Temporal properties of pattern adaptation of relay cells in the lateral geniculate nucleus of cats

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Abstract **The temporal properties of pattern adaptation of relay cells induced by repeated sinusoidal drifting grating were investigated in the dorsal lateral geniculate nucleus (dLGN) of cats. The results showed that the response amplitude declined and the response latency prolonged when relay cells were pattern-adapted in dLGN, like the similar findings in visual cortex. However, in contrast to the result in cortex, the response phase of relay cells advanced. This implies that an inhibition with relatively long latency may participate in the pattern adaptation of dLGN cells and the adaptation in dLGN may be via a mechanism different from that of visual cortex.**

Keywords: pattern adaptation, temporal properties, latency, phase, lateral geniculate nucleus, cat.

In visual system, the response discharge rate of cells reduced gradually with repeated visual pattern stimuli is called pattern adaptation. Pattern adaptation is one of the most important properties in visual pathway. Since Maffei's original work in 1973[1], the adaptation in visual cortex has been widely studied[2—6]. However, almost all studies suggested that pattern adaptation only occurred at cortical cortex level. Recently, several lines of evidence have demonstrated that the dorsal lateral geniculate nucleus (dLGN) cells exhibit some degree of pattern adaptation[7—10].

Despite numerous investigations of adaptation, the mechanism underlying the pattern adaptation is still unclear. Many hypotheses were proposed, such as the transmission exhausting[11], inhibition with long latency[4], excitatory connection network[5] and the alteration of the cell properties[3,8,9]. However, none of them could completely explain physiological results so far. Almost all researches done at pattern adaptation only focussed on the responses decrease in the cell's adapted state[12], and the aftereffects on response properties of cells[2,8]. Temporal properties of pattern adaptation have been ignored except by Saul's work[6]. Saul reported that response timing of cat visual cortex cells was retarded by adaptation. We recorded the PSTH of the same dLGN cell to stimulus before and during grating adaptation to study the effect of adaptation on response timing. Comparing with the cortical results, we tried to give some clues to the understanding of the mechanism for the pattern adaptation.

1 Materials and methods

Fifteen healthy adult cats (weighing 2.3—4.0 kg) were studied in the experiment. The physiological preparation, recording receptive field mapping, visual stimulation and data collection were the same as those described in the previous study[7]. The basic properties of relay cells (such as cell-types, orientation selectivity and spatial frequency) were routinely measured using flashing spots and grating stimuli. The repeated drifting prolonged sinusoidal gratings (as long as 50 s) were used to adapt the relay cells. The orientation and spatial-temporal frequency used were optimal, and the contrast value was always kept at 0.6. Trials were repeated (3—6 times) to reduce the random error of data. The interval between trials was longer than 5 min for the cells to recover.

The data of the adapted and control responses were collected and analyzed on-line or off-line. The response amplitude was defined as the fundamental Fourier component of peristimulus-time histograms (PSTHs). We recorded the responses of cells to 150 periods of drifting sinusoidal gratings (temporal frequency was 3 Hz). The average amplitude of initial 5 periods was defined as the peak value and the average amplitude of last 100 periods as the plateau value. The intensity of adaptation was defined as the ratio of plateau to peak values. In this study, only the cells whose ratio was less than 0.8 were studied. The phase of responses was defined as the phase of the fundamental Fourier components of PSTHs, and the latency was defined as the time from the onset of a stimulus to the cross point between the initial regression line of raising phase and the base line.

2 Results

About 40% (62 out of 156) of relay cells recorded showed significant pattern adaptation (t-test, $P<0.05$). We studied the 33 well-adapted cells whose ratio was less than 0.8.

