 1992). It is not surprising that due to the complicated organization of the association cortex with many intermingled connections (Kaas 1993,

Felleman and Van Essen 1991, Zeki 1993), these mechanisms were at first investigated in the cortico-thalamic pathway of the visual system (Lindström and Wróbel 1990).

The ascending fibers of the principal cells of the lateral geniculate nucleus (LGN) of the cat send collaterals to pyramidal cells of layer 6 of the visual cortex (V1). The cortical neurons project in turn toward the LGN where contacts of their axons on principal cells outnumber all other excitatory synapses (Wilson et al. 1984, Montero 1991). Using intracellular recording techniques we were able to show that cortico-geniculate synapses have a built-in frequency amplification mechanism which reaches maximal values at about the 20 Hz frequency (Lindström and Wróbel 1990). Based on this observation we postulated that beta frequency activity transmitted via the cortico-geniculate pathway can depolarize geniculate cells and therefore increase the input-output gain of the geniculate relay (Lindström and Wróbel 1990, Musia³ et al. 1997).

The role of this rich and potentially powerful descending pathway was obscured for a long time (Geisert et al. 1991, Kalil and Chase 1970) since all experiments were carried out on anesthetized animals and the cells in layer 6 become active only after waking up, as shown by Livingston and Hubel (1981). These authors also demonstrated that bursting activity of pyramidal cells which accompanied the waking periods improved the responsiveness of geniculate cells (comp. also Coenen and Vendrik 1972). It is clear that the possible functions of the cortico-thalamic

rows represent continuously recorded signal from the same electrode in visual cortex (V1') before and after appearance of the preparatory stimuli of corresponding modality; C, D, correlation between beta bursts (marked by vertical markers in A and B) registered by two electrodes in V1 (V1'' signal not shown) during visual (C) and auditory (D) trials. The recorded signal in A and B was filtered in the 16-24 Hz frequency band (adapted from Wróbel 1997b).

projections should be studied in awake animals in which the pyramidal cells in visual cortex are easy to activate and thus operate within their intended physiological limits (Wróbel et al. 1994a, Gray and Di Prisco 1997, Wróbel 1997b). Therefore we planned further experiments on behaving cats which performed conditional tasks requiring shifts in visual attention. We hypothesized that when visual information forms a vital component of a task, the attentive state necessary to gain this information should be accompanied by activation of the cortico-geniculate pathway.

BETA ACTIVITY IN THE CORTICO-GENICULATE SYSTEM INCREASES DURING VISUAL ATTENTION

In an attempt to elucidate whether the spectral power of beta activity increases during visual attention we performed an experiment in which cats were rewarded for proper responses in a spatial differentiation test which required visual or auditory attention in intermingled trials (Bekisz and Wróbel 1993, Wróbel et al. 1994 a,b). In brief, cats were trained in a specially designed small wooden cage equipped in front with two translucent doors. The visual and auditory trials were preceded by a preparatory stimuli of appropriate modality: a diffuse flash of light or noise from a loudspeaker from behind the front wall. During the visual trial the cat had to notice the cue stimulus (1 s duration flash of a small light spot) which appeared with 10 to 20 s delay (randomized) on one of the doors. When pressing this door the cat could grab a piece of meat for a reward. Analogously, a short (1 s) noise from one of the loudspeakers placed behind the sidewalls was a cue for solving the auditory differentiation task. This procedure kept the animal in a state of attention to a given modality, starting from a warning up to the cue stimulus, and shifting it to other modality in the subsequent trial. It is important that during the analyzed period of any

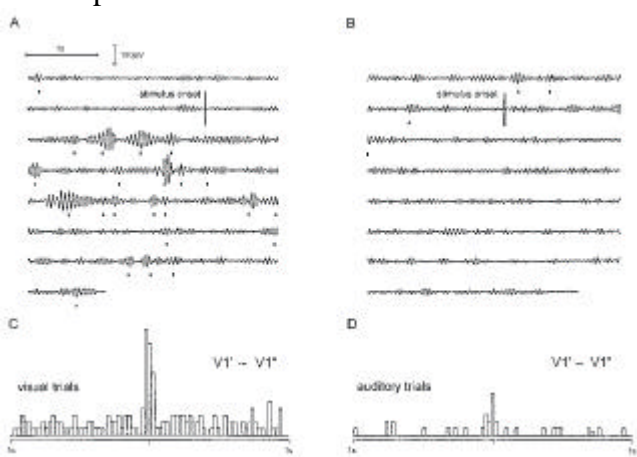


Fig. 5. A, B, increase in amplitude and frequency of appearance of beta bursts recorded from cat's visual cortex during expectation of the visual cue (A) and lack of such changes in auditory differentiation task (B). Consecutive 8

trial the animal was kept in the same (visual or auditory) sensory environment.

