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Contrast adaptation in cat lateral geniculate nucleus and influence of corticothalamic feedback

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Abstract

Contrast adaptation is a basic property of visual information processing. However, important questions about contrast adaptation in the lateral geniculate nucleus (LGN) remain. For example, it is unclear whether the different information channels have the same or distinct contrast adaptation properties and mechanisms. It has been recognized that the visual system is not a one-way ascending pathway, but also contains descending feedback projections. Although studies have explored the role of this feedback system, it is unclear whether corticothalamic feedback contributes to adaptation in the LGN. To investigate these questions, we studied contrast adaptation of LGN neurons in anesthetized and paralysed cats by measuring electrophysiological responses to visual test stimuli before and after adaptation induced by prolonged visual stimulation. After adaptation, contrast response functions were usually shifted towards higher contrasts, indicating decreased contrast gain, and the maximum response decreased. Also, contrast adaptation effects were stronger in Y-cells than in X-cells. Furthermore, adaptation effects were still observed in the LGN when the corticothalamic feedback was inactivated. Changes in the contrast gain of Y-cells were diminished in the absence of feedback, while contrast gain was largely unchanged in X-cells. Our observations confirm that contrast adaptation occurs in LGN neurons and furthermore demonstrate that Y-cells show stronger adaptation effects than X-cells. These results also provide an example of how corticothalamic feedback modulates contrast information processing distinctly in different information channels.

Introduction

Adaptation is a universal phenomenon in sensory systems, and has been analysed extensively in the visual (Maffei *et al.*, 1973; Movshon & Lennie, 1979; Bonds, 1991; Muller *et al.*, 1999; Dragoi *et al.*, 2000), auditory (Malone *et al.*, 2002) and somatosensory (Lee & Whitsel, 1992) systems. Adaptation plays an important role in visual information processing. Recent visual experience can affect subsequent neural responses and visual perception, and this represents a fundamental component of visual information processing. Information processing in the visual system is always dynamically regulated and context-dependent, so deeper insights into the mechanisms of adaptation are necessary for a full comprehension of visual perception. Furthermore, adaptation is a useful probe to study the neuronal plasticity that alters the processing of sensory information. Studies of adaptation are thus beneficial for understanding the functions of sensory plasticity, and for exploring how processing dynamics are adjusted under changing visual conditions (Kohn, 2007).

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The lateral geniculate nucleus (LGN) has traditionally been viewed as a passive 'machine-like' relay for retinal information to the cortex, and early studies indicated that adaptation does not occur in the LGN (Movshon & Lennie, 1979; Ohzawa *et al.*, 1982, 1985; Sclar *et al.*, 1989). More recent electrophysiological investigations have found that some LGN neurons exhibit the type of tonic hyperpolarization phenomenon that is thought to underlie the adaptation effect in primary visual cortex (Carandini & Ferster, 1997; Sanchez-Vives *et al.*, 2000a,b). In addition, a few studies have more directly demonstrated that visual adaptation can also occur at the level of the LGN (Shou *et al.*, 1996; Duong & Freeman, 2007). However, these studies do not focus on whether different types of LGN cells within different functional pathways exhibit the same adaptation effects, and whether cortical feedback contributes to adaptation in LGN.

In the cat LGN, there are two well-characterized types of thalamic relay cells, termed X- and Y-cells, which have different physiological properties and functions. Y-cells have larger receptive fields, show non-linear spatial summation (Hochstein & Shapley, 1976a,b) and have higher contrast sensitivity (Enroth-Cugell & Robson, 1966) than X-cells. Thus, it is possible that X- and Y-cells might have different contrast adaptation effects.

Relay cells of the LGN receive various projections from many areas besides the retina (Wilson, 1993; Sherman & Guillery, 1996; Sillito

et al., 2006). Although the retinal inputs to the LGN are the principal driving signals, corticothalamic feedback exerts subtle influences on spatial and temporal tuning (Marrocco *et al.*, 1982; McClurkin & Marrocco, 1984; Murphy & Sillito, 1987), synchronization of LGN firing (Sillito *et al.*, 1994, 2006) and efficiency of transmission to striate cortex (McClurkin *et al.*, 1994). Corticothalamic feedback might thus contribute to the contrast adaptation of LGN neurons.

Here we compared pre- and post-adapted contrast response functions to measure the effect of contrast adaptation on responsiveness of LGN neurons to sinusoidal gratings of varying contrast. Possible differences in adaptation effects between X- and Y-cells were examined electrophysiologically. Moreover, we explored the effect of corticothalamic feedback on contrast adaptation in the LGN.

Methods

Electrophysiology in adult cats in vivo

All experiments were performed on nine healthy adult cats (six male, three female). Animals were examined with an ophthalmoscope to confirm that they had no optical or retinal problems. The experiments were carried out in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals, and were approved by the Institutional Animal Care and Use Committee of the University of Science and Technology of China.

The preparation of cats and methods for extracellular single-unit recording were as described by Shou *et al.* (1996). Briefly, cats were anesthetized with ketamine HCl (20 mg/kg, i.m.; Ben Venue Lab Inc., Bedford, OH, USA). All pressure points and incision sites were treated with lidocaine HCl (1%; Abbott Labs, Chicago, IL, USA). After intravenous and tracheal cannulae were inserted, the cat was placed in a stereotaxic apparatus. Pupils were dilated with atropine (1%, Kangqi Pharm. Co., Wuhu, China) and appropriate contact lenses were used to protect the corneas. During the experiment, a mixture of urethane (20 mg/kg per hour; SCR, Shanghai, China) and gallamine triethiodide (10 mg/kg per hour; Sigma, St Louis, MO, USA) was infused intravenously to maintain anesthesia and paralysis. End-expiratory CO_2 was maintained at approximately 4%, and body temperature was maintained at 38 °C. Heart rate (about 180–220 beats/min) and electroencephalogram were monitored to assess the level of anesthesia. A hole of 4 mm radius was drilled in the skull at Horsley-Clark A6/L9 for LGN access, and the dura was removed. To record action potentials, a glass-coated tungsten microelectrode (3–5 MΩ) was advanced using a hydraulic micromanipulator (Narishige, Tokyo, Japan). Once the electrode was in position, the hole was filled with a 4% solution of agar in saline and sealed with wax.

