BIOLOGIJA. 2004. Nr. 4. P. 19–25

Analysis of bursting activity in phasic and tonic components of dLGN relay cell responses

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The temporal structure of the cat's dLGN relay cell responses to a stationary circular spot of different diameter was investigated. Each response to a visual stimulus was divided into phasic and tonic parts and the temporal structure was analyzed in those components of response independently. We were interested in bursts – clusters of high frequency action potentials, defined by the distribution of interspike intervals. Interspike interval distribution in the phasic part of response was less variable than in the tonic part. Moreover, there was a much stronger dependence of variability on the firing rate in the tonic part of response, showing that the higher frequency (and therefore more clustered response) reduces this variability, whereas there was no such effect in the phasic part of response. According to our "critical interval" criteria, there were more within-burst spikes in the response, and the frequency of bursts was higher in the phasic than in the tonic part of response (median 61.6% and 21.3 bursts/s *vs.* 52.9% and 8.4 bursts/s). The number of within-burst spikes and the burst frequency highly depended on the firing rate showing a higher number of bursts at higher frequencies instead of burst elongation. More than 70% of bursts were short (composed of 2 or 3 spikes) in both parts of response, although bursts in the tonic part were somewhat shorter than in the phasic. There was no clear within-burst interval dependence on burst length or interval number within a burst.

Key words: LGN, burst, phasic response, tonic response

INTRODUCTION

Neurons in the cortex and subcortical structures fire bursts, which are intrinsically generated stereotypical patterns of closely spaced action potentials. The generation of bursts might arise simply from a large transient input. But in many cases, however, it is clear that bursts are generated by the interaction of synaptic input with intrinsic conductance of the cell. These intrinsic mechanisms create a slow depolarizing wave that triggers multiple axonal spikes [1–3].

Bursts in the visual cortex were first described by Hubel [4], who remarked on the irregularity of single unit spike train. However, burst generation mechanisms have not been established so far. Meanwhile a lot is known about the nature and functional significance of LGN relay cell low-threshold (LT) bursts [reviewed in 3]. Studies in cats, monkeys and humans indicate that bursting appears rhythmically during slow wave sleep or pathological conditions or arrhythmically during alert wakefulness when they may provide an important form of information transfer to the cortex, which is less linear than tonic firing, but provides a better signal detectability [reviewed in 3].

Another level of temporal structure is a sequence of several clearly separable response components elicited by a simple visual stimulus, like a spot of light flashed on and off inside the receptive field. In the case of the most frequent in dLGN "non-lagged" cell type, the onset of a spot-flash first initiates a phasic – high-frequency transient response, which then declines to a more or less constant firing level during the following tonic – sustained response, which continues as long as the stimulus is on [reviewed in 5]. So far, little is known about the significance of the different components of the visual response for the higher level visual processing. It has been suggested that the transient response has an arousing function, elevating the general attention in the visual system; meanwhile sustained response carries information important for an attentive and more detailed evaluation of the visual scene [reviewed in 5]. The tonic part of the response has been found to exhibit a stimulus-dependent temporal waveform and is composed of distinct spi-

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ke interval patterns [reviewed in 5], meanwhile the temporal structure of phasic response has not been investigated. The phasic part of LGN relay cell response traditionally is associated with the burst of spikes, which in turn is caused by LT Ca^{2+} spike. But phasic discharge is evident in responses of retinal ganglion cells [6] which, as generally accepted, do not exhibit Ca^{2+} spikes. Therefore the questions can be raised: what temporal structure characterizes different parts of response and what are the differences in the temporal pattern of two functionally different – phasic and tonic – parts of neuronal response? In order to answer these questions we analysed responses of dLGN relay cells with respect to bursting activity.