Local field potentials were registered with the use of a set of electrodes chronically implanted into the visual cortex (area 17, V1), auditory cortex (A1) and also the visual thalamic nuclei: lateral geniculate nucleus (LGN) and lateral posterior –

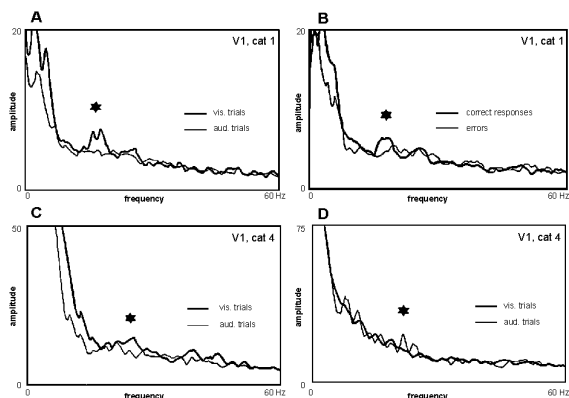


Fig. 6. A, Averaged amplitude spectra calculated from signals recorded from cat's visual cortex during increased visual (thick line) and auditory (thin line) attention in the same experimental session. Each spectrum was obtained from 14 independent signal epochs of 2.5 s duration, taken from successfully ended trials; B, comparison of averaged LFP amplitude spectra from the time periods preceding correct and erroneously ended behavioral responses in the same session; C, D, amplitude spectra showing spectral content of the signal registered from the primary visual (C) and auditory (D) cortices of other cat, calculated from correct trials in one experimental session. Stars indicate the significance in the beta band (t-test, $P < 0.05$).

In the frequency spectra of the visual cortex activity calculated for both animals before the correct response beta band has significantly higher amplitude than in the spectra calculated for auditory and erroneous visual trials. In the spectrum obtained from the auditory cortex, amplitude of the beta band is significantly higher during auditory than visual trials (from Bekisz and Wróbel 1993).

pulvinar complex (LP-P). Fourier analysis (FFT) showed that the amplitude of the beta frequency band calculated for either sensory system indeed grew during the period of increased attention to a specific modality. For example, during the period between a visual preparatory signal and cue stimulus we found an increase of amplitude and frequency of appearance of short (300 - 1000 ms) bursts of beta oscillations both in LGN and V1 (Bekisz and Wróbel 1993, Wróbel et al 1994a, Fig. 5). Such enhanced activity was, however, observed only in the successful trials and was absent in those which ended with an erroneous

response. This observation indicates that the observed beta activity characterizes a specific attentional state of the visual system (Fig. 6A,B,C).

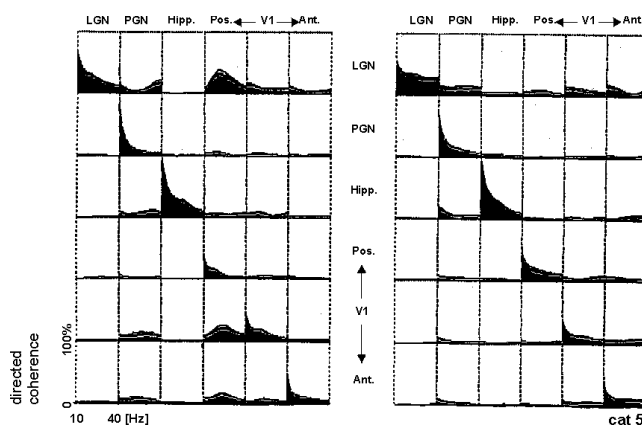


Fig. 7. Directed transfer functions (DTFs) between signals registered from six electrodes implanted under physiological control (LGN: azimuth 2° / elevation 2° ; PGN, perigeniculate nucleus $5^\circ/0^\circ$; three electrodes in V1 from posterior to anterior: $0^\circ/2^\circ$, $2^\circ/0^\circ$, $-1^\circ/-2^\circ$). Hippocampal (Hipp.) electrode was placed in the dentate gyrus. DTF calculated for the signal flow from LGN to other structures are shown in the consecutive boxes of the first column. The signal flow from other structures to LGN is expressed by DTFs shown in the first row of boxes, etc. DTF value represents signal power recorded in the target structure which is related to the temporally preceding (> 5 ms) structure's signal. Each cell on the matrix diagonal contains a power spectrum calculated by the autoregression method from the signal recorded by relevant electrode. All functions are normalized according to the one of the maximal value which was taken for 100%. Left matrix contains functions calculated from the signals recorded during correct visual trials. Right matrix shows relevant DTFs calculated for correct auditory trials. Variability is expressed with corridors showing SEM. Note high DTF values at beta band for signals spreading from posterior electrode in V1 towards LGN and other V1 sites during trials requiring visual attention and lack of such information flow between the same structures during auditory trials (from Wróbel et al. 1994).