(ⅰ) Effect of pattern adaptation on response latency of dLGN cells. Long-time grating stimuli not only reduced the cell's response amplitude, but also made the latency longer. Fig. 1(a) shows the histogram of the difference between the adapted latency and the control one. 18 (54%) cells' latency prolonged significantly during adaptation. The mean latency prolongation during adapta-

tion was 5.7 ms, which was statistically significantly different from zero (t-test, $P<0.02$). The result was similar to that in visual cortex, though the mean latency prolongation in cortical neurons was as long as 10.3 ms[6]. Fig. 1(b) shows the PSTH of a typical relay cell responded to the same drifting grating before and during pattern adaptation. For this cell the response amplitude reduced by about 20% with a latency prolongation of 25 ms, but the phase kept unchanged during pattern adaptation. In addition, about 20% of cells recorded presented this type of response like the cells shown in fig. 1(b).

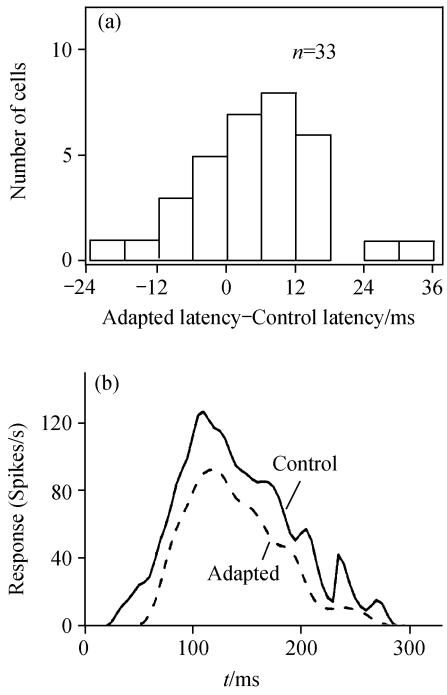

Fig. 1. Effect of pattern adaptation on response latency of dLGN cells. (a) Histogram of the difference between adapted and control latency. The average latency prolongation of the cells was 5.7±13.6 (SD) ms; (b) response curve of a typical cell to drifting grating before and during adaptation. The temporal frequency of grating was 3 Hz, and contrast was 0.6. The latency of cell prolonged 25 ms with the phase almost unchanged when adapting.

(ii) Effect of pattern adaptation on response phase and response duration of dLGN cells. The response latency is the primary measure to describe response timing. However, it only shows the time from stimuli onset to response onset, but does not provide the information about the time course of the response. The difference of first harmonic response phase between the adaptation and the control could be used as an index of the effect of adaptation on the total response of dLGN cells.

Interestingly, the response phase advanced when a cell adapted. The difference between the adapted phase and the control phase is shown in fig. 2(a). The difference in phase values ranged mainly from –22.5° to +16°. The mean phase difference is –10° (t-test, $P<0.01$). This phase advance was observed more significantly in these cells whose latency kept unchanged during adaptation like the cell shown in fig. 2(b). For this cell, the response phase advanced when adapted because the response decrease of the later part was more significant than that of the initial part.

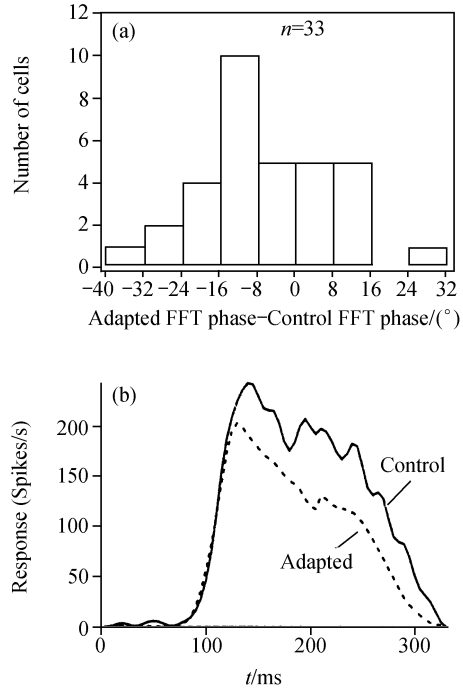

Fig. 2. Effect of pattern adaptation on response phase of dLGN cells. (a) Histogram of the phase difference between the adapted phase and the control one. The response phase of the cells advanced 10 ± 15° (SD) (t-test, $P<0.01$); (b) response curve of a typical cell to drifting grating before and during adaptation. The parameters of stimulus gratings were the same as those in fig. 1.

