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20 Hz bursting beta activity in the cortico-thalamic system of visually attending cats

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Abstract. It has recently been found (Bekisz and Wróbel 1993) that electroencephalographic recordings from the primary visual cortex and lateral geniculate nucleus of cats attending to visual stimuli contained enhanced activity in the 20 Hz frequency band. Here we present the detailed analysis of this activity. It consisted of short (0.1-1 s) bursts of oscillations which tended to appear simultaneously in the visual cortex and lateral geniculate nucleus. There was an increase of amplitude and frequency of appearance of such burst events in both of the investigated visual centres, which resulted in a power increase in 16-24 Hz band during situation requiring visual attention. The present findings provide additional evidence for cortical influence upon the thalamic information processing.

Key words: oscillatory bursting activity, 20 Hz beta frequency, attention, cortico-geniculate synchronization, cat

INTRODUCTION

Recent years have brought an increase in research on the oscillatory activity exhibited by numerous brain areas. Rhythmic activities of frequencies below 14 Hz (delta waves and spindle oscillations) accompany the functional organization of thalamic and cortical networks during sleep (Steriade et al. 1993). On the other hand, oscillations of similar frequency (7-14 Hz) were observed in certain types of vigilant behaviour (Bouyer et al. 1992, Chatila et al. 1992). The synchronizations of higher frequencies in the so-called gamma band (above 30 Hz) have been postulated to serve as a feature-linking mechanism at different levels of cortical sensory processing (Eckhorn et al. 1988, Gray et al. 1989). In our laboratory we have recently recorded an increase in beta activity (about 20 Hz) in the lateral geniculate nucleus (LGN) and primary visual cortex (VCx) of cats attending the visual scene during the differentiation paradigm (Bekisz and Wróbel 1993). We postulated that this type of activity is propagated from the cortical site by descending cortico-thalamic pathway which, by means of a synaptic potentiation mechanism (Lindström and Wróbel 1990), enhances the gain of thalamic relay during visual perception. This hypothesis was put forward long ago (Hernandez-Peon 1966) but has not since been confirmed by empirical evidence.

The excess of 20 Hz band of activity in the cortico-thalamic component of the visual system during attentive behaviour, as found in our experiments (Bekisz and Wróbel 1993), strongly supports the hypothesis of central control of incoming sensory information. In the present paper we describe further the properties of this 20 Hz rhythmic beta activity which, we think, is a neural correlate of attention processes. Support for this notion comes from the observation that the 20 Hz oscillations appeared predominantly during correct performance of a visual discrimination task. Such activity was rarely found at the same sites when an animal made an error or during acoustic trials.

METHODS

Four 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 x 45 x 45 cm) wooden cage and faced two translucent doors situated 5 cm apart. The cat and the doors were separated by a transparent removable screen. The visual stimulus was a small (0.5 x 2 deg) slit 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 (linear speed of about 10 cm/s) at the same time making smaller oscillations in the vertical plane. After ten to twenty seconds the slit was stopped on one of the doors, indicating that a piece of meat was hidden behind that door. Then the stimulus was switched off. After a 1-3 seconds delay the transparent screen was raised and the cat could reach for the reward by pressing the correct door. The incorrect door remained locked and the animal could not open it. When the cat pressed the incorrect door, the correct one was locked as well, so the animal was not allowed to correct an error.

The acoustic stimulus was a noise produced by a pocket-radio loudspeaker, with a fundamental frequency of 5 kHz and with an intensity modulated with a 2.5 Hz frequency between 50 dB 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 sidewall. After ten to twenty seconds the stimulus was switched off, and there was a 1-3 seconds delay before the cat was allowed to press one of the doors. The reward was hidden behind the door to the side on which the auditory stimulus had been turned off.

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. In trained animals both visual and acoustic stimuli were repeated 12 times in each session during one experimental day. For one cat (Cat 1), the visual stimulus was also presented and oscillated in the vertical plane between the doors (neutral position) during the acoustic task to provide similar light-flux input in both visual and auditory modality tasks. The recordings obtained from this cat did not differ from those of the other animals. Training was considered complete when animals reached 90% performance accuracy during 3 successive experimental days. Ten to fifteen sessions (one session a day, each lasting about half an hour) were sufficient for all cats to learn the task.

After the completion of training, surgery was performed under Nembutal anaesthesia (35 mg/kg with subsequent supplementary doses, premedication - combelen 0.2 mg/kg and 0.01 ml atropine (0.05% atropinum sulfuricum)). Tungsten recording electrodes were inserted under electrophysiological control: two in the left lateral geniculate and/or perigeniculate nucleus and one in the contralateral hippocampus. The LGN electrode was lowered to the central part of the nucleus, aiming at the representation of the area centralis. A row of three chromonickel electrodes, about 1.5 mm apart, was placed in the left primary visual cortex of all animals. In two cats an additional electrode was inserted into the ipsilateral auditory cortex. The electrodes and a plug were fastened to the skull using dental cement. The recordings started 5 to 7 days after surgery with one session a day, four sessions a week. After the experiment, the cats were anaesthetized with an overdose of Nembutal and perfused with 4% paraformaldehyde in 0.1% phosphate buffer for histological verification of the recording sites.

The electroencephalographic (EEG) signals (1 Hz - 0.5 kHz) were amplified and stored on FM magnetic type recorder (Racal V-store). For the computerized off-line data analysis, signal frequencies higher than 100 Hz were filtered out and the remaining signals were digitized with a 200 Hz sampling rate.