Were our hypothesis of cortical control of thalamic transmissions in an attentive state true, beta activity should be propagated through the descending pathway. This we were able to confirm (Bekisz and Wróbel 1993, Wróbel et al. 1994a; Fig. 7) by calculating the Directed Transfer Function (DTF), a method developed to measure the direction and frequency content of the flow of activity between different brain locations (Kamiński and Blinowska 1991). Our preliminary data also indicated that such dynamic cortical input activates retinotopically relevant LGN

representations (central *vs* peripheral; Wróbel et al. 1994b). The DTF analysis therefore supported our hypothesis that beta activity is correlated with the mechanism of visual attention and is exerted *via* the cortico-geniculate pathway. Available EEG data from human subjects suggest that beta signals between higher visual processing levels may also be spread by descending routes (Thatcher et al. 1986, Takigawa and Kidiyoor 1991).

Our experiments revealed that the amplitude of beta activity recorded from V1 area varied with electrode location. These observations suggested that attention related activation of the visual cortex may be organized in a specific functional pattern. In order to verify this hypothesis we have calculated the normalized correlation coefficient with zero time-lag (Roelfsema et al. 1997) for all pairs of filtered beta signals recorded from different sites, in each animal. On auditory trials most of the Pearson correlation coefficients had positive values indicating that beta activity in the visual cortex was globally synchronized. During situations requiring visual attention, most of the correlation coefficients decreased except those with extremely high original values ($> 0,75$). For few such pairs the synchronization of the recorded signals was higher in the visual than auditory trials (Krakowska et al. 1995; Fig. 8; comp. also Llinas 1994, Murthy and Fetz 1996). These results suggest that in a visually attentive situation beta activity in the visual cortex is organized in a specific functional pattern (Ahissar et al. 1992, Arieli et al. 1995) according to theoretically suggested demands of the "searchlight" hypothesis (Olshausen et al. 1993).

Attention related changes in human EEG activity was originally correlated with variation of the alpha band power (Berger 1930, Ray and Cole 1985, Vanni et al. 1997). There were observations, however, indicating that enhanced beta activity accompanied certain intellectual tasks (Ray and Cole 1985) and some investigations suggested that this enhancement may be used as an arousal index (Cardenas et al. 1997). Our preliminary results show that the amplitude of the beta frequency spectrum registered by occipital electrodes decreases with increased visual attention (Wróbel 1998, Fig. 9B). Paradoxical decreases of beta band amplitude may result from setting the underlying cortical activity into a specific pattern similar to that evoked by attentional mechanisms in the cat's