To study whether cortical feedback affects contrast adaptation in the LGN, areas 17 and 18 of four cats were irreversibly inactivated with liquid nitrogen. Briefly, a craniotomy was performed to expose the visual cortex. A Q-tip was immersed in liquid nitrogen and then touched to the cortical surface four or five times in 1 min (Shou *et al.*, 1996). The inactivated region covered at least the central 15° of visual space according to retinotopic maps (Tusa *et al.*, 1978, 1979). We only recorded neurons in LGN at eccentricities of up to 10° so all relevant corticothalamic (feedback) inputs were inactivated. To verify the effectiveness of the physical lesion, recording was performed in layer 6 to confirm that cortical neuron activities had been abolished.

Visual stimulation

The visual stimulus patterns were drifting sinusoidal gratings displayed on a CRT monitor (1024 × 768, 85 Hz, Philips 107P, Suzhou, China) that was placed 57 cm from the cat's eyes. The CRT's luminance non-linearities were corrected by an inverse-gamma function applied with the software. The mean luminance of the monitor was about 60 cd/m^2, and the environmental luminance on the cornea was near 0.1 lux. The program used to generate the stimulus was coded in MATLAB (Mathworks, Natick, MA, USA) using the extensions provided by the high-level Psychophysics Toolbox (Brainard, 1997) and low-level Video Toolbox (Pelli, 1997). Here, contrast was defined as the Michelson contrast:

$$\text{Michelson contrast} = (L_{\max} - L_{\min})/(L_{\max} + L_{\min})$$

where $L_{\max}$ and $L_{\min}$ are the maximum and minimum luminance of a sinusoidal grating, respectively.

When an individual neuron was isolated, its receptive field was mapped by consecutively presenting light spots of varying diameter to determine the optimal size. For each cell, the optimal spatial frequency and orientation were measured, with the temporal frequency fixed at 4 Hz. The pre-adapted trial consisted of a single randomized sequence of 1-s test stimuli of varying contrast (from 0.02 to 1.0 in equal logarithmic steps), each preceded by a 5-s mean luminance stimulus. Then a 40-s adaptation stimulus was displayed. Finally, the post-adapted test sequence was shown in which each grating was preceded by a 5-s 'top-up' of the adapting stimulus (Fig. 1A). Two adaptation protocols were used. The only difference between them was the contrast of the adapting stimuli. In one protocol, the contrast of adaptation stimuli was fixed at 0.99. In the other protocol, we first measured a contrast response function that was fit with a Naka-Rushton equation (see below for details), and then empirically set the adapting contrast as half of the C_{50} (Fig. 1B). We attempted to test each neuron with both adapting protocols, but some neurons were tested only with one protocol due to limited recording time.

Each 'test-adapt-test/top-up' trial sequence was followed by a recovery period of at least 10 min. Six to ten such trials were recorded. The pre-adaptation response of the next trial (after the 10-min delay) was actually a recovery response, so additional recovery response measurements were not necessary.

Data collection and analysis

After the response of an isolated cell was amplified with a microelectrode amplifier (Dagan, Minneapolis, MN, USA), signals were fed into a window discriminator and audio monitor (Winston Electronics, St Louis, MO, USA), digitized by a data acquisition board (National Instruments, Austin, TX, USA) controlled by IGOR software (WaveMetrics, Lake Oswego, OR, USA), and then saved for off-line analysis.

Based on the responses to drifting and contrast-reversing gratings, LGN neurons were classified as either X- or Y-cells (Hochstein & Shapley, 1976b). Some of the cells that were recorded in C-layers had lower spatiotemporal frequency preferences, which suggested these neurons might be W-cells (Sur & Sherman, 1982) – these cells were excluded from further analyses.

To obtain contrast response curves, post-stimulus time histograms (PSTHs) of the grating responses (bin width 10 ms) were first constructed. For X-cells, the fundamental Fourier components measured for each stimulus contrast were used to draw the contrast response curve. For Y-cells, mean responses were used. To characterize contrast response curves both before and after adaptation, data were fitted by the Naka-Rushton equation (Albrecht & Hamilton, 1982):

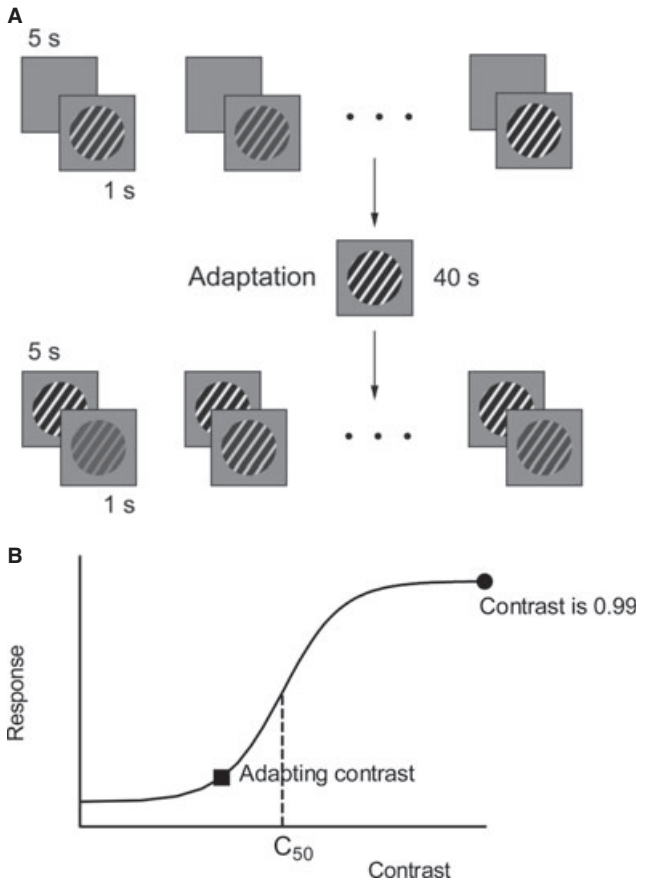

FIG. 1. Stimulation protocol for contrast adaptation experiments. (A) Responses to drifting gratings at nine contrasts (1 s for every presentation) recorded before and after adaptation. The adaptation stimulus is a drifting grating, presented for 40 s. To maintain the adaptation level, a 5-s 'top-up' drifting grating precedes every test stimulus after adaptation. Each trial is followed by a recovery period of at least 10 min to ensure that the adaptation effect disappears before the next trial begins. (B) We used two adaptation protocols. For one protocol, the adaptation stimulus contrast was set to 0.99. For the other protocol, the adapting contrast was always less than the pre-adapted C_{50}, as determined from a Naka-Rushton curve fit to a pre-adapted contrast response function (half of the C_{50}).

$$R = R_{\max}\frac{C^n}{C^n + C_{50}^n} + m$$

where R is the neuron's response to contrast C, $R_{\max}$ is the maximum attainable response and represents the response gain, C_{50} is the contrast evoking half maximal response and represents the contrast gain, and n and m are free parameters. In preliminary analyses, we found that n was little affected by adaptation, so in the curve-fitting, C_{50}, $R_{\max}$ and m were allowed to have different pre-adapted and post-adapted values, while n was assumed to be fixed under both conditions. For some LGN cells, the contrast response function did not reach saturation. In these situations, the upper and lower $R_{\max}$ bounds for the fit were set at ±10% of the maximum measured response above spontaneous (Crowder *et al.*, 2006).