To better show the frequency content of the investigated signal as it changed in time we have applied the dynamic spectral analysis method (Sciarretta and Erculani 1977) and constructed Fast Fourier Transform (FFT) planes, as shown in the Fig. 2. The FFT plane shows FFT spectra calculated for many consecutive time epochs and organized in increasing time order, one after another. Each epoch was 256 samples (1.28 s) long. Before Fourier transformation the raw data within the epoch were multiplied by the cosinusoidal window function. This function reached maximal value in the middle of the epoch and decreased down to zero towards its both ends. The use of such a procedure reduces the noise in the spectrum and also improves the time resolution of the dynamic spectral analysis method. The time shift between the onset of two consecutive epochs from which the neighbouring FFT spectra were calculated was 40 samples (0.2 s) and the resulting overlap was 216 samples (about 1.08 s).

Further elaboration of the EEG was made after the signals were digitally band-pass filtered with cut-off frequencies 16-24 Hz. To obtain the cumulative amplitude function the mean value of the filtered signal from the whole trial was calculated and then the absolute values (moduli) of the differences between each successive sample and the mean were recorded cumulatively as shown in detail in Fig. 3A.

The temporal relationship between the bursts' appearance in different brain structures was calculated by the ordinary crosscorrelation method. The burst event was defined by setting the threshold amplitude and reckoning the mid-point of the period in which the amplitude of the oscillations exceeded the set value. To discriminate two neighbouring bursts the assumption was made that different bursts had to be separated by a period of at least 20 consecutive samples (two periods of 20 Hz oscillation).

RESULTS

Typical examples of electroencephalograms (EEGs) recorded from the lateral geniculate nucleus (LGN) and primary visual cortex (VCx) obtained during the period when the cat observed the visual stimulus in order to discriminate the place of its disappearance are shown in Fig. 1A and C. Close inspection of the records showed that the underlying activity synchronized from time to time with about 20 Hz frequency, forming remarkable beta fre-

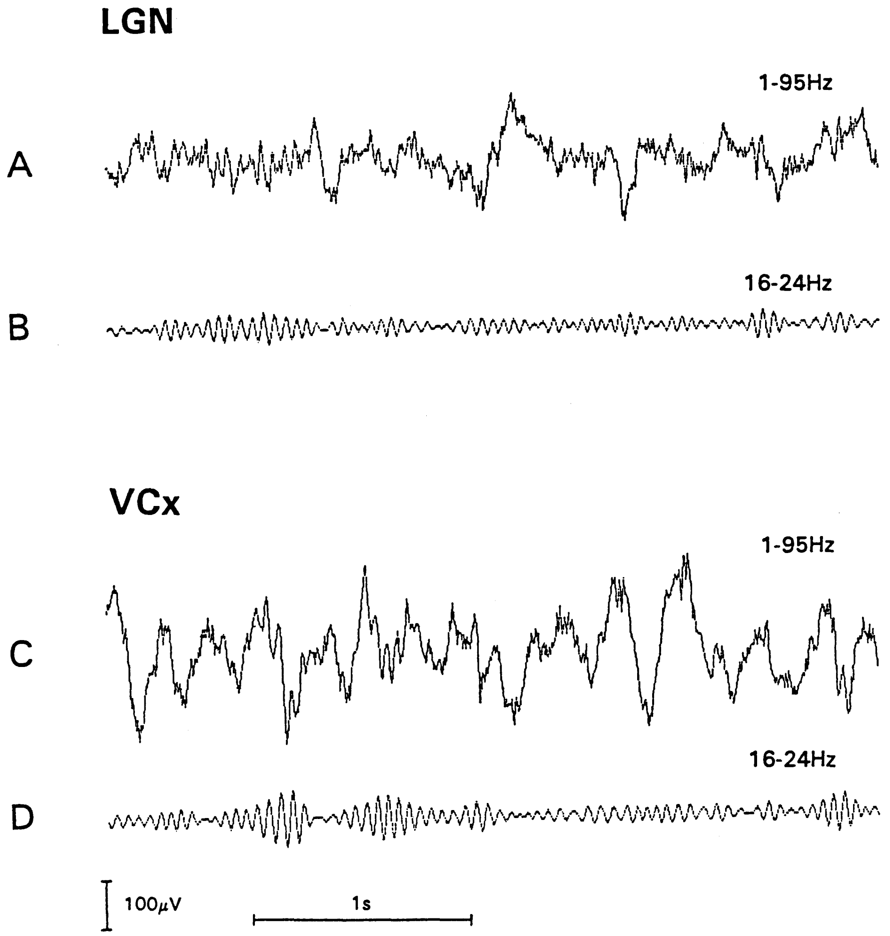

Fig. 1. A, C, the 1-95 Hz range EEG signal recorded from LGN (A) and VCx - area 17 (C) during the visual trial. Among slow waves one can easily detect the periods of oscillations with a frequency of about 20 Hz; B, D, - band-pass filtered data with cut-off frequencies 16-24 Hz.

quency oscillations. The content of this frequency band has been filtered and shown below each record (Fig. 1B and D). The filtered signals clearly show the individual bursts of activity of about 20 Hz frequency as they appear in both structures. Such high amplitude bursts were consistently present only in those visual trials which ended with a correct behavioral response, like the example shown in Fig. 1. When present, these bursts lasted from 0.1 to 1 s. They were less apparent during unsuccessful visual trials or during the auditory trials (Figs. 2 and 3).

We also detected similar high amplitude bursts in auditory cortex during acoustic trials. Such prominent 20 Hz bursts also appeared in the hippocampus but regardless of the behavioral situation (either visual or acoustic). Thus, within the scope of our recording sites, the increase of the bursting activity during visual behaviour was limited to the geniculo-cortical system.