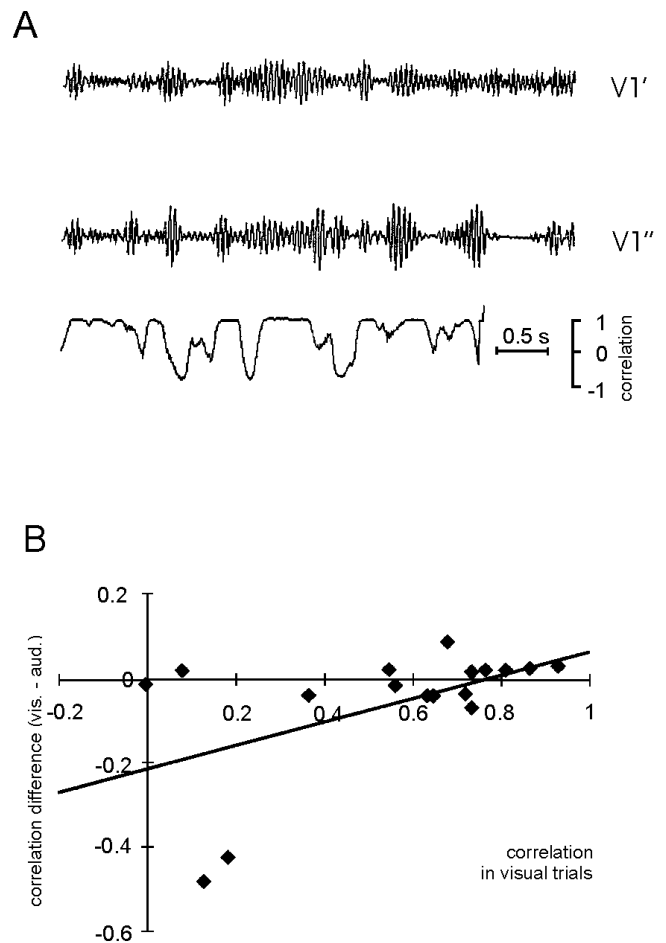


Fig. 8. A, An example of local field potentials simultaneously registered by two electrodes (V1', V1'') in the visual cortex of the cat during experiment on spatial differentiation of visual or auditory trials (comp. Figs. 5-7) and their current correlation. The signals contain only filtered out beta frequencies (16-24 Hz). B, Relation of averaged correlation coefficients of the signals from visual trials calculated for different pairs of electrodes placed in V1 and difference between these values and coefficients calculated for the same electrode pairs during auditory trials. Pooled data from four cats. Straight line (by least squares method) marks on the abscissa the value 0.75 above which the strength of the correlation grows during visual (in comparison to auditory) trials. See text for details. (Krakowska et al., 1995).

visual cortex (Fig. 8). Skin electrodes tend to average EEG signal from a large area of the occipital cortex and the amplitude largely depends on the synchronization of all contributing sources. Accordingly, cortical activity of small amplitude but synchronized over large cortical areas may be recorded as a relatively strong signal compared to a highly synchronized but limited neuronal pool (v. Stein et al. 1993, Menon et al. 1996). In accordance with such interpretations are results indicating that visual stimulation increases beta

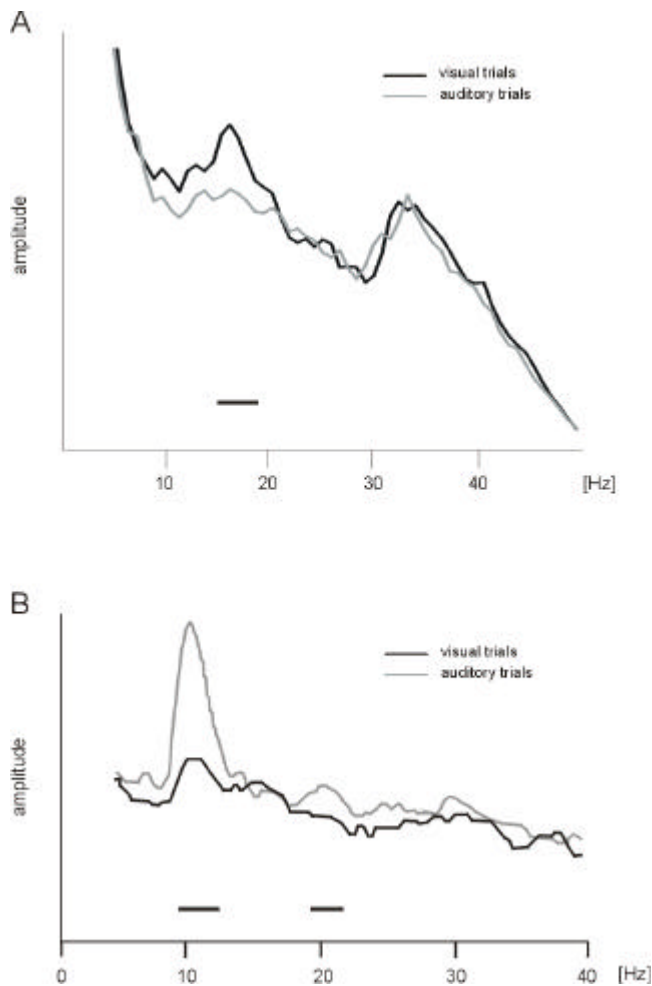


Fig. 9. A, Increase of the amplitude of the beta band (17-20 Hz) in the frequency spectrum of LFP registered in LPI-c (lateral zone of lateral posterior complex, caudal part) during attentive expectation of the visual cue stimulus, compared with the signal spectrum recorded in the auditory situation. Horizontal line above abscissa marks the frequency limit in which spectra differ significantly ($p < 0.05$). B, Average EEG frequency - amplitude spectrum registered from the occipital electrode in the subject in similar experiment as described for cats. During anticipation of visual differentiation stimulus, beta band has significantly lower amplitude than during corresponding auditory trials (Wróbel et al. unpublished).

activity solely in those parts of the cortical representations of the visual field which are engaged in attentive processing (Lutzenberger et al. 1995, Gomez et al. 1998).