To quantify the changes in C_{50} and $R_{\max}$, $C_{50\ \mathrm{shift}}$ and $R_{\max\ \mathrm{shift}}$ were used (Crowder *et al.*, 2006):

$$C_{50\,\mathrm{shift}} = \frac{C_{50\,\mathrm{post}} - C_{50\,\mathrm{pre}}}{C_{50\,\mathrm{post}} + C_{50\,\mathrm{pre}}}$$

$$R_{\max\,\mathrm{shift}} = \frac{R_{\max\,\mathrm{post}} - R_{\max\,\mathrm{pre}}}{R_{\max\,\mathrm{post}} + R_{\max\,\mathrm{pre}}}$$

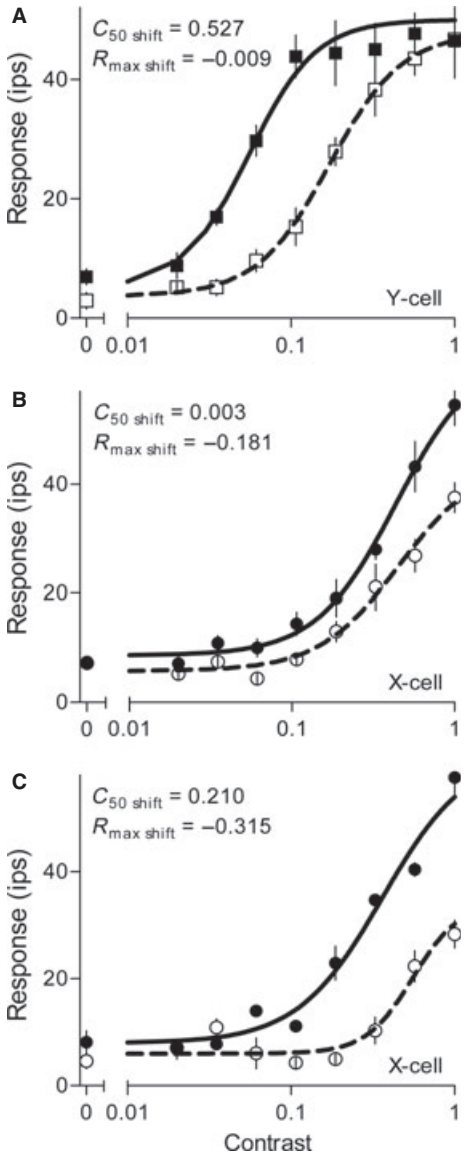

FIG. 2. Contrast adaptation in lateral geniculate nucleus (LGN) neurons. (A) The adaptation effect in a typical LGN cell. The post-adapted contrast response function (open symbols, dotted line) is shifted toward the right from the pre-adapted function (closed symbols, solid line). The primary effect of adaptation is to reduce the contrast gain. (B) Contrast adaptation in a second LGN cell, in which the maximum response substantially decreases, while the contrast gain exhibits only a minor change. (C) A representative cell in which adaptation causes a significant reduction in both contrast gain and response gain.

The $C_{50\ \mathrm{shift}}$ and $R_{\max\ \mathrm{shift}}$ can vary between −1 and 1 are zero when there is no adaptation (no changes in response after the adapting stimulus). A positive $C_{50\ \mathrm{shift}}$ means that adaptation causes a rightward shift in contrast gain, whereas a negative value indicates a leftward shift. A positive $R_{\max\ \mathrm{shift}}$ indicates that the maximum firing rate increases, whereas a negative value indicates that the maximum response decreases after adaptation.

To estimate the statistical significance of changes in C_{50} and $R_{\max}$ for individual LGN neurons, bootstrap analyses were used. For each LGN neuron, we re-sampled data from all pre-adapted trials to create 1000 bootstrap sample datasets. Every re-sampled dataset was fitted using the same method used in fitting the measured responses. Thus, we obtained 1000 estimates of pre-adaptation. In the same way, 1000

estimates of post-adaptation were constructed. We were then able to estimate the mean and variance of pre- and post-adapted response functions, and calculate the statistical significance. All data in the graphs and text are expressed as mean ± SEM. Statistical analyses were performed using SPSS 13.0 (Chicago, IL, USA).

Results

We recorded responses before and after adaptation from five normal cats and four cortex-inactivated cats.

Effect of contrast adaptation in LGN cells

Previous studies in visual cortex reported that the primary effect of contrast adaptation is a decrease in contrast gain, although the response gain is also reduced after adaptation (Ohzawa *et al.*, 1982, 1985). To explore the effect of adaptation in LGN neurons, we measured the responses of cat LGN neurons before and after adaptation. A sample response curve generated from a single neuron is shown in Fig. 2A. Before adaptation (closed symbols, with solid line to show curve-fit), the C_{50} of this neuron was 0.053 ± 0.002. After adaptation, the C_{50} increased to 0.171 ± 0.032 ($P < 0.001$, *t*-test). The R_{max}, however, was little changed after adaptation (from 45.01 ± 3.852 to 44.22 ± 1.822 impulses per second (ips), $P = 0.853$, *t*-test). In this neuron, adaptation caused the post-adapted contrast response function to significantly shift rightward from the pre-adapted response, indicating a reduction in contrast gain. A second sample is shown in Fig. 2B. In contrast to the cell shown in Fig. 2A, adaptation caused a strong reduction in R_{max} from 55.53 ± 4.454 to 38.50 ± 4.394 ips ($P = 0.007$, *t*-test), while the C_{50} shifted only slightly from 0.385 ± 0.047 to 0.387 ± 0.065 ($P = 0.980$, *t*-test). Figure 2C presents a response curve from a third representative cell in which contrast adaptation markedly decreased both the contrast gain (C_{50} shifted from 0.362 ± 0.061 to 0.555 ± 0.026, $P = 0.004$, *t*-test) and the response gain (R_{max} shifted from 54.414 ± 6.392 to 28.321 ± 0.692 ips, $P < 0.001$, *t*-test). According to bootstrap analyses for each neuron, 76.26% (151/198) of LGN neurons showed significant increases in C_{50} and 48.99% (97/198) of cells showed significant decreases in R_{max}.