The appearance of the beta frequency bursts in association with attentive visual behaviour was a consistent finding in the data obtained from three out of four investigated animals. The forth cat did not show significant changes in beta bursting activity in any stage of the experiment. This cat had learned the task rapidly and responded with no apparent behavioral signs of attention but with the same high performance score (90%). Consequently, we think that for this cat the task was to easy and therefore "attention-related" activity was difficult to detect.

The 20 Hz activity illustrated in the Fig. 1 is obscured in a raw signal by more prominent waves of lower frequency. The ratio of the power calculated for the two bands can be estimated from the FFT

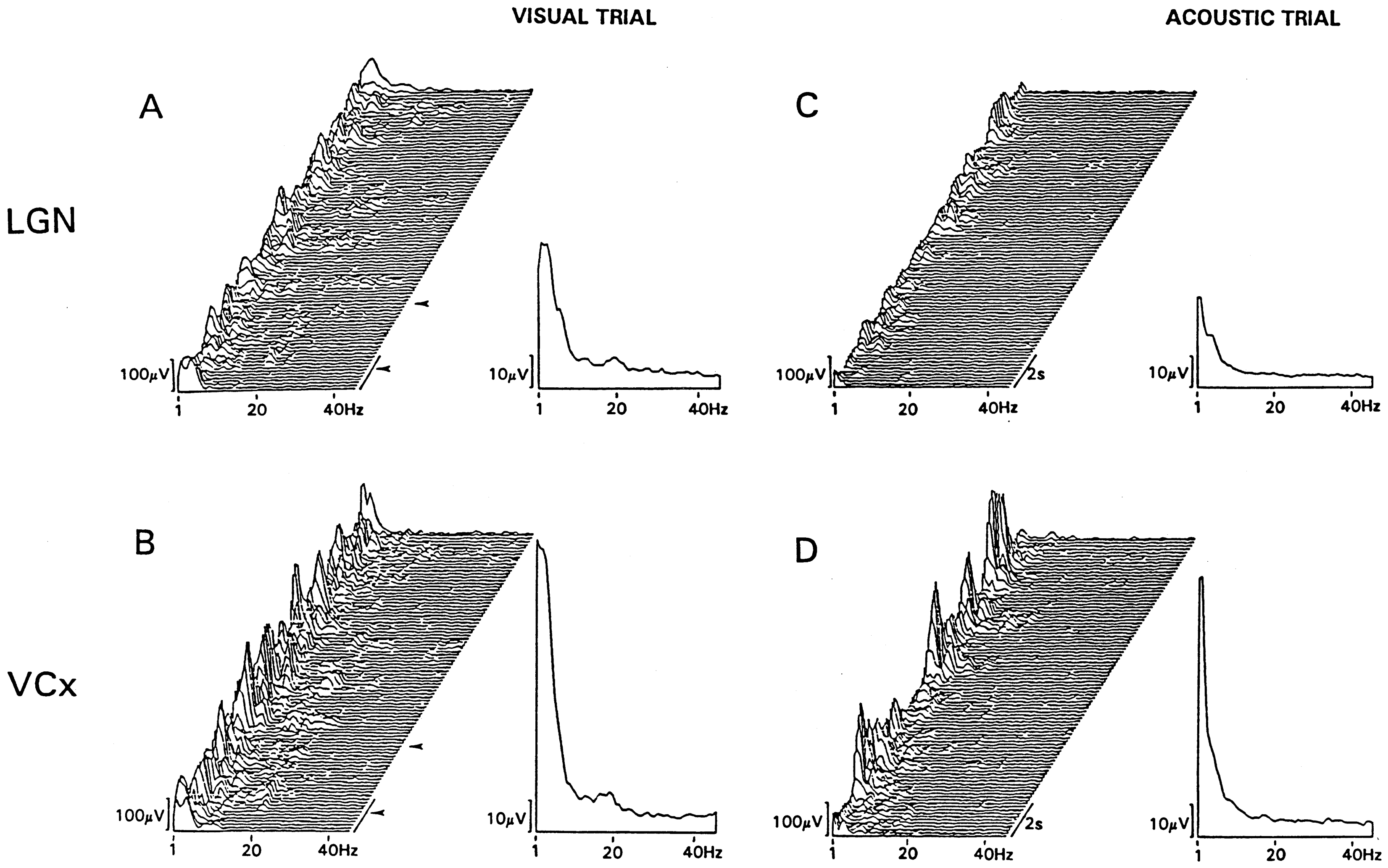

Fig. 2. The analyzed EEG activity recorded during two consecutive trials from one experimental day. Left, visual trial; right, acoustic trial. Upper row, LGN; lower, the most posterior recording site on VCx (electrode no. 2, in Fig. 7). Dynamic spectral analysis is presented in the form of three-dimensional maps - FFT planes. Lowermost amplitude spectrum on each of the planes was calculated from the epoch starting with the beginning of the trial, the next one - from the epoch shifted by 40 samples (0.2 s), and so on (see Methods). Thus the oblique axes of the plane represent the time domain. The mean spectra obtained for the whole trials are shown to the immediate right of each FFT plane. Arrowheads denote the period of the visual trial as presented also in Fig. 1.