GENERAL HYPOTHESIS ON THE ROLE OF BETA ACTIVITY IN VISUAL ATTENTION

Our experiments showed that enhanced beta activity appears during visual attention not only in the primary visual cortex and LGN but also in the

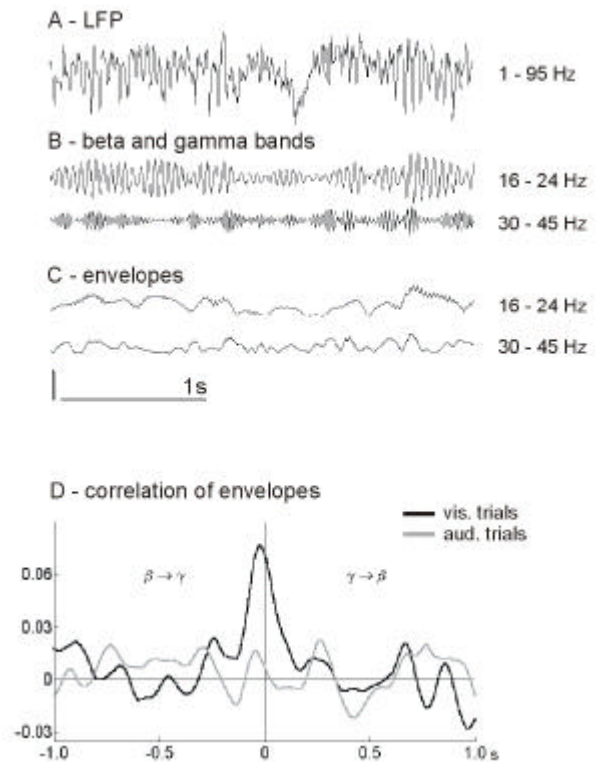


Fig. 10. A, B, C, An example of the LFP registered from the cat's primary visual cortex during experiment on spatial differentiation of visual and auditory stimuli (A), the same signal filtered to show beta and gamma contents (B) and their envelopes (C). D, Correlation between beta and gamma activity with zero time shift is higher in visual than auditory trials (adapted from Bekisz and Wróbel 1999).

higher visual areas (V2, PMLS, not illustrated) and lateral posterior and pulvinar complex (LP-P; Fig. 7 and 9A). LP-P neurons receive descending fibers from layer 5 of the visual cortex and send feedback projections to the recipient cortical layers of primary and higher visual areas (Guillery 1995; Fig. 1). Thus LP-P seems to be in a key position for controlling the bottom-up and top-down streams of visual information processing. Previous investigations have suggested that LP-P is engaged in control of visual attention and selection of salient visual objects (Chalupa 1991, Garey et al. 1991, Robinson and Paterson 1992). Theoretical considerations propose that LP-P is vital for integration of elementary visual features into percepts (Niebur et al. 1993, Olshausen et al. 1993) and even that activity of cortical layer 5 neurons express conscious states (Crick 1994). Our results are in agreement with a model which assigns the role of attention related excitation of specific visual

assemblies to the LP-P (Olshausen 1993). According to this model LP-P would provide a source of modulatory activity (searchlight) gating the information about salient stimuli to higher visual centers. From the other side LP-P activity would be controlled by higher centers in a voluntary attention and recall processes. Such an integrative role of the LP-P complex requires further investigation. Designing all structures encompassed by beta activity during attentive behavior and finding directions of the information flow in this system may reveal basic processes for visual perception.

We assume that beta activity causes background excitation within specific parts of the visual system with the help of a frequency potentiation mechanism at the synaptic level of the recurrent loops (Lindström and Wróbel 1990). Such activation would allow high frequency synchronization (Steriade et al. 1996) during putative feature binding process (Eckhorn et al. 1988, Gray et al. 1989, Roskies 1999). In favor of such a hypothesis, our recent recordings from the cat's lateral geniculate nucleus and visual cortex have shown that attention related bursts of beta activity tend to correlate in time with gamma bursts (Bekisz and Wróbel 1999, Fig. 10). Similar phase correlations between beta and gamma cortical rhythms were observed during visual stimulation in visual cortex of behaving monkey (Schanze and Eckhorn 1997), although these authors discuss their findings in the view of visual feature linking across different temporal and spatial scales.

The present hypothesis about the role of cortico-thalamic beta activity in attentive perception is quite general and can be easily adapted to higher visual processing levels and also to other sensory systems. Our preliminary data support this notion, showing that large amplitude beta bursts can be observed in the primary auditory cortex of the cat during attentive listening (Bekisz and Wróbel 1993, Fig. 6). We thus ascribe to beta activity a general role of an attention carrier, similar to the previously proposed role of the alpha band in idle arousal and gamma synchronous oscillations in feature integration processes. The three resonance frequency bands of the visual pathway may therefore be understood as activation channels used to shift the state of the visual system to consecutively higher functional processing levels: from idle arousal, through attention up to

perception. The presented data suggest that each of these levels might emerge from the background set by the previous one.