To quantify the strength of these adaptation effects, we measured the population distribution of $C_{50\ shift}$ and $R_{max\ shift}$ (Fig. 3A and B). The mean value of $C_{50\ shift}$ was 0.170 ± 0.014 (different from 0, $P < 0.001$, $n = 198$, *t*-test), indicating that on average contrast adaptation caused a substantial reduction in contrast gain. Similarly, the mean value of $R_{max\ shift}$ was −0.030 ± 0.009 (different from 0, $P = 0.010$, *t*-test), indicating that the maximum firing rate was also reduced after adaptation, although the amplitude of $R_{max\ shift}$ was not as large as $C_{50\ shift}$. These results indicated that LGN neurons exhibit reliable contrast adaptation effects characterized mainly by reductions in contrast gain, similar to the adaptive response changes measured in visual cortex.

To explore whether cortical feedback contributes to contrast adaptation of cat LGN neurons, contrast response functions were obtained in four cortex-inactivated cats. Bootstrap analyses indicated that that 70.11% (122/174) of neurons exhibited a significant increase in C_{50} (decrease in contrast gain) while 50.00% (87/174) showed a significant decrease in R_{max}. These proportions were similar to those measured in LGN cells from normal cats (for C_{50}, $P = 0.181$; for R_{max}, $P = 0.846$, Pearson chi-square test). Figure 3C and D show the distributions of $C_{50\ shift}$ and $R_{max\ shift}$ of LGN neurons without

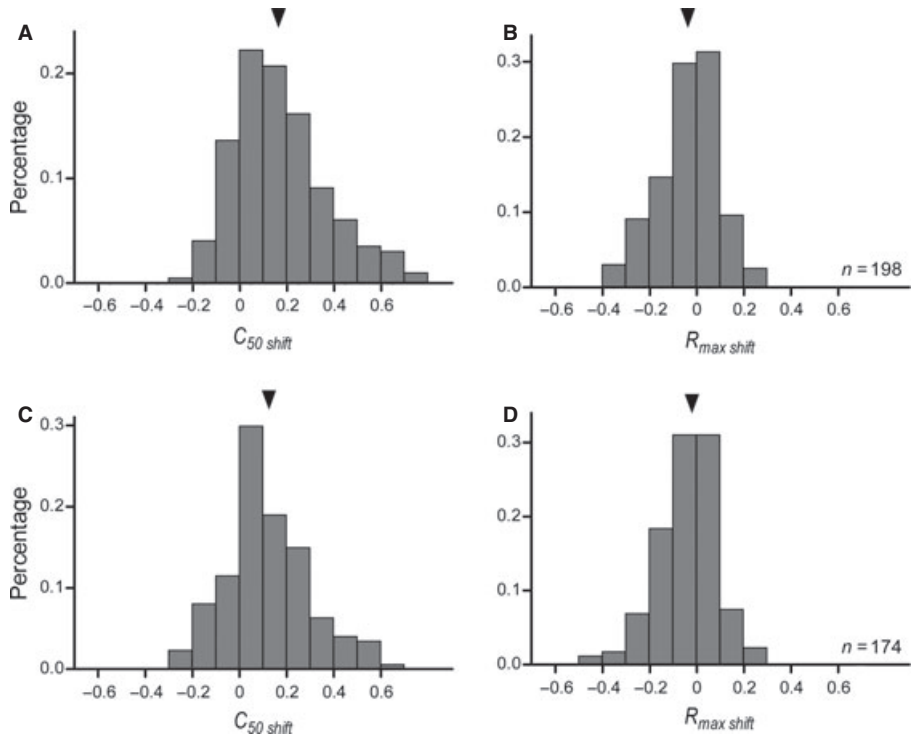

FIG. 3. Histograms showing the distribution of changes in parameters fitted to contrast response functions for a population of LGN neurons. In normal cats, contrast adaptation causes the contrast response function to shift rightward (A) ($C_{50\ shift}$ 0.170 ± 0.014, $P < 0.001$, *t*-test) and the maximum response to decrease (B) ($R_{max\ shift}$ −0.030 ± 0.009, $P < 0.010$, *t*-test). When cortical feedback is inactivated, adaptation still causes substantial changes (C and D) ($C_{50\ shift}$ 0.125 ± 0.014, $P = 0.002$; $R_{max\ shift}$ −0.035 ± 0.009, $P < 0.001$, *t*-test), but the amplitude of shift in C_{50} is less in cortex-inactivated cats ($P = 0.028$, *t*-test). Arrowheads indicate the means.

feedback. Across the population, the mean value of $C_{50\ shift}$ was 0.125 ± 0.014 (different from 0, $P = 0.002$, $n = 174$, t-test), which was less than the shifts observed in LGN neurons with intact feedback ($P = 0.028$, t-test). The mean value of $R_{max\ shift}$ was −0.035 ± 0.009 (different from 0, $P < 0.001$, t-test), which was similar to that found in normal cats ($P = 0.694$, t-test). These analyses indicate that LGN neurons without cortical feedback still exhibit contrast adaptation, but the magnitude of the shift in contrast gain was reduced.

The adaptation effects of ON and OFF center cells were also separately analysed. In normal cats, the $C_{50\ shift}$ appeared to be larger in ON cells (0.192 ± 0.020), although this effect did not reach statistical significance compared with OFF cells (0.140 ± 0.019, $P = 0.061$, t-test). No difference was found in the $R_{max\ shift}$ of ON and OFF cells (−0.023 ± 0.012 vs. −0.039 ± 0.131, $P = 0.353$, t-test). When cortical feedback was inhibited, adaptation still caused significant shifts in C_{50} of ON cells (0.146 ± 0.020) and OFF cells (0.098 ± 0.018), but $C_{50\ shift}$ was not significantly different between ON and OFF center cells ($P = 0.082$, t-test). These two types of cells also exhibited similar adaptive changes in $R_{max\ shift}$ (−0.029 ± 0.012 vs. −0.043 ± 0.144, $P = 0.479$, t-test).

Differences in adaptation effect between X- and Y-cells

Figure 4A and B show representative data from X- and Y-cells. In both cell types, an obvious decrease (rightward shift) in contrast gain was observed. The magnitude of the shift distinguished X- from Y-cells, however. Usually, the shifts of Y-cells were larger than those of X-cells, suggesting a greater decrease in contrast gain following adaptation.