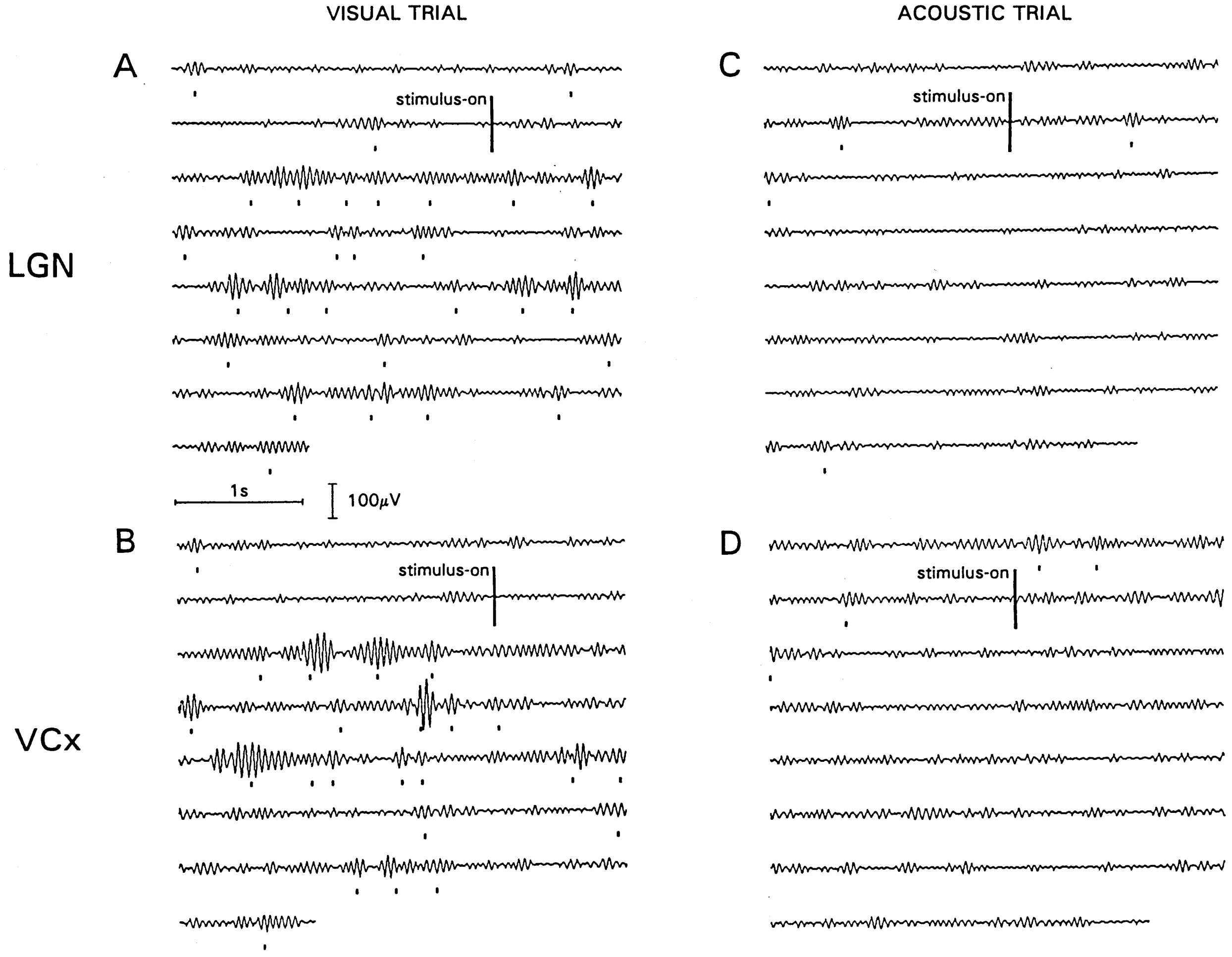

Fig. 3. Filtered signals showing bursting activity within the 16-24 Hz frequency range during visual (left column) and acoustic (right column) trials. A, C, LGN recorded activity; B, D, activity from the posterior recording site of VCx as marked in Fig. 7 (electrode 2). The same trials presented in Fig. 2 are represented here. Traces in each quarter represent continuous recordings during trials. The vertical marker in the second line indicates the moment of turning the stimulus on (beginning of the trial). Note more frequent and higher amplitude bursts during the visual trial recorded in both structures. Small dots under each individual traces indicate the mid-points of the oscillatory events amplitudes which exceed the set threshold level (see Methods). Note the simultaneous occurrence of many such bursts in LGN and VCx.

planes shown in the Fig. 2. Although the activity below 10 Hz dominated overall during trials, both in the VCx and LGN recording sites, the short events of enhanced activity within the 16-24 Hz frequency band were typically also apparent (compare also Fig. 1, in which part of the visual trial is presented). These events were frequently well-distinguished from neighbouring background, indicating that they may represent specific phenomena in the frequency domain.

The typical 16-24 Hz frequency content that was enhanced during the visual trials is illustrated for one of such trial in the left column of Fig. 2. In contrast, we could not trace a stable activity within the beta band on the FFT plane obtained from a consecutive acoustic trial (right column of Fig. 2). In other animals, we could also observe some bursts within this specific (16-24 Hz) range during acoustic trials, but they were always significantly fewer and less prominent than those observed in visual trials. The elevation at the 16-24 Hz frequency band is clearly visible in the mean FFT spectra calculated for the whole period of visual trials, as are shown to the right of each FFT plane. In contrast, the EEG power measured within these amplitude spectra appeared to fall more smoothly with frequency during rest (not shown) and auditory trials (right column of Fig. 2).

The other point illustrated by Fig. 2 is the smaller power measured during acoustic trials for the whole spectra regardless of the frequency band as observed for both LGN and VCx data. This drop in the overall activity in the visual system during acoustic trials was not a consistent finding and will not be discussed in detail here.

