Spectral shifts of very slow (0-0.5 Hz) potential oscillations in the structures of brain visual system during different illumination changes in freely moving rats

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Abstract

Recent publications have shown different forms of very slow oscillatory phenomena in the brain visual system structures. The present study was performed to test the hypothesis that extracellular very slow brain potential (VSBP) oscillations in lateral geniculate complex (LGC) and primary visual cortex (PVC) are responding concurrently to illumination changes. The results support the aforementioned suggestion and revealed similar patterns of VSBP modification within a frequency band of 0.1-0.25 Hz in both the LGC and PVC in response to darkness, illumination, and photostimulation. Thus, a possible role for VSBP oscillations in the central mechanisms of vision should be strongly considered.

Keywords: Very slow brain potential oscillations, Lateral geniculate complex, Primary visual cortex, Neurophysiology of central vision

1. Introduction

It has been documented that neurons of the lateral geniculate complex (LGC) and primary visual cortex (PVC) express strong intrinsic oscillatory activity in the frequency domain below 0.5 Hz. For example, Albrecht and her colleagues discovered very slow

rhythms in rat lateral geniculate neurons with frequencies of 0.025-0.01 Hz [1]. They also reported that such oscillatory behavior of LGC neurons was modulated by the level of illumination. Very slow (less than 0.3 Hz) oscillatory activity of PVC neurons has also been described in cats [13]. Secondly, there are indications in several reports that very slow extracellular brain potentials could be involved in visual threshold and perception level regulation [4]. Additionally, it was demonstrated that there is very slow endogenous rhythmicity with similar frequencies in functions of the visual system [15]. Moreover, previous studies of our laboratory [6, 7] have supported the relevance of the aforementioned findings for very slow brain potential (VSBP) oscillation in the cortex of the visual system (Area V1). It was demonstrated that such activity could be significantly and specifically altered by varying the illumination from dark to light and vice versa. Taken together, these data raise an intriguing question about the possible role of VSBP oscillatory activity in the mechanisms in the neuroprocessing of visual information.

According to the current terminology [2, 8, 9], very slow (infra-slow or ultra-slow) brain potential oscillations have the frequency range of 0-0.5 Hz. Based on waveform period, these processes are subdivided into several ranges [2, 9]. These are: (1) oscillations in the domain of seconds, known also as second oscillations, which have the period of 2-10 seconds (frequency domain of 0.1-0.5 Hz); (2) multi-second oscillations, which have the period of 10-60 seconds (frequency domain of 0.0167-0.1 Hz); and (3) minute and multi-minute oscillations with periods of 1 minute or more (frequency domain of approximately 0.0167 Hz and less). Formerly this type of brain activity was studied in classical CNS electrophysiology using other labels (e.g., DC-shifts, DC-potentials, steady state potentials, etc.) [2, 8, 9, 12]. Accumulating evidence indicates that VSBP oscillations are closely related to the neurophysiological mechanisms in the functional state regulation of CNS sub-cortical

structures and also some cortical areas [8, 9]. This type of brain activity may reflect some aspects or mechanism of sensory information processing in the CNS.

Though intriguing, the functional role of extracellular VSBP oscillatory dynamics as a mechanism of brain visual information neuroprocessing is not yet established. The present study was undertaken to investigate the possible functional role of VSBP electrical activity in the mechanisms of central vision and, specifically, to test the hypothesis that extracellular VSBP oscillations in the LGC and PVC are responding to changes in ambient illumination in specific and similar ways.

2. Methods

The subjects were five freely moving male albino rats. All procedures were conducted in accordance with humane principles of laboratory animal care (NIH publication No. 86-23, revised 1985). Our experimental procedures have been described in detail in earlier reports, including their theoretical, technical, and electrophysiological bases [5, 6, 7]; therefore, only the main points will be reiterated here. Under general anesthesia (Nembutal®, 40 mg/kg i.p.), and in accordance with a rat brain stereotaxic atlas [14], two gold electrode pairs were stereotaxically implanted in the LGC and PVC in order to record long-term chronic bipolar extracellular potentials in these brain sites. Experimental sessions were started 14 days after the implantation procedure. Each animal was placed in a Faraday's chamber and isolated in a special separate cage with light source on the top and light-reflecting, non-transparent walls. Freely moving within this cage, the animals were then exposed to three different background illumination levels: darkness (0 lux), continuous light (2000-2500 lux), and rhythmic photostimulation (frequency, 4 Hz; minimum intensity, 0 lux; maximum intensity, 2500 lux). Each illumination condition was maintained for 1024 seconds (though there were several exceptions, not less than 512 seconds, for sessions in which the rats were highly active). Electrophysiological recordings of VSBP oscillations from the aforementioned brain areas

were obtained under following experimental conditions during each of 30 daily sessions: darkness, ambient illumination, and rhythmical photostimulation. After the end of experimental series, the rats were devitalized using an injection of Nembutal® (100 mg/kg i.p.). Electrode positions were determined histologically, post mortem.