We examined the results of bootstrap analyses of these data. Eighty per cent (68/85) of Y-cells and 73.45% (83/113) of X-cells showed significant increase in C_{50}, and no difference was found between the proportions of X- and Y-cells showing this adaptive effect ($P = 0.284$, Pearson chi-square test). Similarly, 45.88% (39/85) of Y-cells and 51.33% (58/113) of X-cells showed a significant decrease in R_{max} following adaptation and the proportions were similar ($P = 0.448$, Pearson chi-square test). Thus, both X- and Y-cells showed contrast adaptation effects and the percentages of cells that exhibited substantial changes in contrast gain or response gain after adaptation were similar.

The distributions of shifts in C_{50} and in R_{max} of X- and Y-cells were also analysed. Adaptation caused substantial shifts in C_{50} for both X-cells ($C_{50\ shift}$ 0.139 ± 0.017, different from 0, $P < 0.001$ $n = 113$, t-test) and Y-cells ($C_{50\ shift}$ 0.211 ± 0.023, $P < 0.001$, $n = 85$, t-test). The average shift in C_{50} of Y-cells was significantly larger than that of X-cells ($P = 0.010$, t-test, Fig. 5A). In contrast, the mean values of $R_{max\ shift}$ for X- and Y-cells were similar (X-cells: −0.0221 ± 0.011; Y-cells: −0.0406 ± 0.0154; $P = 0.315$, t-test, Fig. 5B). These results suggested that Y-cells showed stronger adaptation effects, reflected primarily in a decrease in contrast gain rather than a change in response gain.

Contrast adaptation of X- and Y-cells without feedback

To explore whether cortical feedback has different effects on contrast adaptation in each information channel, we re-examined the adaptation effects in X- and Y-cells without feedback. Figure 4C and D present representative X- and Y-cell response curves in cortex-inactivated cats. Adaptation effects still existed in X- and Y-cells without feedback,

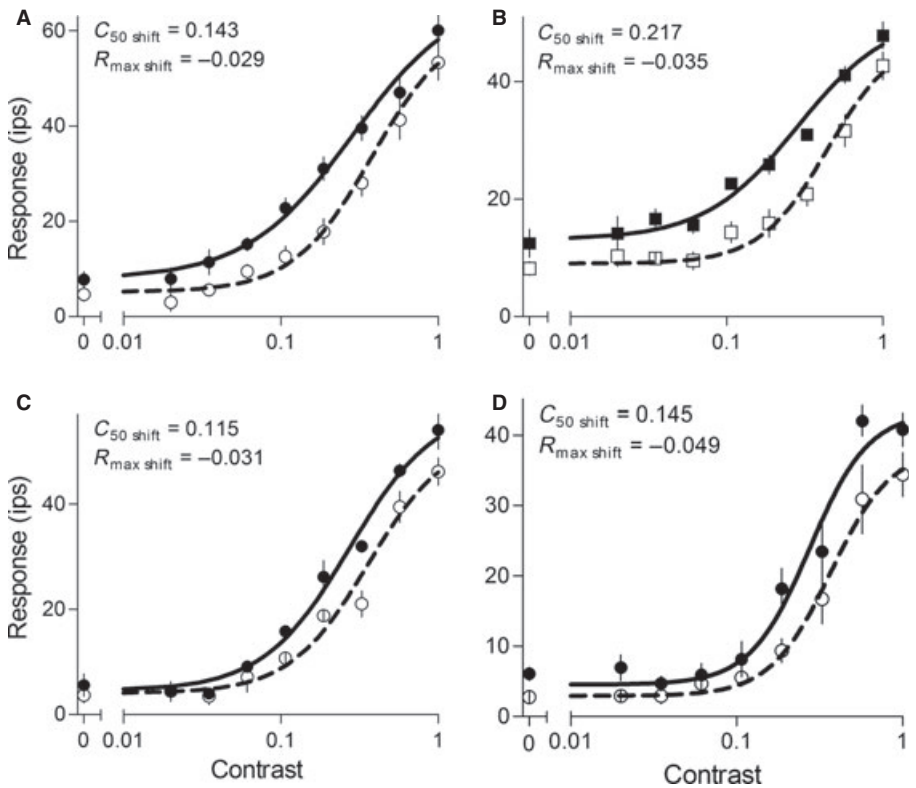

FIG. 4. Contrast response functions before and after adaptation for four representative X- and Y-cells with and without cortical feedback. Filled and empty circles (X-cell)/blocks (Y-cell) denote responses in pre-adapted and post-adapted conditions, respectively. Solid and dotted lines are Naka-Rushton curve-fits to the data points. (A) Normal X-cell, (B) normal Y-cell, (C) X-cell without feedback, (D) Y-cell without feedback. Most X- and Y-cells show similar contrast adaptation effect to these samples. The adaptation effect of the X-cell (A) is weaker than that of the Y-cell (B) in the normal LGN. However, the shift in contrast gain of the X-cell (C) is similar to that of the Y-cell (D) when the cortex is inactivated.