MATERIALS AND METHODS

Methods in detail have been described elsewhere [6, 7]. Adult cats (2.0–3.5 kg) were prepared (arterial and venous cannulation, tracheotomy, bilateral cervical sympathectomy, and craniotomies) under anaesthesia. Anaesthesia was induced by xylazine (1 mg/kg i.m.) and ketamine hydrochloride (10 mg/kg i.m.), and maintained during surgery by halotane (0.5–1.5%) in N_2O/O_2 (75/25–70/30). After surgery the animal was immobilized (gallamine triethiodide, initial dose 40 mg, maintenance dose 10 mg/kg/h), and anaesthesia was maintained throughout the experiment by halothane (0.2–1.2%) in N_2O/O_2 (75/25–70/30). We monitored continuously arterial blood pressure, heart rate, electroencephalogram (EEG), end tidal CO_2 (4%), and rectal temperature (38 °C). At the end of the experiment the animal was deeply anesthetized with pentobarbitone sodium (50 mg/kg i.v.).

Responses from single units in the A-laminae of dLGN were recorded extracellularly with glass-insulated tungsten electrodes (exposed tip 6–8 μm), or with glass pipettes filled with 0.9% NaCl (15–25 MΩ *in vivo*).

After isolation of a single cell, its receptive-field center was plotted by means of hand-held stationary light and dark spots, as well as grating stimuli. The cells were classified as X or Y, and lagged or nonlagged as described previously [7]. Only responses of nonlagged cells were analysed in this study.

For each cell, we recorded the response to a series of stationary light or dark circular spots (for ON- and OFF-center cells respectively) that varied stepwise in diameter. The spot sizes varied from spot that covered only a small part of the receptive-field center to spots that exceeded the receptive field. The stimuli were presented on a computer-controlled video-monitor. Responses to spots with diameters larger than the periphery of RF were excluded from analysis. Diameters of selected stimuli ranged from 0.1 deg to 12 deg.

The contrast and background luminance was fixed for each series of spot sizes. The contrast and background luminance was selected so as to ensure a clear response to the spots and the maximum response to be well below response saturation for the cell [6].

Using peri-stimulus-time histograms (PSTH), a 500 ms long response to stimulus presentation was divided into different components: spontaneous activity, phasic (high-frequency transient response) and tonic (sustained response) parts (Fig. 1). Only phasic and tonic parts of response, which we also call “discharges”, were investigated in this study.

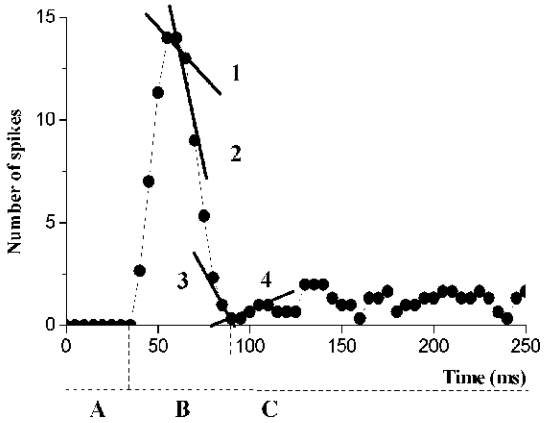

Fig. 1. Separation of different response components. PSTH (bin 5 ms) was calculated from all cell responses to a spot of particular diameter. The curve obtained was smoothed (moving average method, smoothing interval 3 PSTH bins) because of response variability. The slope of sliding linear regression was used for response separation. The first line was fit to the three points starting at the maximum response (line 1). The second line was fit to three points starting at the point next to maximum response (line 2), and so on. Calculations were repeated till the slope changed to a zero or an opposite value. Regression equations of two lines were used for finding the intersection point – the ending (beginning) of the response component. Two lines were taken for this calculation: the first when the slope changed to zero or an opposite value (line 4), and the second before the change of slope sign (line 3). Spontaneous activity (A) was separated from the phasic part (B) while declining the left slope, and the phasic part was separated from the tonic part (C) while declining the right slope

The interspike interval histogram (ISIH) was calculated for responses of a particular cell to each stimulus and was defined based on this “critical interval” (Fig. 2). Like other authors who explored ISIHs or used a particular interspike interval for burst identification [8–13], we think that the characteristic bimodal shape of ISIH reflects the intervals occurring within and between bursts (see Fig. 2

and Discussion). Therefore the critical interval criterion was used to classify response events to bursts, within-burst spikes and isolated spikes. If the interspike interval was smaller or equal to the "critical", spikes were referred to within-burst spikes. If the interspike interval was longer, spikes were referred to isolated spikes. Two or more consecutive within-burst spikes were called a burst.