REFERENCES

- Adrian E.D. (1953) The physiological basis of perception. In: Brain Mechanisms and Consciousness (Eds. E.D. Adrian, F. Bremer, H.H. Jasper) Blackwell, Oxford, pp. 237-248.
- Ahissar E., Vaadia E., Ahissar M., Bergman H., Arieli A., Abeles M. (1992) Dependence of cortical plasticity on correlated activity of single neurons and on behavioral context. *Science* 257: 1412-1415.
- Ahlsen G., Lindström S., Lo F.S. (1985) Interaction between inhibitory pathways to principal cells in the lateral geniculate nucleus of the cat. *Exp. Brain Res.* 58: 134-143.
- Arieli A., Shoham D., Hildesheim R., Grinvald A. (1995) Coherent spatiotemporal patterns of ongoing activity revealed by real-time optical imaging coupled with single unit recording in cat visual cortex. *J. Neurosci.* 73: 2072-2093.
- Basar E. (1980) EEG brain dynamics. Relation between EEG and brain evoked potentials. Elsevier. Amsterdam.
- 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. *NeroReport* 10: 3589-3594.
- Berger H. (1930) Über das elektroencephalogramm des Menschen: Zweite Mitteilung. *J. Psychol. Neurol. (Lpz)*, 40: 160-179. (English translation in *Electroenceph. clin. Neurophysiol. Suppl.*, 1969, 28: 75-93).
- Bressler S.L. (1990) The gamma wave: a cortical information carrier? *TINS.* 13: 161-162.
- Cardenas V.A., Gill P., Fein G. (1997) Human p50 suppression is not affected by variations in wakeful alertness. *Biol. Psychiatry* 41: 891-901.
- Castro-Alamancos M.A., Connors B.W. (1997) Thalamocortical synapses. *Progr. Neurobiol.* 51: 581-606.
- Chalupa L.M. (1991) Visual function of the pulvinar. In: *Vision and Visual Dysfunction*, Vol 4 (Ed. A.G. Leventhal) The Macmillan Press, Houndmills. pp. 140-159.

- Childers D.G., Perry N.W. (1970) Alpha-like activity in vision. *Brain Res.* 25: 1-20.
- Coenen A.M., Vendrik A.J. (1972) Determination of the transfer ratio of cat's geniculate neurons through quasi-intracellular recordings and the relation with level of alertness. *Exp. Brain res.* 14: 227-242.
- Crick F. (1994) The astonishing hypothesis. The scientific search for the soul. Charles Scribner's sons, New York.
- Eckhorn R., Bauer R., Jordan W., Brosch M., Kruse W., Munk M., Reitboeck H.J. (1988) Coherent oscillations: a mechanism for feature linking in the visual cortex? *Biol. Cybern.* 60: 121-130.
- Felleman D.J., Van Essen D.C. (1991) Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, 1: 1-47.
- Garey L.J., Dreher B., Robinson S.R. (1991) The organization of visual thalamus. In: *Vision and Visual Dysfunction*, Vol. 3 (Ed. B. Dreher, S.R. Robinson) The Macmillian Press, Houndmills. pp. 176-234.
- Geisert E.E., Langsetmo A., Spear P.D. (1981) Influence of the cortico-geniculate pathway on response properties of cat lateral geniculate neurons. *Brain Res.* 208: 409-415.
- Giannitrapani D. Scanning mechanisms and the EEG (1971) *Electroenceph. clin. Neurophysiol.* 30: 139-146.
- Gomez C.M., Vazquez M., Vaquero E., Lopez-Mendoza D., Cardoso M.J. (1998) Frequency analysis of the EEG during spatial selective attention. *Int. J. Neurosci.* 95: 17-32.
- Graille C., Rougel-Buser A. (1996) Posterior parietal electrocortical (ECoG) "attention rhythms" in macaque during a visually guided manual task. *Europ. J. Neurosci. Suppl.* 9: 122.
- Gray C.M., Konig P., Engel A.K., Singer W. (1989) Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature* 338: 334-337.
- Gray C.M., Di Prisco G.V. (1997) Stimulus dependent neuronal oscillations and local synchronization in striate cortex of the alert cat. *J. Neurosci.* 17: 3239-3253.
- Guillery R.W. (1995) Anatomical evidence concerning the role of the thalamus in cortico-cortical communication. A brief review. *J. Anat.* 187: 585-592.
- Hernandez-Peon R. (1966) Physiological mechanisms in attention. In: *Frontiers in physiological psychology.* (Ed. R.W. Russel). Academic Press, New York.
- Herculano-Houzel S., Munk M.H.J., Neunschwander S., Singer W. (1999) Precisely synchronized oscillatory firing patterns require electrophysiological activation. *J. Neurosci.* 19: 3992-4010.
- Hughes G.W., Maffei L. (1966) Retinal ganglion cell response to sinusoidal light stimulation. *J. Neurophysiol.* 29: 333-352.
- Kaas J.H. (1993) The organization of visual cortex in primates: problems, conclusions, and the use of comparative studies in understanding the human brain. In: *The Functional Organization of the Human Visual Cortex* (B. Gulyas, D. Ottoson and P. Roland, eds.) Pergamon Press, Oxford, pp. 1-11.
- Kalil R.E., Chase R. (1970) Corticofugal influence on activity of lateral geniculate neurons in the cat. *J. Neurophysiol.* 33: 459-474.
- Kamiński M.J., Blinowska K.J. (1991) A new method of the description of the information flow in the brain structures. *Biol. Cybern.* 65: 203-210.
- Krakovska D., Waleszczyk W., Bekisz M., Wróbel A. (1995) General 20 Hz synchronization within cortico-thalamic division of the cat's visual system shifts to specific pattern during visual attention. *Europ. J. Neurosci. Suppl.* 8: 38.
- 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.
- Livingstone M.S., Hubel D.H. (1981) Effects of sleep and arousal on the processing of visual information in the cat. *Nature (Lond.)* 291: 554-561.
- Llinas R. (1994) Unpublished results, cited in: T.M. Mc Kenna, T.A. Mc Mullen, M.F. Shlesinger: *The brain as a dynamic physical system.* *Neuroscience* 60: 587-605.
- Lopes da Silva F. (1991) Neural mechanisms underlying brain waves: from neural membranes to networks. *Electroenceph. Clin. Neurophysiol.* 79: 81-93.
- Lopes da Silva F., Van Rotterdam A., Storm van Leeuwen W., Tielen A.M. (1970a) Dynamic characteristics of visual evoked potentials in the dog. I. Cortical and subcortical potentials