The time resolution of FFT planes was not sufficient to distinguish all neighbouring bursts as separate events. The large overlap between consecutive epochs used in our dynamic spectral analysis smeared the relatively short 20 Hz burst events in the time domain. For detailed analysis of the appearance of the beta bursts we used the filtered signals that are presented in the Fig. 3. Here we present the records from two consecutive trials: visual (left side of Fig. 3) and acoustic (right side). The upper records are taken from the geniculate recording site whereas the lower ones represent the activity measured from the cortical electrode. All eight traces in each quadrant of the figure show continuous recordings.

It is apparent from Fig. 3 that the observed 20 Hz bursts had much larger amplitudes during the visual than acoustic trials both in geniculate and cortical recording sites. The dots underneath each signal indicated those bursts which were selected for further calculations by exceeding an arbitrary amplitude threshold. The threshold set for a given electrode remained the same for all recordings throughout the experiment. Note that the frequency of appearance of these bursts was much higher during visual than acoustic trials.

To better characterize the dynamics of the filtered signal within the 16-24 Hz range we applied a special method of building up the cumulative curves which included changes of both amplitude and frequency of appearance of the bursts. These curves are cumulative records of the values of amplitudes (ordinate) for all samples measured until a given experimental time (abscissa) as shown in the Fig. 4 (cf. also the Methods). Figure 4 shows the beginning of two cumulative curves during consecutive visual and acoustic trials as measured from the same electrode placed in the LGN. The filtered signals from which the cumulative curves were built are presented below them. It can easily be seen that bursts of high amplitude present during the visual trial raise the curve much more (Fig. 4A) than those of smaller amplitude recorded during the acoustic trial. As a result, the curve obtained during a visual trial was much steeper than that characterizing the

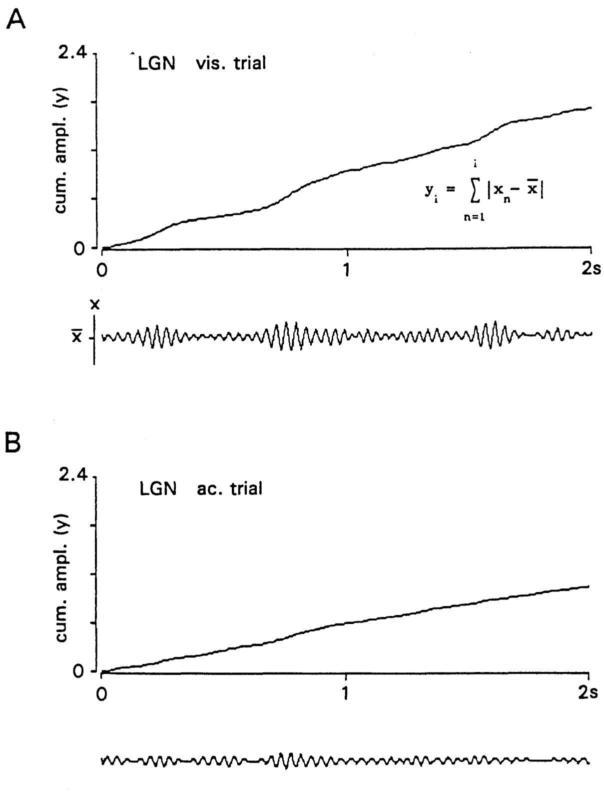

Fig. 4. The beginning periods of the two consecutive LGN recordings (filtered frequencies 16-24 Hz only) from visual and acoustic trials with expanded time axes to show details of the cumulative function method. Note also the stepping course of the cumulative function obtained during visual trial, which represents high amplitude bursting. Consequently the cumulative value after 2s of recording was much higher at the visual trial. The ordinate unit corresponds to 5 mV.

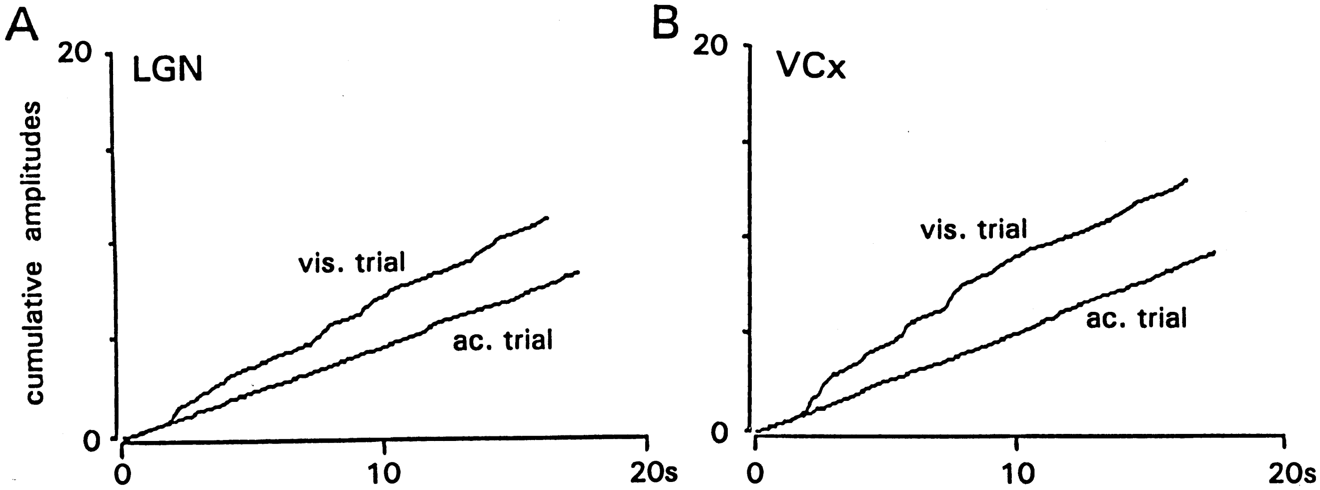

Fig. 5. The EEG activity in the 16-24 Hz band during successive visual and acoustic trials as characterized by the cumulative amplitude functions. The cumulative curves calculated for recordings obtained during visual trial are steeper then those from acoustic trial both in LGN (A) and VCx (B) activity. The position of the electrode in VCx is marked by no. 2 in Fig. 7. The ordinate unit is the same as in Fig. 4.

acoustic trial, thus indicating more of the 20 Hz frequency signal content.