To describe the curve shape and time course of responses more specifically, the difference of the adapted and control response duration (i.e. the time between the ones corresponding to the response phase and latency) histogram was shown in fig. 3. Longer duration means that the cell responds to a grating stimulus longer. As shown in fig. 3, the duration shortened significantly during adaptation. The mean decrease value in duration was –17±20 ms, which is statistically significant (t-test, $P<0.001$).

3 Discussion

In this study, the temporal properties of pattern adaptation of relay cells were firstly studied in cat dLGN. The latency prolonged and the response phase advanced when the cell was adapted. The cells' response duration also decreased significantly. However, the extent of pat-

tern adaptation in dLGN is weaker than in the visual cortex. This may suggest that the mechanism of pattern adaptation in dLGN is partially different from that in visual cortex, and that the inhibition with relative long latency may play an important role in pattern adaptation of dLGN cells.

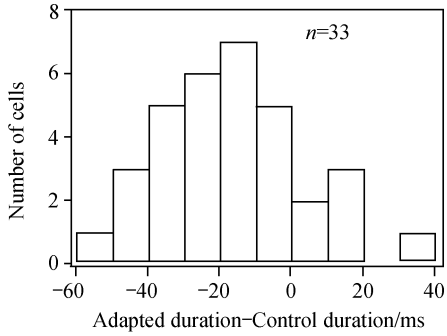

Fig. 3. Histogram of the difference in response duration between the adapted and the control conditions. The response duration was defined as the time between the ones corresponding to the response phase and latency. The mean value of duration difference was −17 ± 20 ms (SD, *t*-test, $P < 0.001$).

As shown in fig. 1, most but not all dLGN neurons prolonged the response latencies, like the similar result in visual cortex (for details, see fig. 11 in ref. [6]). There were about 30% (10 out of 33) dLGN neurons whose latencies shortened, just the same as cortical cells (29%). It may be caused by the variability of the neuron firing, or may imply that there are other mechanisms for adaptation, such as the pre-excitation of synaptic resulting from the accumulation of excitatory transmitter after long time stimuli.

Lots of hypotheses of the mechanism for the pattern adaptation have been suggested. Recently, some experiments suggested that the membrane hyperpolarization of cortical cell played a key role in adaptation and adaptation aftereffect[3,8]. The cell could not response easily to stimuli when the membrane hyperpolarized, so the response amplitude decreased and latency prolonged. Using intracellular recording we also found the membrane of some cells in dLGN hyperpolarized when adapting, though the degree was lower than that in visual cortex (Zhou et al. unpublished data). However, if the unselective inhibition caused the pattern adaptation, it would only prolong the latency, without any effect on the response phase. In fact, about 20% of cells we recorded presented this type of response as shown in fig. 1(b).

However, the above hypothesis could not explain the adaptation phenomena when using the current injection to mimic the membrane hyperpolarization in visual cortex[8]. Our results also suggested that the adaptation in most dLGN cells could not be explained by the hyperpolarization. The latency of the cell changed little, while the amplitude of later part of response decreased significantly (fig. 2(b)), suggesting that a long-latency inhibition may participate in the adaptation. It was the inhibition that advanced the response phase of most cells. The cortical studies demonstrated that adapting delayed the average response phase[6] though there existed some cells whose phase advanced when adapting. This implies that the adaptation mechanism in dLGN is, at least partially, different from that in visual cortex, and the inhibition with long-latency may play a more important role in dLGN than in visual cortex. This inhibition may come from feedback inhibitory pathway, or mediated by the $GABA_B$ receptor pathway in dLGN and thus, needs to be further studied using pharmacological methods.

Another possible explanation for the timing difference between dLGN cells and visual cortex cells is the difference in short-term synaptic plasticity between the two kinds of cells. The earlier short-term depression (STD) of synapses is more significant in visual cortex than in dLGN, while the later STD of synapses is more significant in dLGN cells[13].

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