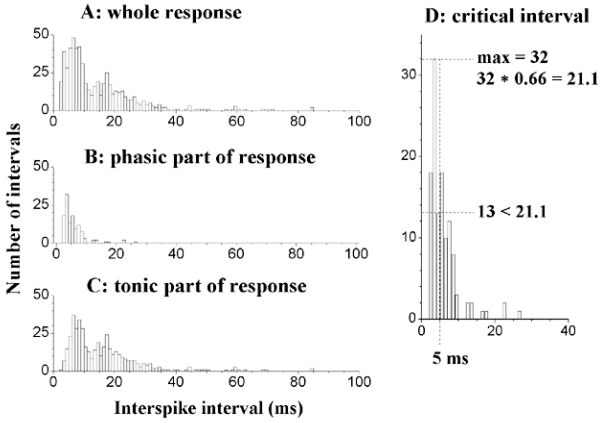

Fig. 2. Interspike interval histograms (ISIH) built from responses of Y on relay cell to spot size 0.9 deg. Note the bimodal distribution of whole response ISIH showing peaks at 7 ms and 18 ms (A). Similar ISI (peaks at 7 ms and 18 ms) persist during tonic discharge (C), except shortest intervals which predominate during phasic discharge, showing a peak at 4 ms (B). Calculation of the "critical interval" (D). The same ISIH as in (B) is shown here on a larger scale. The ISIH peak value (32) was multiplied by 0.66, and a value smaller or equal to the product (21.1) was looked for. The abscissa value shows the "critical interval" (5 ms in this case).

Since the assumption of a normal distribution was not satisfied (χ^2 test $p < 0.05$), comparisons between groups were performed by the nonparametric Wilcoxon matched pairs test. The Spearman correlation coefficient was calculated, median values and percentiles (25–75%) were reported for the same reason.

RESULTS

Temporal characteristics of 42 dLGN relay cell responses to stationary circular spots of different diameters were investigated. We do not present X and Y cells as separate groups, because we found no significant differences in the temporal structure of X or Y cells.

The phasic part of response lasted on average 53.0 ms (43.1–63.3 ms). No correlation was found between the duration of phasic discharge and the phasic response firing rate (Spearman r = –0.17), indicating that the time window of phasic discharge is constant for a particular cell at different firing frequencies when the degree of receptive field excitation varies because of a different diameter of the stimulus.

The frequency of phasic discharge was 2.6 times higher than that of tonic when the firing rate was calculated from responses to spots of different diameter (median 92.5 spikes/s (63.1–127.8 spikes/s) and 34.9 spikes/s (15.5–54.1 spikes/s), respectively; $p < 0.01$, Wilcoxon matched pairs test).

Inter-spike interval distribution

Phasic and tonic discharges are very different in their firing frequency, therefore ISIHs were built not for the whole period of stimulus presentation, but for time windows corresponding to phasic or tonic discharges independently for a particular cell and particular spot size. Critical interval distributions showed that during the phasic part of response critical intervals lasted on the average 5 ms (4–8 ms), during the tonic part 15 ms (12–20 ms), and the differences were significant ($p < 0.01$ Wilcoxon matched pairs test) (Fig. 3). According to Cattaneo et al., [9] the value of the most probable interspike interval in the discharge of all cortical complex cells is constant and independent of stimulus parameters in a given cell and varies only slightly from cell to cell, between 2 and 4 ms; also, Ruksenas et al. [12] showed the prevalence of intervals with the duration of 2–6 ms in responses of Clare–Bishop area neurons.