The cumulative curves obtained from LGN and VCx electrodes for two consecutive visual and acoustic trials in the same experiment are shown in the Fig. 5. As a result of the more frequent and higher amplitude bursts present in the visual trial, the visual cumulative curves were steeper in both recording sites. This observation was shown to be significant (Mann-Whitney U-test, $P<0.05$) for all cats except the one that failed to show behavioral signs of attention, as discussed above. All curves measured during visual trials were also irregular, with steps reflecting the high amplitude bursting activity. It was typical for bursting to occur at the same point in time at both recording sites. This observation confirmed that the bursting in the VCx and LGN are related phenomena, as reported previously (Bekisz and Wróbel 1993).

To assess the relationship between the bursting activity in the VCx and LGN we have correlated the two events with the typical crosscorrelation technique. Each burst in which amplitude exceeded an arbitrary level was marked as a nonlasting time event (cf. Fig. 3 and the Methods). These events recorded from the VCx and LGN tended to occur simultaneously, as shown in Fig. 3.

The crosscorrelation histograms of events occurring in concert at different recording sites as recorded during one experimental day are presented in Fig. 6. The histological verification of the recording sites matched with the retinotopic organization in LGN and VCx is shown in Fig. 7.

In the left column of Fig. 6 the correlograms of bursts occurrences in the LGN and different sites of the primary visual cortex (area 17) are shown. The central peak in the presented correlograms indicate the level of coincidental burst appearances at the two recording sites. Usually we attempted to place the cortical electrodes in primary visual cortex close to the region representing the area centralis (a.c.). Indeed, all our cortical recording sites were within three degrees of this region as judged by comparing the established cortical maps (Tusa et al. 1978). The LGN recording sites covered larger representation of the visual map (azimuth: from 0 to 10 deg / elevation from -10 to +20 deg of visual angle). We noticed that when the LGN electrode was further away from the a.c. region (for about 10 deg or more), the correlations were weaker. Typically, the