Extracellular bipolar recordings were obtained with aforementioned implanted LGN and PVC gold electrode pairs (inter-electrode distance, 2 mm). The rostral electrodes were connected to the positive amplifier input, while caudally located to the negative amplifier input. High impedance (200 MΩ) differential multi-channel low-noise (internal noise in 0-0.5 Hz bandpass, less than 3 μV) universal AC/DC-amplifier with DC-offset compensation (model UU-93, IEM, St.-Petersburg, Russia) was used for the electrophysiological measurements. The summary bioelectrical signal was artificially separated in 2 frequency domains using corresponding high- and low-pass amplifier filter settings: 0.1-0.5 Hz (second oscillation band) and 0.001-0.1 Hz (multi-second and minute oscillation bands). Amplified signals were continuously digitized on-line at a sampling frequency of 1 Hz using an analog-to-digital converter (model KPCI-3101, Keithley Instruments, Inc., Cleveland, Ohio, USA) and stored on disk for pre-processing and further off-line analysis.

We selected the following data sets for subsequent analyses: (a) second oscillations band, 256 data points; (b) multi-second oscillation band, 512 data points; and (c) minute oscillations band, 1024 data points, respectively. Each segment was subjected to the fast Fourier transformation (FFT) and power spectra analysis.

3. Results

The electrophysiological recordings generally showed a predominance of VSBP oscillations in the frequency domain of seconds and multi-second oscillations with occasional non-regular fluctuations in the domain of minutes in both the LGC and PVC brain sites (see Figure 1, Panels A, B, C, & D). The power spectra analysis for second oscillations (0.1 to 0.5

Hz) is also reported in Figure 1 (Panels E & F). Several 2 x 99 repeated measures ANOVAs were performed with these spectra. The power in each frequency bin was one repeated measure in the analysis and the type of illumination was the other. Greenhouse-Giesser and Huynh-Feldt corrections were employed where appropriate [10]. Two separate ANOVAs of the power spectra were conducted for each site. One ANOVA compared darkness with rhythmical photostimulation. An illumination x frequency interaction for the LGC site, $F(98, 196) = 2.61$, $EMS = 3.33 \times 10^{-11}$, $p < .01$, indicated that rhythmical photostimulation elicited significantly more power at the lower frequencies than did darkness, but a similar pattern of activity at the PVC site was not statistically significant. Another ANOVA compared ambient illumination with rhythmical photostimulation. Once again, an illumination x frequency interaction for the LGC site, $F(98, 196) = 4.77$, $EMS = 2.15 \times 10^{-11}$, $p < .01$, revealed than rhythmical photostimulation elicited significantly more power at the lower frequencies than did ambient illumination, and again, a similar pattern at the PVC site was not significant.

In addition, the power in each frequency bin of the mean power spectra for the LGC was correlated with that for the PVC for each illumination condition. The correlations between the LGC and PVC for darkness, ambient illumination, and rhythmical photostimulation were .60, .64, and .80, respectively. Each of these correlations was significantly different from zero ($p < 0.01$).

There were no apparent differences in the multi-second oscillatory domain or minute fluctuations domain in response to darkness, light exposure, and photostimulation, and therefore the details of these analyses will not be discussed.

4. Discussion

The most important finding of this investigation was the dramatic increase in power in the in the oscillatory domain of seconds during exposure to rhythmical photostimulation relative to constant sensory input conditions – i.e., either constant darkness or ambient

illumination. This finding confirms the hypothesis that extracellular VSBP oscillations in the LGC and PVC are responding to changes in ambient illumination in specific and similar ways. This outcome and other findings of the present study suggest several tentative conclusions:

1. Extracellular VSBP oscillations within LGC and PVC are, obviously, implicated in some mechanisms of CNS visual information neuroprocessing.

2. Oscillations in the domain of seconds in LGC and PVC are most the sensitive to environmental illumination changes relative to other types of very slow oscillations. Several interpretations are suggested: (1) second oscillations may reflect specific visual attention shifts depending on the type of visual stimuli, and this assumption is consistent with some previously proposed hypotheses on functional role of second oscillations [2]; and (2) second oscillations in the brain visual system may be involved in the mechanisms of background illumination encoding. Our results suggest that if such encoding exists it might be provided mainly by the changes in second oscillation power or amplitude, rather than spectrum or frequency shifts within this range.

3. Multi-second oscillations and minute fluctuations are not remarkably altered by simple visual stimuli such as those used in the present study, suggesting that they are not associated with specific mechanisms of vision. This leads to the preliminary conclusion that they reflect some other process (e.g., arousal-dependent, non-specific spontaneous oscillations or fluctuations of geniculate and cortical neuronal excitability). They may be controlled by brainstem nuclei (e.g., locus coeruleus, raphe nuclei, etc.) via multiple ascending projections of these systems to thalamus and occipital cortex. Previously published research of our group [5] demonstrated spontaneous multi-second and minute oscillations in locus coeruleus and frontal neocortex system activity. It was also reported that serotoninergic neurons of dorsal

raphe nuclei might modulate the activity of intergeniculate leaflet neurons very slow oscillatory activity pattern [3].