Figure 3 shows a weak inverse correlation between the critical interval and the firing rate in corresponding parts of response evoked by stimuli of different diameters (during phasic discharge Spearman r = –0.38, during tonic discharge Spearman r = –0.49). A significant though not strong correla-

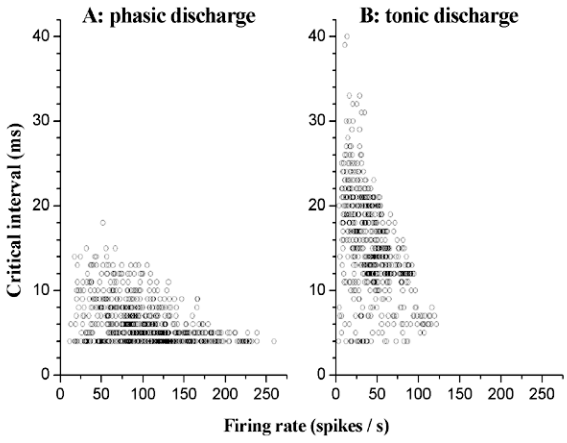

Fig. 3. Relation between firing rate and length of critical interval during phasic (A, n = 644) and tonic (B, n = 561) discharge. Here, as well as in other scatter plots, each data point was based on calculations for responses to a particular spot size from a particular cell. There was a weak to moderate inverse correlation between the length of critical interval and firing rate in both parts of response (Spearman r = –0.38 during phasic discharge and Spearman r = –0.49 during tonic discharge)

tion indicates the predominance of shorter interspike intervals during a higher firing frequency.

The duration of interspike intervals is much more variable during tonic than during phasic discharge (Figs. 2 and 3). For a more objective estimation, interspike interval variability was quantified by the coefficient of variation (*Cv* = SD/mean), showing a relative variation. The variability during phasic discharge (median *Cv* 0.6 (0.5–0.7)) is smaller than during tonic discharge (median *Cv* 0.7 (0.6–0.8)) and this difference is statistically significant ($p < 0.01$ Wilcoxon matched pairs test). Values of $Cv \leq 1$ indicate a less variability than it would be if the length of interspike intervals should be determined by a Poisson process [14]. Figure 4 shows firing during the phasic part being quite regular and constant at different firing frequencies (Spearman r = –0.07), whereas firing during the tonic part was found to be much more irregular, especially at lower firing frequencies (Spearman r = –0.53).

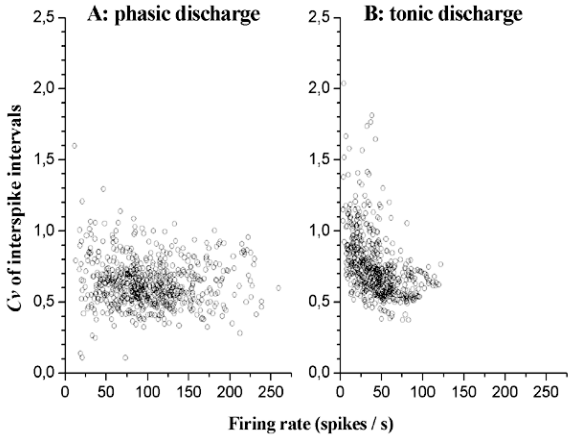

Fig. 4. Relation between firing rate and C*v* of interspike intervals during phasic (A, n = 644) and tonic (B, n = 561) discharge. There was no significant correlation during phasic discharge (Spearman r = –0.07), meanwhile there was a moderate inverse correlation between *Cv* and firing rate during tonic discharge (Spearman r = –0.53).

Structure of bursts

All response spikes were divided into within-burst spikes and isolated ones based on critical interval only. Analysis of distribution of response's spikes showed that there were 1.5 times more within-burst spikes than isolated ones in the phasic (median 61.6% (43.9–79.1%) and 38.4% (20.9–56.1%); $p < 0.01$ Wilcoxon matched pairs test) and 1.2 times in the tonic part of response (52.9% (36.4–72.4%) and 47.1% (27.6–63.6%); $p < 0.01$, in both cases Wilcoxon matched pairs test). These values show that within-burst spikes compose a larger part of phasic than of tonic discharge ($p < 0.01$ Wilcoxon matched pairs test).