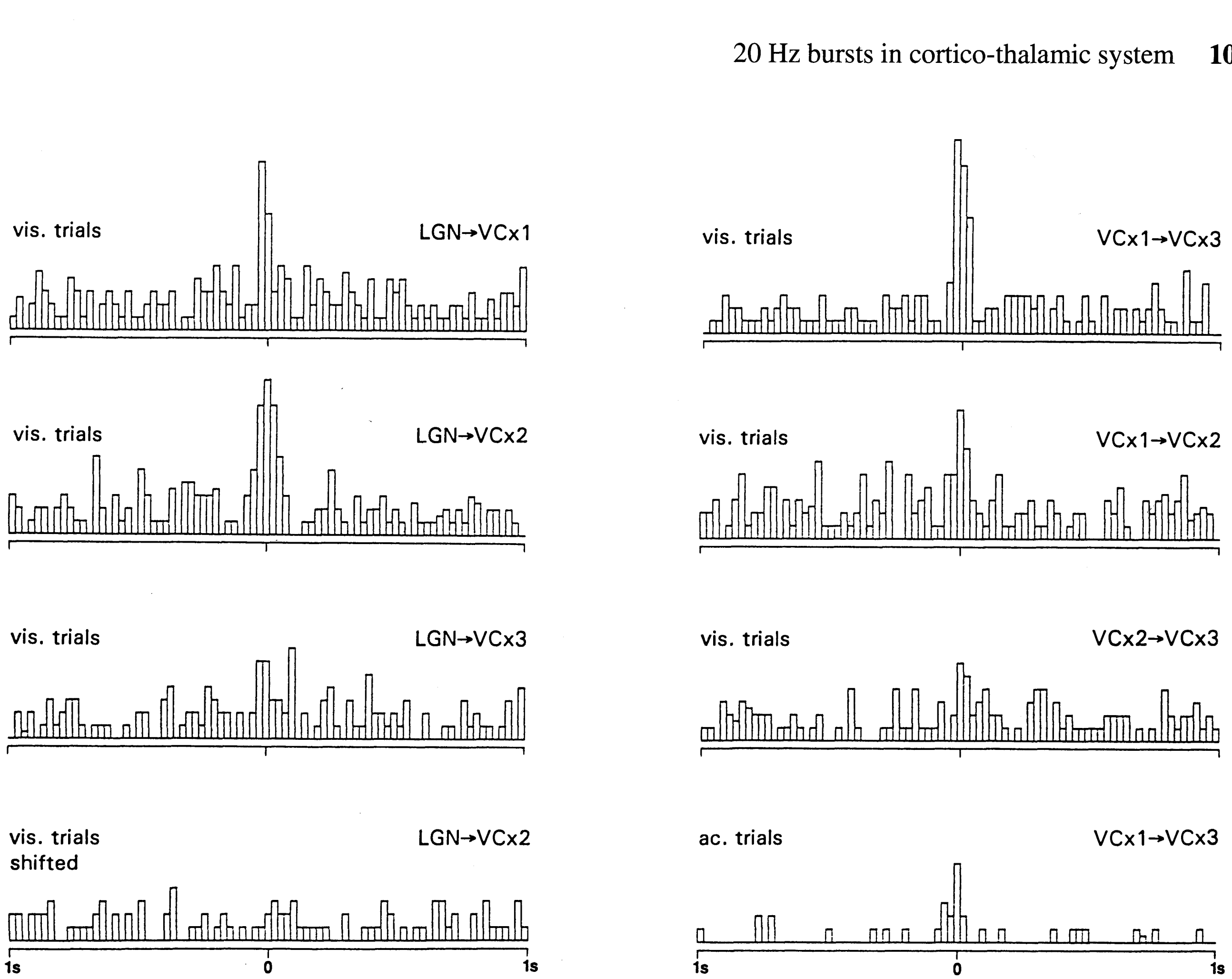

Fig. 6. Coincidental LGN and VCx 20 Hz bursting activity visualized by the crosscorrelation method. Burst events from all positive trials in one experimental day were selected by the threshold method as shown by examples in Fig. 3. The recording sites in the VCx are numbered in correspondence with Fig. 7. Note the high probability of coincidental appearances of burst events occurring at LGN and posterior cortical recording sites. Compare the estimated retinotopic positions of the recording sites given in Fig. 7. Shifted correlogram at the bottom-left position (between LGN and VCx 2 recordings) is an example to indicate significance of the presented correlations. The bin width was 25 ms and the window was 40 bins (1 s). The right sides of the correlograms are labelled to indicate the correlation directions; the left, unlabelled sides show correlation values for the opposite direction.

higher correlations were obtained in more closely aligned sites of LGN and VCx. Our accuracy, limited by the small number of electrodes, does not allow for more specific descriptions of this observation. The correlation of bursting recorded from closely positioned cortical electrodes and the same LGN electrode varied without any obvious relationship (Fig. 6). The possible source for the dispersion of the correlation strength could be the columnar organization of the VCx, with dominance columns supplied more by either ipsi- or contra-inputs (Hubel and Wiesel 1962, LeVay et al. 1978). Whether the eye dominance is important for the observed correlations remains to be determined.

The lowermost correlogram in the right column in Fig. 6 shows the correlation obtained during an acoustic instead of visual trial. The overall number of bursts counted in the acoustic trial was much diminished, as the bursts were of smaller amplitude (compare Fig. 3). The small central peak in the correlation histogram indicated that the same synchronization mechanism was still present, however, as it contributed also to the development of the prominent peaks seen during the visual trials.

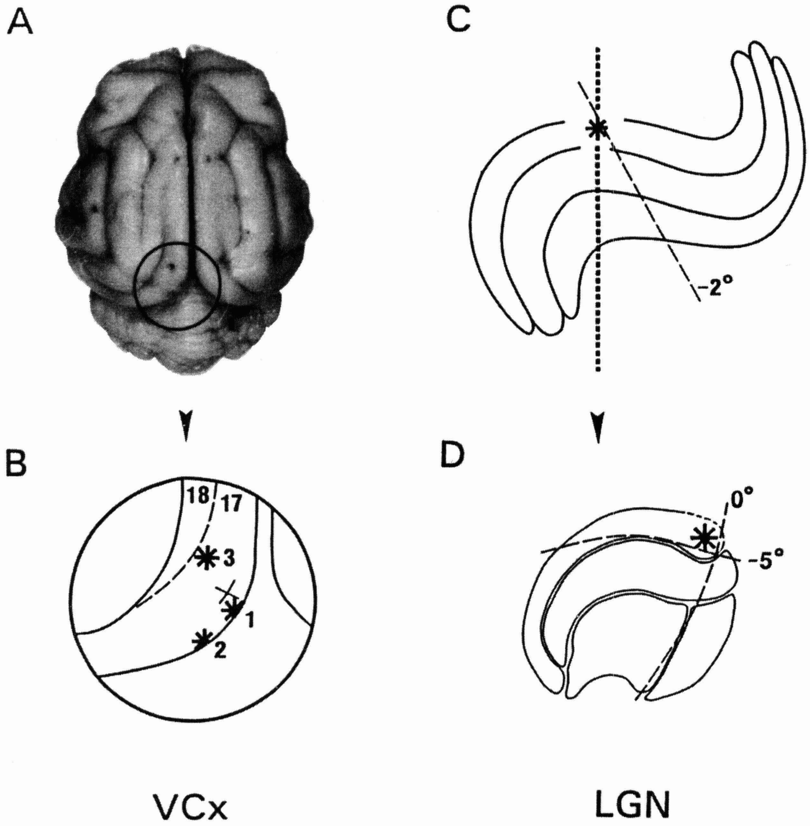

Fig. 7. The histological verification of the recording sites. The retinotopic alignment of the recording sites as estimated according to the data of Sanderson (1971) and Tusa et al. (1978), and described in azimuth/elevation degree values. LGN: +1/-2; VCx 1: +2/0; VCx 2: +0.5/+2.5; VCx 3: -1.5/-1.5. B, schematic enlargement of the region of the brain limited on the photograph (A) by the circle; stars, recording sites; cross, crossing of the vertical and horizontal meridian; dashed line, border between areas 17 and 18. C, drawing of a parasagital section of through the LGN; vertical line indicates the level of the coronal section shown in D. In C and D: star, recording site; dashed lines, isoelevations (-2, -5), isoazimuth (0).