- evoked by sine wave modulated light. *Clin. Neurophysiol.* 29: 246-259.
- Lopes da Silva F., Van Rotterdam A., Storm van Leeuwen W., Tielen A.M. (1970b) Dynamic characteristics of visual evoked potentials in the dog. II. Beta frequency selectivity in evoked potentials and background activity. *Electroenceph. Clin. Neurophysiol.* 29: 260-268.
- Lutzenberger W., Pulvermuller F., Elbert T., Birbaumer N. (1995) Visual stimulation alters local 40 Hz responses in humans: an EEG-study. *Neurosci. Lett.* 183: 39-42.
- McCormick D.A., von Krosigk M. (1992) Corticothalamic activation modulates thalamic firing through glutamate "metabotropic" receptors. *Proc. Natl. Acad. Sci. USA.* 89: 2774-2778.
- Menon V., Freeman W.J., Cuttillo B.A., Desmond J.E., Ward M.F. Bressler S.L., Laxer K.D., Barbaro N., Gevins A.S. (1996) Spatio-temporal correlations in human gamma band electrocorticograms. *Electroenceph. Clin. Neurophysiol.* 98: 89-102.
- Montagu J.D. (1966) The relationship between the intensity of repetitive photic stimulation and the cerebral response. *Electroenceph. Clin. Neurophysiol.* 23: 152-161.
- 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.
- Motokawa K., Ebe M. (1953) Selective stimulation of color receptors with alternating currents. *Science.* 116: 92-94.
- Mundy-Castle A.C. (1951) Theta and beta rhythm in the electroencephalograms of normal adults. *EEG Clin. Neurophysiol.* 3: 477-486.
- Murthy V.N. and Fetz E.E. (1996) Oscillatory activity in sensorimotor cortex of awake monkeys: synchronization of local field potentials and relation to behavior. *J. Neurophys.* 76: 3949-3967.
- Musia³ P., Bekisz M., Wróbel A. (1997) Spectral characteristics of lateral geniculate and cortical responses evoked by electrical stimulation of chiasma change with attentional mode in behaving cats. *Proc. 2nd ENA Meeting. Strassbourg.* p 102.
- Niebur E., Koch C., Rosin C. (1993) An oscillation-based model for the neuronal basis of attention. *Vision Res.* 18:2789-2802.
- Olshausen B.A., Anderson C.H., Van Essen D.C. (1993) A neurobiological model of visual attention and invariant pattern recognition based on dynamic routing of information. *J. Neurosci.* 13: 4700-4719.
- Ray W.J., Cole H.W. (1985) EEG alpha activity reflects attentional demands, and beta activity reflects emotional and cognitive processes. *Science* 228: 750-752.
- Robinson D.L., Peterson S.E. (1992) The pulvinar and visual salience. *TINS* 15: 127-132.
- Roelfsema P.R., Engel A.K., Konig P., Singer W. (1997) Visuo-motor integration is associated with zero time-lag synchronization among cortical areas. *Nature* 385: 157-161.
- Roskies A.L. (ed.) (1999) Reviews on the binding problem. *Neuron* 24: 7-110.
- Schanze T. and Eckhorn R. (1997) Phase correlation of cortical rhythms at different frequencies: higher order spectral analysis of multiple-microelectrode recordings from cat and monkey visual cortex. *Int. J. Psychophysiol.* 26: 171-189.
- Schwartz F. (1947). *Über die Reizung des Seheorgans durch doppelphasige und gleichgerichtete elektrische Schwingungen.* *Z. Sinnesphys.* 69: 158-172.
- Singer W. (1977) Control of thalamic transmission by corticofugal and ascending reticular pathways in the visual system. *Physiol. Rev.* 57: 386-420.
- Spekreijse H., van Norren D., van den Berg T.J.T.P. (1971) Flicker responses in monkey lateral geniculate nucleus and human perception of flicker. *PNAS.* 68: 2802-2805.
- von Stein A., Rappelsberger P., Filz O., Petsche H. (1993) EEG-Korrelate bildlicher Vorstellung; eine Amplituden- und Kohärenzuntersuchung. *Z. EEG-EMG* 24: 217-224.
- Steriade M. (1993) Cellular substrates of brain rhythms. W: E. Niedermeyer, F. Lopes da Silva (red.), *Electroencephalography: basic principles, clinical application and related fields.* Wyd. III, Williams and Wilkins, Baltimore. str. 27-62.
- Steriade M., Gloor P., Llinas R.R., Lopes da Silva F.H., Mesulam M.M. (1990) Basic mechanisms of cerebral rhythmic activities. *Electroenceph. Clin. Neurophys.* 76: 481-508.