Figure 5 shows a strong correlation between the number of within-burst spikes and the firing rate in the phasic as well as in tonic part of response to different spot sizes (Spearman r = 0.76 in both cases). A positive correlation between the number of within-burst spikes and firing frequency predicts two ways in bursting activity at higher frequencies: bursts become longer (in number of spikes) or burst length does not change, but the number of bursts increases. The latter possibility is most likely, because a very strong correlation was found between the frequency of bursts and firing rate in both parts of response (Spearman r = 0.93 in phasic and Spearman r = 0.96 in tonic (Fig. 6)). The frequency of bursts was 2.5 times higher in the phasic (median 21.3 bursts/s (13.8–30.6 bursts/s)) than in the tonic part of response (8.4 bursts/s (4.3–13.9 bursts/s)) ($p < 0.01$ Wilcoxon matched pairs test).

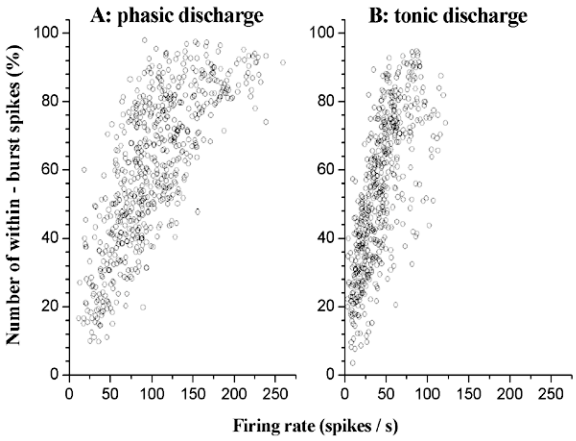

Fig. 5. Relation between firing rate and number of within-burst spikes during phasic (A, n = 644) and tonic (B, n = 561) discharge. There was an equally strong correlation between the number of within-burst spikes and firing rate in the phasic and in tonic parts of response (Spearman r = 0.76 in both cases).

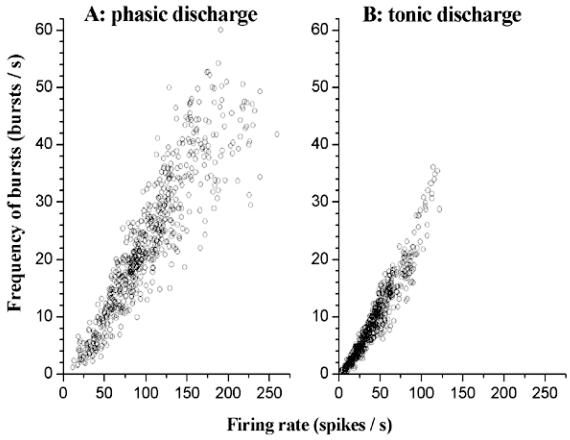

Fig. 6. Relation between firing rate and frequency of bursts during phasic (A, n = 644) and tonic (B, n = 561) discharge. There was a very strong correlation between frequency of bursts and firing rate in phasic (Spearman r = 0.93) and tonic (Spearman r = 0.96) parts of response.

Most of bursts were short – about 74% of bursts in the phasic and about 81% in the tonic part of response were composed of 2 or 3 spikes. Clusters of the same length consisting of 2–3 impulses are typical of the response in the primary visual cortex [8, 9] and Clare–Bishop area neurons [12]. The number of shortest bursts can be underestimated in our results, because two or three short bursts with very short within-cluster intervals could be integrated occasionally because of a longer critical interval. The number of bursts consisting of more than 7 spikes shows this probability because it was found out of the proportion to shorter bursts (Fig. 7).