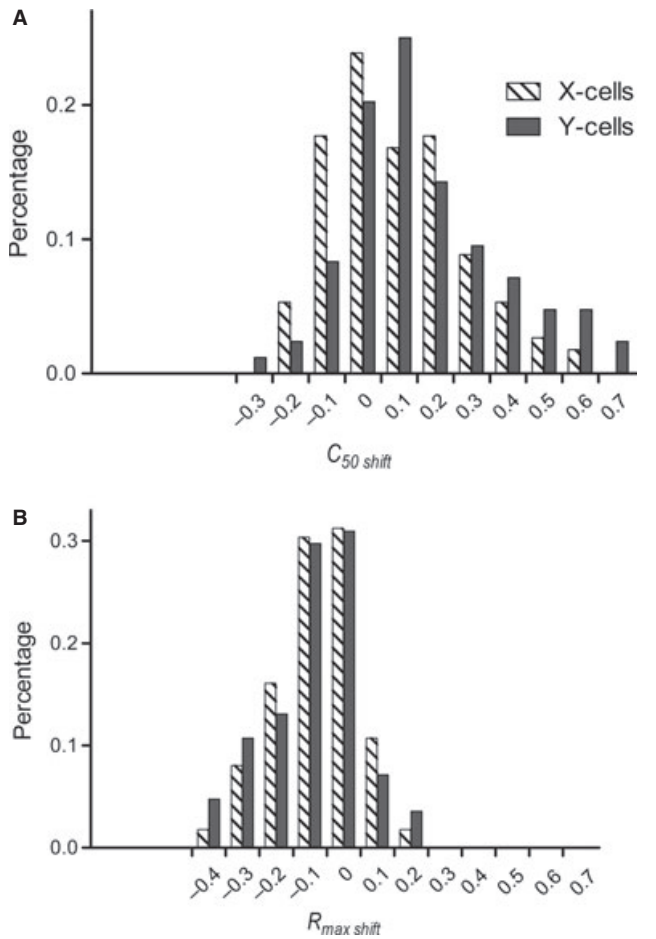

FIG. 5. Distribution of shifts in contrast gain and response gain for X- and Y-cells in normal cats. (A) X-cells show smaller shifts in C_{50} than Y-cells ($C_{50\ shift}$ 0.139 ± 0.017 vs. 0.211 ± 0.023, $P = 0.010$, *t*-test). (B) Contrast adaptation causes similar changes in R_{max} for X- and Y-cells ($R_{max\ shift}$ −0.0221 ± 0.011 vs. −0.0406 ± 0.0154, $P = 0.315$, *t*-test).

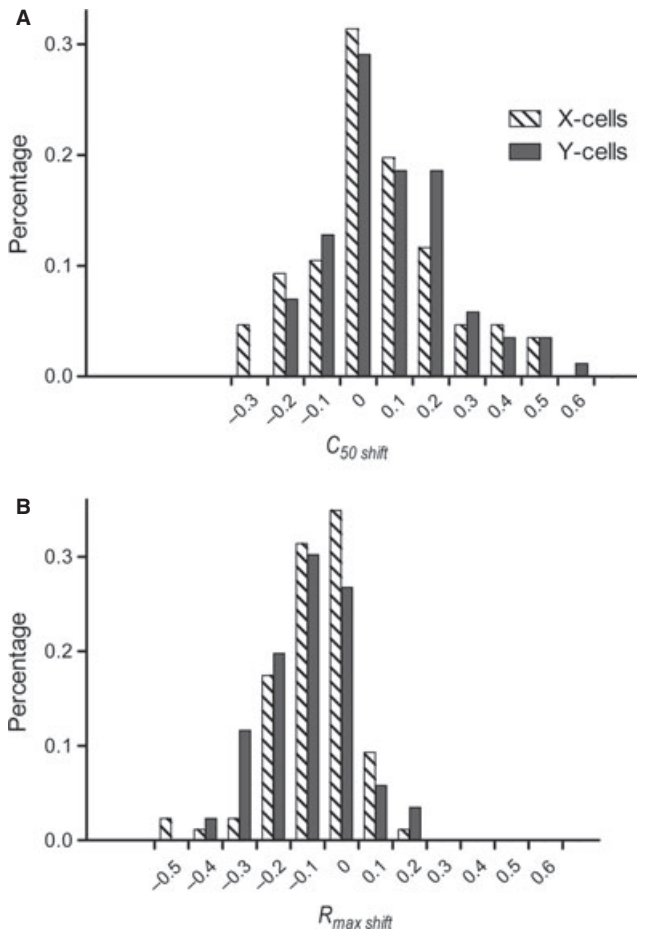

FIG. 6. Distribution of shifts in contrast gain and response gain for X- and Y-cells in cortex-inactivated cats. When cortical feedback is inactivated, X- and Y-cells show similar changes in C_{50} (A) ($C_{50\ shift}$ 0.106 ± 0.020 vs. 0.143 ± 0.019, $P = 0.172$, *t*-test) and R_{max} (B) ($R_{max\ shift}$ −0.026 ± 0.013 vs. −0.044 ± 0.014, $P = 0.351$, *t*-test).

indicating that adaptation is not totally dependent on feedback. Compared with the results from normal cats, the $C_{50\ shift}$ of the sample X-cell was only slightly lower in the absence of feedback (Fig. 4C). The $C_{50\ shift}$ of the Y-cell apparently decreased, however, when cortical feedback was inactivated (Fig. 4D).

In cortex-inactivated cats, 71.26% (62/87) of X-cells and 68.97% of Y-cells showed a substantial reduction in contrast gain, and 47.13% (41/87) of X-cells and 52.87% (46/87) of Y-cells showed significant reductions in response gain. The percentages of X- and Y-cells that showed a significant reduction in contrast gain or in response gain were similar (for C_{50}, $P = 0.740$, Pearson chi-square test; for R_{max}, $P = 0.448$, Pearson vhi-square test) and these frequencies were also not significantly different from X- and Y-cells in cats with intact corticothalamic feedback (all $P > 0.1$, Pearson chi-square test). Thus, it can be inferred that LGN neurons adjust their responsiveness according to outside information even in the absence of cortical feedback.

We also analysed the distributions of $C_{50\ shift}$ and $R_{max\ shift}$ in X- and Y-cells without feedback to assess the magnitude of these changes. When the cortical feedback was inactivated, adaptation still caused the post-adapted contrast response function to shift rightward for both X-cells ($C_{50\ shift}$ was 0.106 ± 0.020, different from 0, $P < 0.001$, $n = 87$, *t*-test) and Y-cells ($C_{50\ shift}$ was 0.143 ± 0.019, $P < 0.001$, $n = 87$, *t*-test). Unlike the results from normal LGN cells, however, the $C_{50\ shift}$ of X- and Y-cells were not significantly different in the absence of corticothalamic feedback ($P = 0.172$, *t*-test, Fig. 6A). Compared with the results from normal LGN cells, shifts in contrast gain of Y-cells without feedback were significantly smaller ($P = 0.023$, *t*-test), but there was no significant difference in the $C_{50\ shift}$ between X-cells with and without cortical feedback ($P = 0.210$, *t*-test). In cortex-inactivated cats, both X- and Y-cells showed significant changes in $R_{max\ shift}$ (X-cells: −0.026 ± 0.013, different from 0, $P = 0.046$; Y-cells: −0.044 ± 0.014, $P = 0.002$, *t*-test) after adaptation but these shifts were not significantly different between X- and Y-cells ($P = 0.351$, *t*-test, Fig. 6B). Furthermore, the changes in response gain were not significantly different from the normal LGN neurons (for X-cells, $P = 0.800$; for Y-cells, $P = 0.869$, *t*-test). These results indicated that cortical feedback contributed to contrast adaptation of Y-cells, particularly the reduction in contrast gain, but had little effect on any aspect of X-cell adaptation.