- Steriade M., Amzica F., Contreras D. (1996) Synchronization of fast (30-40 Hz) spontaneous cortical rhythms during brain activation. *J. neurosci.* 16: 392-417.
- Tallon-Baudry C., Bertrand O. (1999) Oscillatory gamma activity in humans and its role in object representation. *TICS* 3: 1-18.
- Takigawa M., Kidiyoor R.G. (1991) Analysis of high frequency and in human EEG by differentiation and directed coherence. *Neurosciences* 17: 289-295.
- Thatcher R.W., Krause P.J., Hrybak M. (1986) Cortico-cortical associations and EEG coherence: a two-compartmental model. *Electroenceph. Clin. Neurophysiol.* 64: 123-143.
- Treisman A., Gelade G. (1980) A feature-integration theory of attention. *Cogn. Psychol.* 12: 97-136.
- Utlett G.A., Johnson L.C. (1958) Pattern, stability and correlates of photic-electroencephalographic activation. *J. nerv. ment. Dis.* 126: 153-168.
- Vanni S., Revonsuo A., Hari R. (1997) Modulation of the parieto-occipital alpha rhythm during object detection. *J. Neurosci.* 17: 7141-7147.
- 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* 221: 411-436.
- Wróbel A. (1997a) Attention related oscillatory activity within sensory systems. *Acta Neurobiol. Exp.* 57: 38.
- Wróbel A. (1997b) W poszukiwaniu integracyjnych mechanizmów działania mózgu. In: *Mózg a zachowanie*. PWN, Warszawa. p. 460-486. (in polish).
- Wróbel A. (1998) Beta frequency burst - elementary event of attention span. In: *Time and timing in neural systems*. Abstr. Satellite Symp. FENS in Strzêkocino. p. 42-44.
- Wróbel A., Bekisz M., Waleszczyk W. (1994a) 20 Hz bursts of activity in the cortico-thalamic pathway during attentive perception. In: C. Pantev, Th. Elbert, B. Lutkenhoner (eds.): "Oscillatory event related brain dynamics" Plenum Press London. NATO A/Life Sciences. Vol. 271.
- Wróbel A., Bekisz M., Kublik E., Waleszczyk W. (1994b) 20 Hz bursting beta activity in cortico-thalamic system of visually attending cats. *Acta Neurobiol. Exp.* 54: 95-107.
- 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.
- Zeki S. (1993) *A vision of the brain*. Blackwell Scientific Publications, Oxford, 366p.