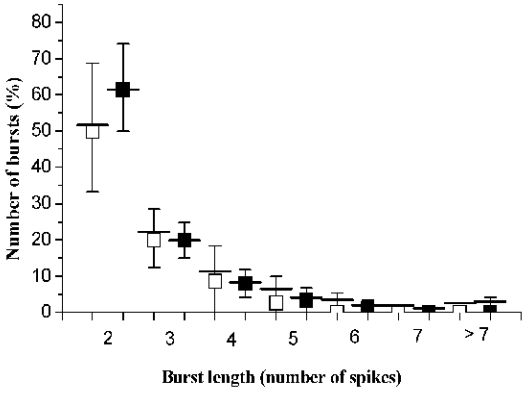

Fig. 7. Distribution of bursts of certain length during phasic (open squares) and tonic (filled squares) discharges. During tonic discharge there were more shortest (composed of 2 spikes) and longest (composed of more than 7 spikes) bursts than during phasic, whereas during phasic part there were more bursts of intermediate length (composed of 4, 5, 6, and 7 spikes) than during tonic discharge (Wilcoxon matched pairs tests are significant at $p < 0.01$, except for those of >7 spikes $p = 0.02$). Plot details: squares = median; horizontal line = mean; whiskers range = 25–75%

On average three spikes compose a burst in the phasic (median 2.8 spikes (2.4–3.4 spikes)) as well as in the tonic (2.7 spikes (2.4–3.2 spikes)) part of response. Results of the Wilcoxon matched pairs test show that bursts during phasic discharge are longer than during tonic ($p < 0.01$). This is more obvious from Fig. 8 showing that there are more longer bursts in the phasic part of response. A moderate correlation was found between burst length and firing rate in the phasic part of response (Spearman $r = 0.50$), while in the tonic part of response this correlation was weak (Spearman $r = 0.38$). However, scatter plots show a tendency of longer bursts appearance during higher frequency, and this is consistent with the finding that bursts during phasic discharge are longer than during tonic (Fig. 8).

The defining feature of bursts in cortically projecting thalamic neurons is a progressive increase in the duration of successive interspike intervals within a burst [15–17]. However, our data do not confirm this rule. All within-burst intervals ranged between 2 and 6 ms (median 3.5 ms (2.6–5.0 ms) in phasic and between 5 and 15 ms (median 9.8 ms (7.3–13.0 ms)) in tonic response without any clear regularity with respect to the burst length or interval position within the burst. Within-burst intervals for groups of spikes concerned as Ca^{2+} bursts were investigated separately, but the results were similar to those for bursts not complying with requirements for Ca^{2+} bursts.

DISCUSSION

Interspike interval disribution

Analysis of interspike intervals from visual cortical [10, 11], LGN relay cells [5, 16, our data], as well as the bursting neuron model [18] do not yield a uniform or Poisson distribution of the interval values. Most cells produce a bimodal distribution with a prominent peak at short intervals (contributing to within-burst intervals) and a lower, broader peak or plateau at longer intervals, showing that many of the spikes are gathered in bursts rather than having intervals distributed in a more continuous (Poisson-like) manner [10]. Distinctive peaks at shortest intervals during distinctive discharges of the same cell, as well as a clear bi- or multimodal interval distribution of tonic discharge (Fig. 2) indicate the presence of distinct burst generation mechanisms. As suggested by DeBusk et al., [10] interval peaks provide strong evidence for the existence of both intrinsic and network-mediated burst mechanisms in the striate cortex. The same could be referred to LGN relay cells too. Funke and Worgotter [revie-

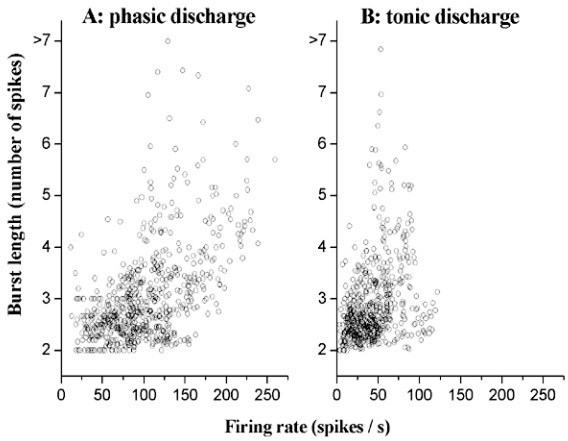

Fig. 8. Relation between firing rate and mean burst length during phasic (A, n = 644) and tonic (B, n = 561) discharge. There was a moderate correlation between burst length and firing rate during phasic discharge (Spearman $r = 0.50$) and this correlation was weak during tonic discharge (Spearman $r = 0.38$)

wed in 5] showed that the multi-modal distributions of the preferred spike intervals of LGN relay cells are obviously caused by a fundamental firing frequency (fundamental spike interval) of retinal origin, which generates multiple intervals and is not produced by a mixture of different, independent firing frequencies. This multi-modal pattern is generated by the interaction of excitatory retinal inputs with local inhibition in the LGN.