In visual trials one can trace the dependent bursting between the neighbouring cortical recording sites (Fig. 6, right column, upper correlograms). More distant electrodes, however, recorded less correlated bursting activity (right column, correlogram VCx 2 - VCx 3). With the correlation method used we cannot judge to what extent the cortical correlations depend on second-order connections, e.g. the common input from the geniculate source. The special method of calculating the directed transfer functions was applied previously (Bekisz and Wróbel 1993) and demonstrated that at least some part of the correlation seen between the cortical electrodes was of internal cortical origin. The shifted correlogram shown at the bottom of the left column of Fig. 6 indicates that the peaks of the correlograms shown above are of a real significance.

DISCUSSION

In this study we have shown that the characteristic activity with frequency of about 20 Hz (within the beta band) which appears in the lateral geniculate nucleus (LGN) and visual cortex (VCx) of cats attending the visual scene consists of short bursts of oscillations. The increase of the beta band content was associated with the increase of both frequency of appearance and average amplitude of bursts. We further confirmed the previous report from our laboratory (Bekisz and Wróbel 1993) that the activity described in both visual structures was specific and correlated exclusively with attentive visual behaviour. Finally we were able to show that bursts recorded from VCx and LGN tend to coincide in time regardless of the behavioral context. The correlation measured with the threshold method is most strongly expressed during visually attentive task, when the largest and most frequent bursts appear at the same time. These findings confirm the notion about the interrelation of cortical and thalamic activities during sensory information processing as postulated previously (Lindström and Wróbel 1990, Bekisz and Wróbel 1993).

Two points of the above findings should be discussed separately. Our support for describing as "attentive" the period of high beta activity in the visual centres during which cats had to perceive the visual stimulus came from the observation that the appearance of such activity was related reliably to correct performance of the subsequent visual task. The question arises whether the 20 Hz oscillatory activity was not evoked instead by a stimulus-dependent mechanism. We ruled out this possibility by accompanying the acoustic trial with a nonsignalling visual stimulus in between the doors. Such a stimulus did not evoke any additional beta activity in the investigated visual centres and the results obtained in this cat did not differ from those of other animals. Recently we repeated our experiment with the absence of any stimuli during the waiting period (not published). In such a paradigm the visual or acoustic context of the trial was marked at the beginning of each trial by presenting specific cue stimuli (see also, Lopes da Silva 1991). During such a stimulus-free situation we could also observe the increase of the beta bursts activity in waiting time when the trial ended in correct responses.

Secondly, we believe that the beta band content of activity of the visual centres is actually increased during the visually attentive situation because both during the auditory task and during intertrial stimulus-free situations this activity was low and fitted the smooth curves of amplitude spectra as in the right column of Fig. 2. We believe that the proper cortical mechanism must be activated in order to evoke potentiation and enhance gain in the geniculate relay. Such a situation would occur during attentive seeing. There are, however, data indicating that other possibilities need to be considered. Hernandez-Peon et al. (1957) and Horn (1960) found suppression of postsynaptic field potentials evoked by light-flash stimulation in the visual cortex during attentive hearing. Horn (1976) called this phenomenon the "transmission blockade". Additional experiments are needed to check for the beta content of the EEG in the behavioral situation used by Horn.

It is well known that vigilance is associated with desynchronization of the EEG (Steriade and Llinas 1988, Steriade et al. 1993). Recent investigations on anaesthetized animals suggest that the "desynchronized" EEG is comprised of fast oscillations of small amplitudes and different frequencies, serving as a carrier for coordination between cortical areas (Bressler 1990, Engel et al. 1991). These data did not allow one to determine whether synchronous oscillations influence the activity of thalamic cells (see discussion in Steriade et al. 1991). Ghose and Freeman (1992) argued that the gamma rhythms appearing in the cortex might have their source in the thalamic nuclei, on the basis of spontaneously appearing, common oscillatory inputs. Recent experiments by Sillito et al. (1993) seem to indicate, however, that corticofugal feedback may also correlate the firing of geniculate cells. In nonanaesthetized animals the beta rhythms have been found by Lopes da Silva (1991) to appear in the cortex. On the other hand Bouyer et al. (1980) assigned the source of similar rhythms to the thalamus. In this respect, it is interesting that the two sources cortical and thalamic can also generate alpha waves (Steriade et al. 1990, Lopes da Silva 1991). Our finding suggesting a cortical origin of beta rhythms transmitted from the visual cortex towards the lateral geniculate nucleus (Bekisz and Wróbel 1993) needs support from independent experiments with different methodological approaches. There is need for further studies in order to localize the origin of high frequency oscillations in the brain.

It was recently proposed that the beta frequency activity in the cortico-thalamic pathway, which appears during visually attentive processing, can drastically change the excitability of geniculate cells and therefore increase the amount of visual information transmitted by this nucleus (Lindström and Wróbel 1990, Bekisz and Wróbel 1993). This idea recalls the "searchlight hypothesis" postulated some time ago by R. Jung (1967) and presented in the modern form by Crick (1984). He proposed that the attention control system should contain a mechanism for transiently strengthening the synaptic effects produced by rapid bursts of high frequency, exactly as found in the experiment by Lindström and Wróbel (1990). However, Crick (1984) believed the responsible neurons to be located in the reticular nucleus. The reticular nucleus contains only inhibitory interneurons and cannot, therefore, link direct excitatory feedback as required by our hypothesis.

Such a focus on the role of the feedback pathways in attentive perception is appealing, because it can be applied to other stages of visual processing and also to other sensory systems. Preliminary recordings from the acoustic cortex have revealed beta oscillatory bursts during attentive hearing (Bekisz and Wróbel 1993). More data are, however, required to replicate the present findings in auditory system.

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