RESPONSE SELECTIVITY AND g-FREQUENCY FLUCTUATIONS OF THE MEMBRANE POTENTIAL IN VISUAL CORTICAL NEURONS

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ABSTRACT

With *in vivo* intracellular recordings we show that the rapid, γ-range fluctuations of the membrane potential occur during responses to visual stimuli in both simple and complex cells in cat visual cortex. The strength of these rapid fluctuations correlated with the stimulus optimality. Furthermore, the amplitude of the γ-fluctuations correlated with the phase of stimulus-imposed slow changes of the membrane potential. The combination of these features makes cortical neurons capable to encode the slow changes in the visual world in a kind of amplitude modulation of the high frequency fluctuations. This assures reliable transformation of the membrane potential changes into spike responses without compromising the temporal resolution of visual information encoding in the low frequency range.

MATERIALS AND METHODS

We did intracellular recordings from visual cortex cells in 9 adult cats. The details of surgery, maintenance of animals and recording techniques are described elsewhere (Volgushev et al., 2002). For visual stimulation we used moving gratings of different orientation, presented for 4-6 sec in a pseudorandom sequence. Power spectra were calculated using fast Fourier transformation of 4096 ms epochs of the membrane potential traces, starting with the beginning of grating movement.

RESULTS

We demonstrate, that (i) rapid, γ-range fluctuations of the membrane potential occur during responses to visual stimuli in both simple and complex cells; (ii) the strength of the γ-range fluctuations correlates with stimulus optimality and (iii) γ-frequency fluctuations of maximal amplitudes are phase-locked to the positive peaks of stimulus-induced, low frequency changes of the membrane potential.

To study the relationship between the stimulus optimality and the spectral composition of the membrane potential fluctuations we used two complementary approaches. First, we compared the power spectra of the membrane potential traces during the responses to stimuli of different orientations. In most of the 26 cells studied, fluctuations of the membrane potential in the γ-frequency range (25-70 Hz) were strongest during presentation of the optimal stimulus. For the whole sample, the γ-power of the membrane potential fluctuations were stronger than during presentation of stimuli of any other orientation ($p<0.001$, paired samples tests). Second, we found a strong and significant correlation between the γ-power of the membrane potential fluctuations and spiking during responses to stimuli of different orientations in the majority of cells (23 out of 26). In 21 of these cells the correlation coefficient was higher than 0.75 ($p<0.001$). Taken together, these data demonstrate that changing the stimulus orientation led to parallel changes of the spike responses and the membrane potential fluctuations in the γ-range: stronger spike responses were associated with a stronger γ-power.

Next, we assessed the possible difference in the strength of the γ-range membrane potential fluctuations between complex and simple cells. Cells were classified as simple of complex according to the spike response modulation index, which is defined as the half of the peak-to-peak modulation divided by the mean increase of the spiking frequency (Dean & Tolhurst, 1983; Skottun et al., 1991). The modulation index is higher than 1 in simple cells, but is less than 1 in cells with complex receptive fields. The strength of the γ-range fluctuations of the membrane potential was positively correlated with the spike response modulation index, indicating that simple cells had stronger γ-range fluctuations of the membrane potential.

Finally, we studied a phase relation between the low frequency changes of the membrane potential and the strength (amplitude) of γ-range fluctuations, extracting the response components of certain frequency band from the responses to visual stimuli. The γ-range fluctuations of the membrane potential occurred predominantly on the depolarizing peaks of the low frequency membrane potential modulation. Several approaches, which we used to quantify this relation, showed its significance and reliability in both simple and complex cells.

DISCUSSION

Contrary to previous studies, in which γ-range oscillations of the membrane potential were found predominantly in complex cells in the visual cortex (Jagadeesh et al., 1992; Anderson et al., 2000b), our quantitative analysis showed, that in the simple cells fluctuations in the γ-range are not only present, but are even stronger than in the neurons with complex receptive fields. Thus, γ-frequency fluctuations of the membrane potential is a general property of visual cortical cells, and the advantages of the γ-frequency fluctuations for generation of precise patterns of action potentials may be exploited in both simple and complex cortical neurons

Our analysis demonstrated that the strength of the γ-frequency fluctuations of the membrane potential correlates with stimulus optimality: stronger spike responses were associated with a stronger γ-power. Taken together with the earlier data which showed the inverse relation between the threshold of spike generation and the rate of the membrane potential rise (Azouz & Gray, 2000); the correlation between the gain at which membrane depolarization is translated into trains of action potentials and the γ-power of the membrane potential (Volgushev et al., 2002); as well as in vitro data (Mainen & Sejnowski, 1995; Nowak et al., 1997; Volgushev et al., 1998), these data support the notion that γ-range fluctuations of the membrane potential enhance the spike generation in cortical neurons, and thus contribute to improvement of the response selectivity.

A mechanism similar to stochastic resonance has been recently suggested to be exploited in the visual cortex to detect weak signals and to enhance contrast invariance of orientation specificity (Troyer et al., 1998; Anderson et al., 2000a). However, a potential drawback of the stochastic high frequency noise is that outside a narrow range of the relations between the spike generation threshold and the amplitudes of noise and signal, it disturbs encoding of the low frequency temporal structure of a stimulus (Ho & Destexhe, 2000). Our finding, that γ-range fluctuations of maximal amplitudes are phase-locked to the positive peaks of stimulus-induced, low frequency changes of the membrane potential show that visual cortex neurons may use a kind of amplitude modulation of the high frequency component to encode the temporal structure of the response in the low frequency range. The use of the amplitude-modulation encoding may expand the borders of applicability of stochastic resonance to the function of nerve cells.

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