Our critical interval roughly can be compared to the 'fundamental interval' of Funke and Worgotter [reviewed in 5], which was the first interval band of the sustained activity. The same authors showed that the increase in the fundamental interval (decrease in fundamental firing frequency) is correlated with the decreasing mean firing rate during the tonic light response. Increasing the stimulus size does not affect (or affects very little) the fundamental interval duration, but results in a redistribution of the activity into the longer interval bands [reviewed in 5]. We also found a weak inverse correlation between the critical interval and the firing rates in corresponding parts of response. This signifies a prevalence of longer intervals at lower firing rates, although we noticed that the general pattern of the interval distribution (position of the peaks, number of interval bands) was relatively invariant at different firing frequencies for a particular cell.

Structure of bursts

Our results on the structure of bursting activity are similar to those from visual cortex. Snider et al. [13] reported that on average 60.5% of the spikes were contained in bursts (61.6% in the phasic and 52.9% in the tonic part of response in our case). A very strong correlation between the frequency of bursts and the firing rate (Spearman r > 0.9 in both parts of response, Fig. 6) is consistent with findings of DeBusk et al. [10] that burst frequency observed in visual cortex cells as well as in LGN fibers was essentially linear with firing rate and this relationship was constant for a given cell, regardless of the stimulus parameter that was varied to produce variation in average firing rate. According to authors, this behavior implies that the initiation of burst events is a straightforward reflection of the net excitation of the cell.

Burst length (on average 3 spikes) was found very similar to that of Reinagel et al. [17] found for LGN Ca^{2+} burst length. The mean number of spikes per burst was 3.0 ± 1.4 (X cells) or 2.7 ± 0.5 (Y cells) in their study.

We found phasic bursts to be somehow longer than tonic (Fig. 8). Geniculo-cortical projections involve some degree of convergence [19], and strong phasic discharges are needed from a number of presynaptic geniculate cells to drive the cortical cell. The longer bursts are much more likely to cause a spike in a postsynaptic cell than shorter bursts [13], therefore the prevalence of longer bursts in phasic response of LGN relay cells can be explained by the necessity to have the necessary number of spikes to evoke a response from the cortical network.

DeBusk et al. [10] reported a linear relationship between the firing rate and burst length (spikes per burst) observed in LGN fiber responses. This relationship was not so clear in our data, maybe because of prevalence of two- and three-spike bursts.

Low-threshold Ca^{2+} bursts

It is generally accepted that LGN bursts derive from low-threshold Ca^{2+} spikes which can be distinguished by empirical criteria developed from intracellular recordings by Lu et al. [20]. Criteria are based on a temporal pattern of action potentials thus permiting the use of extracellular recording to study LT spiking. They showed that when two or more action potentials separated by ≤4 ms are preceded by at least 100 ms of quiescence, the probability of an underlying low-threshold Ca conductance (I_T) is better than 0.99. These criteria correspond to what has been used in studies of bursting activity in anesthetized, paralyzed [17, 21], and awake, behaving cat [22, 23], monkey [24] and rabbit [25]. Therefore we also used these criteria for LT Ca^{2+} burst identification, except the silence period of ≥50 ms instead of ≥100 ms. Lu et al. [20] found that a silent period of ≥50 ms followed by brief interspike intervals was successfully identified an LT burst; other authors also noticed that the first action potential in a burst may occasionally occur after a silent period as short as 50 ms [23, 24]. While exploring our data using criteria of the preceding silent period of ≥50 ms and following an interspike interval of ≤4 ms, we managed to find Ca^{2+} bursts in the very beginning of phasic discharge only. ISIH built from relay cell responses evoked by visual stimulation were similar to those recorded from LGN by Funke and Worgotter [reviewed in 5], where almost all interspike intervals of LGN cells fell in the range of 2–50 ms, and from visual cortex [10] where there is no evidence for an extended silent period preceding cortical bursts.