To further investigate the influence of cortical feedback, pre- and post-adapted contrast response functions were analysed for LGN neurons with and without feedback (Fig. 7). Before adaptation, normal Y-cells had smaller C_{50} than Y-cells without feedback (0.252 ± 0.015 vs. 0.291 ± 0.012, $P = 0.041$, *t*-test). After adaptation, normal Y-cells had similar contrast gain to Y-cells without

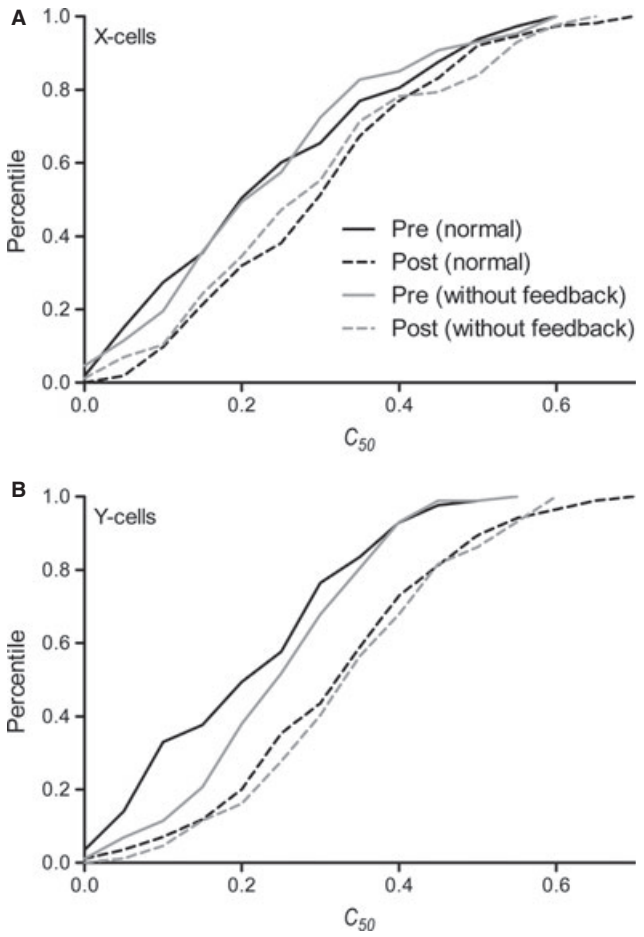

FIG. 7. Cumulative distributions of C_{50} before and after adaptation in X-cells (A) and Y-cells (B) with and without feedback. Black and gray lines represent LGN cells with and without feedback, respectively. Solid and dashed lines represent pre- and post-adapted states, respectively. (A) For X-cells, cortical feedback has little effect on the C_{50} of pre-adaptation ($P = 0.967$, t-test) and post-adaption ($P = 0.873$, t-test) contrast response functions. (B) For Y-cells, the feedback significantly affects the C_{50} of pre-adaption response ($P = 0.041$, t-test), but hardly affects the post-adaptation response ($P = 0.436$, t-test).

feedback (0.365 ± 0.016 vs. 0.382 ± 0.014, $P = 0.436$, t-test). Therefore, the shifts in C_{50} of Y-cells without feedback were smaller than those in Y-cells with feedback due to a higher C_{50} in pre-adapted Y-cells in the absence of feedback. For X-cells, however, the C_{50} distribution was similar for both pre-adapted (0.283 ± 0.0154 vs. 0.275 ± 0.016, $P = 0.967$, t-test) and post-adapted responses (0.345 ± 0.014 vs. 0.332 ± 0.017, $P = 0.873$, t-test), indicating that the contrast response functions of X-cells were little affected by cortical feedback. Feedback had a slight effect on pre- and post-adapted maximal firing rate. For X-cells, no statistically significant difference was found in R_{max} of both pre-adapted (normal LGN cells – 43.345 ± 1.738; LGN cells without feedback – 39.129 ± 1.310, $P = 0.054$, t-test) and post-adapted responses (42.043 ± 1.766 vs. 37.814 ± 1.461, $P = 0.066$, t-test). Cortical feedback also had no distinct effect on the R_{max} of Y-cells (pre-adapted – 40.451 ± 2.179 vs. 38.115 ± 2.161, $P = 0.448$; post-adapted – 39.379 ± 2.205 vs. 36.557 ± 1.779, $P = 0.322$, t-test). From these results, it can be inferred that cortical feedback mainly affected the pre-adapted response functions (especially in contrast gain) of Y-cells, and had little effect on the post-adapted response.

Relationship between adaptation effect and adapting contrast

In the visual cortex, it has been reported that the adaptation effectiveness becomes greater with increasing adapting contrast. To quantify the relationship between adapting contrast and shifts in contrast gain and response gain in LGN neurons, the relative adapting strength (A_S) was introduced (Crowder *et al.*, 2006):

$$A_s = \frac{C_{adaptor} - C_{50\,pre}}{C_{adaptor} + C_{50\,pre}}$$

where $C_{50\ pre}$ is the C_{50} of the pre-adapted contrast response function and $C_{adaptor}$ is the adapting contrast. Obviously, while the adapting contrast was 0.99, A_S was always larger than zero. To study the relationship over an extensive range of adapting contrasts, many neurons were adapted with a contrast that was less than $C_{50\ pre}$. In this situation, the A_S would be negative. In preliminary analyses, no systematic differences were observed in the relationship between X- and Y-cells, so results concerning the effects of adapting contrast were determined without differentiating between X- and Y-cells.

The magnitude of the increase in C_{50} was related to the adapting contrast (Fig. 8A). That is, an adapting stimulus with high contrast (larger A_S) was associated with a larger change in C_{50}, while an adapting stimulus with lower contrast led to smaller $C_{50\ shift}$. The goodness of fit (R^2) of the relationship between A_S and $C_{50\ shift}$ was 0.411. The slope (0.252 ± 0.022) was significantly non-zero ($F_{1,197} = 134.4$, $P < 0.001$, F-test). Compared with the effect in cortex, however, this effect was relatively weak in the LGN, especially when A_S was small. Thus, the relationship between C_{50} and R_{max} was not as obvious in LGN as in cortex. Although R_{max} values decreased after adaptation, the decrease was not related to the adapting contrast ($R^2 = 0.007$, slope −0.057 ± 0.014, $F_{1,197} = 1.356$, $P = 0.246$, F-test, Fig. 8B).