It is necessary to mention that there are very few publications that address the issue of very slow oscillations in the brain visual system. Our results on the presence in LGC and PVC recordings of multi-second oscillations and fluctuations in the domain of minutes are consistent with some current reports on this topic. The presence of ultra-slow (ultradian) isoperiodic activity with a period of about 105-124 seconds was shown in the intergeniculate leaflet neurons, which is known as a part of lateral geniculate complex and located between its dorsal and ventral parts [3, 11]. This work also demonstrated the sensitivity of this frequency domain to the level of environmental illumination [3]. Another publication [1] described very slow oscillations (0.025-0.01 Hz) in the neuronal activity of LGC in anaesthetized and freely moving rats. In addition, it was reported that very slow activity of LGC neurons could be significantly altered by exposure to light and darkness conditions. Continuous illumination apparently blocked these very slow oscillations, presumably this was associated with GABA-ergic neurotransmission mechanisms within aforementioned nucleus [1]. Endogenous oscillations in the frequency domain of seconds in visual cortex neurons were also described in anaesthetized cats in some previous articles [13]. These published data coincide with the results of our research on (1) the presence in both the LGC and PVC of oscillations in the domain of seconds and (2) the sensitivity of this frequency range to illumination level changes.

Some other publications indirectly agree with our experimental data as well. These were addressed to the issue of very slow fluctuations of functions in central parts of the brain visual system. For example, some psychophysiological data have shown very slow fluctuations of mental activity and visual threshold in the frequency domain of 0.02-0.068 Hz [15]. In the recent research of M. Devrim et al. (1999) on the slow cortical potential shifts in

the human visual system, it was demonstrated that spontaneous slow cortical potential shifts modulate the detection of visual stimuli at sensory threshold. It has been shown that the stimulus detection performance was higher in negative compared to positive cortical potential shifts. Accordingly, these authors suggest their findings demonstrate that cortical negativity reflects increased excitability of neural networks, thereby facilitates the detection of threshold stimuli [4].

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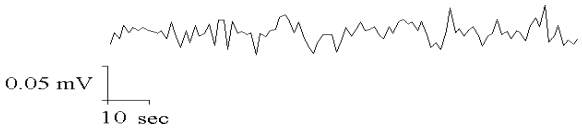
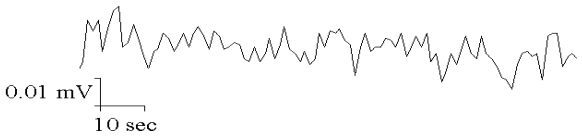
Figure 1

Panel A: LGC, Darkness

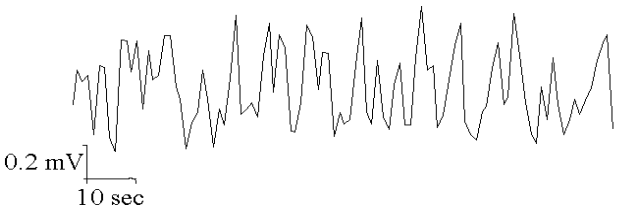


Panel B: LGC, Photostimulation

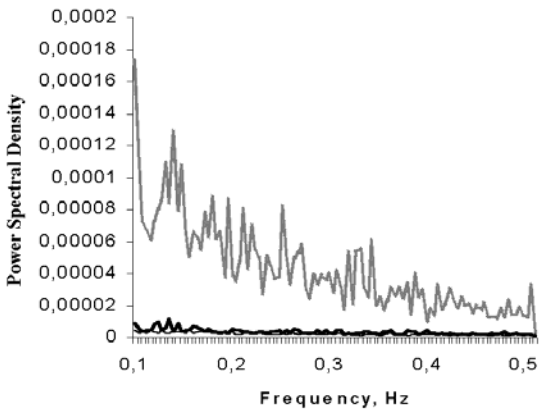
Panel C: PVC, Darkness



Panel D: PVC, Photostimulation



Panel E: LGC, Spectral Analysis



Panel F: PVC, Spectral Analysis

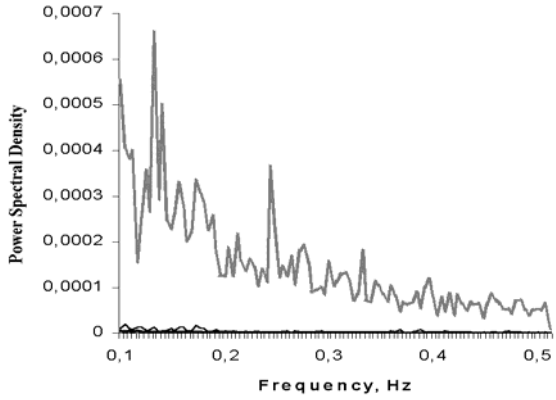


Fig. 1. Examples of typical very slow brain potential (VSBP) oscillation recordings in the frequency domain of seconds in lateral geniculate complex (LGC) in Panels A and B and primary visual cortex (PVC) in Panels C and D of the rat under conditions of darkness and photostimulation are shown. The power spectral analysis of VSBP oscillations in the domain of seconds under darkness (thin line), ambient illumination (thick line) and photostimulation (thin grey line) are shown in Panel E for LGC (averaged over n=30 graphs) and in Panel F for PVC (averaged over n=30 graphs).