All LT Ca^{2+} bursts we found during phasic discharge were the first events in this part of response. The number of responses with Ca^{2+} burst in the beginning of response varied from 0.1% to 70.6% in the neurons investigated, but only 7 (17%) neurons had 50% or more responses starting with Ca^{2+} burst. Ca^{2+} bursts during tonic discharge were very rare, with no preferable position in time (*i.e.* the first, intermediate or last event). Twelve (29%) neurons had no Ca^{2+} in their tonic discharges at all. The probability of tonic discharge with presence of Ca^{2+} burst varied from 0.3% to 8.1% in the rest of neurons. The variability in

bursting among LGN neurons during sleep and wakefulness [23] indicates that either LGN neurons vary in the degree to which the I_T channel is expressed, and/or there are significant differences in intrinsic circuitry. Calcium imaging and whole cell *in vitro* studies suggest that the I_T channel and its kinetics are homogeneous among relay cells [26, 27]. Qualitative and quantitative differences exist among relay cell afferents. Beside obvious differences in X, Y, or W retinal afferents, there is evidence suggesting that intrinsic, brainstem, and corticothalamic afferents vary in their density and distribution [reviewed in 3]**.** These differences in circuits offer an obvious avenue for heterogeneity.

ACKNOWLEDGEMENTS

Authors are indebted to Prof. Paul Heggelund for his support and advice enabling appearance of this paper.

Received 13 September 2004
Accepted 12 November 2004

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ÐONINIO KELINIO KÛNO PERDAVIMO LÀSTELIØ FAZINËS IR TONINËS ATSAKO DALIØ PLIÛPSNINIS AKTYVUMAS

Santrauka

Buvo tirta katës šoninio kelinio kûno perdavimo neuronø fazinës bei toninës atsako daliø laikinë struktûra. Ekstralàsteliniu bûdu buvo registruojamas perdavimo neuronø atsakas á kintamo skersmens ðviesias ar tamsias dëmeles. Tyrime naudoti 42 neuronø atsakai. Atsakas á fazinæ bei toninæ atsako dalis buvo skirstomas remiantis postimuline laiko histograma, o veikimo potencialai á pliûpsninius ir izoliuotus buvo skirstomi remiantis tarpimpulsiniø intervalø histograma.

Toninëje atsako dalyje tarpimpulsiniø intervalø kintamumas buvo didesnis nei fazinëje. Be to, toninëje atsako dalyje tarpimpulsiniø intervalø kintamumo priklausomybë nuo impulsacijos daþnio bei pliûpsniniø impulsø kiekio buvo didesnë nei fazinëje, o tai rodo, jog didesnis impulsacijos daþnis (uþtikrinantis labiau pliûpsniná atsakà) sumaþina ðá variabilumà.

Nustatyta, kad fazinëje atsako dalyje buvo daugiau pliûpsniniø impulsø ir pliûpsniø daþnis buvo didesnis nei toninëje atsako dalyje (mediana 61,6% ir 21,3 pliûpsniai/s *vs*. 52,9% ir 8,4 pliûpsniai/s). Rasta stipri teigiama pliûpsniniø impulsø kiekio, taip pat ir pliûpsniø daþnio priklausomybë nuo impulsacijos daþnio, rodanti, jog esant aukðtam impulsacijos daþniui daugëja pliûpsniø, o ne vyksta pliûpsnio ilgëjimas. Daugiau nei 70% pliûpsniø abejose atsako dalyse buvo trumpi (sudaryti ið 2 ar 3 impulsø), nors pastebëta, jog toninëje atsako dalyje pliûpsniai yra nedaug trumpesni nei fazinëje. Aiðkios vidupliûpsniniø intervalø ilgio priklausomybës nuo pliûpsnio ilgio ar intervalo vietos pliûpsnyje nerasta.