We also studied this relationship in LGN neurons without feedback (Fig. 8C and D). The results in cortex-inactivated cats were similar to those in normal cats, suggesting that this effect is independent of feedback. The $C_{50\ shift}$ became larger with an increase in adapting contrast ($R^2 = 0.354$, slope 0.220 ± 0.023, $F_{1,173} = 93.29$, $P < 0.001$, F-test), while $R_{max\ shift}$ was not related to A_S ($R^2 = 0.021$, slope −0.037 ± 0.019, $F_{1,\ 173} = 3.740$, $P = 0.055$, F-test). In summary, for LGN neurons, the shifts in contrast gain are related to adapting contrast, but response gain is independent of the adaptor.

Discussion

Although contrast adaptation in the LGN of anesthetized cats has been shown previously, the data presented here constitute the first demonstration that Y-cells exhibit a stronger adaptation effect than X-cells and that this difference may be come from the corticothalamic feedback.

Contrast adaptation in the visual system

The shifts in contrast gain and response gain after adaptation were the main issues addressed in this study. These two parameters have important physiological implications. Although the dynamic range of a neuron is limited, the change in contrast gain can modify the dynamic range to match the prevailing stimulus contrasts. The decrease in response gain involves a reduction in the firing level at high rates, and may simply reflect a 'fatigue' effect (Movshon & Lennie, 1979; Ohzawa *et al.*, 1982, 1985).

Our results demonstrated that contrast adaptation caused changes in the responsiveness of LGN neurons, due primarily to a reduction in contrast gain. These effects are similar to those observed in cortex.

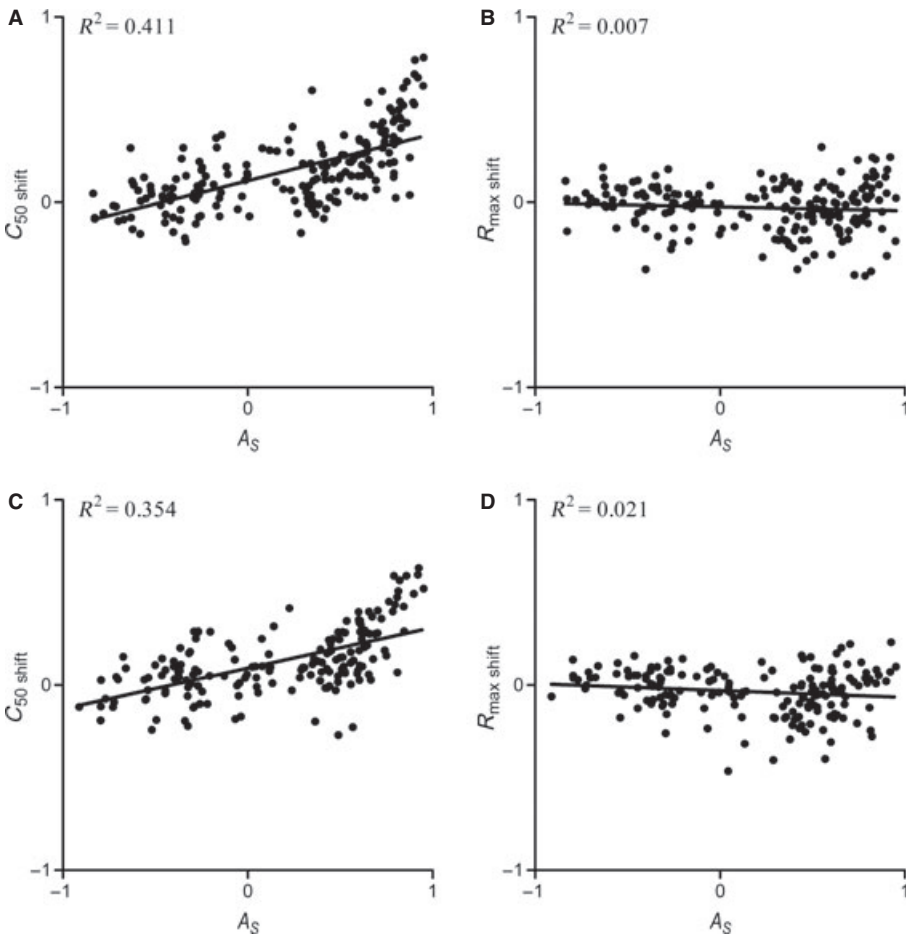

FIG. 8. Effects of adapting contrast on the C_{50} and R_{max} values. Relative strength of $C_{50\ shift}$ and $R_{max\ shift}$ values are plotted against the relative adapting contrast (A_S), which is normalized in relation to each neuron's C_{50}. Solid line indicates linear regression. The goodness of fit (R^2) values are given in the top left of each scatter plot. The $C_{50\ shift}$ is nearly linear with relative adapting strength in normal LGN neurons (A, slope 0.252 ± 0.022, $P < 0.001$, F-test). Even when cortical feedback is inactivated, the relationship between $C_{50\ shift}$ and A_S remains (C, slope 0.220 ± 0.023, $P < 0.001$, F-test). However, no relationship between $R_{max\ shift}$ and A_S is found in LGN neurons with (B, $P = 0.246$, F-test) and without feedback (D, $P = 0.055$, F-test).

One study in primates also indicated that adaptation may originate in retinal ganglion cells (Solomon *et al.*, 2004), so it is possible that cortical adaptation may reflect an adaptation effect in the early visual pathway. It is unlikely, however, that the adaptation effect observed in cortex simply inherited from the input neurons. First, contrast adaptation effects in cortex were stronger than those in the LGN and retina (Ohzawa *et al.*, 1985; Shou *et al.*, 1996; Solomon *et al.*, 2004), suggesting that adaptation effect reflects both adaptations in inputs and intrinsic information processing. Second, unlike the effect in visual cortex, contrast adaptation in the LGN is not sensitive to spatial frequency (Duong & Freeman, 2007), further suggesting that the mechanisms of contrast adaptation in striate cortex and in LGN are distinct. Furthermore, we found that the percentages of LGN neurons exhibiting significant shifts in contrast gain or in response gain were independent of the cell type and of cortical feedback. Thus, adaptation is an intrinsic attribute of neurons, and each processing stage of the visual system may adjust its limited dynamic range to match the prevailing contrasts of the current visual scene.

Different adaptation properties of X- and Y-cells

The visual information processing system comprises several parallel and independent information channels, and each channel performs distinct functions in vision (Kaplan & Benardete, 2001; Callaway, 2005). In the LGN of cat, X- and Y-cells represent two major neuronal types (Sherman, 1985). An important difference between X- and Y-cells is the structure of their receptive fields. Unlike X-cells, non-linear subunits contribute to the receptive fields of Y-cells (Hochstein & Shapley, 1976a). Studies have indicated that non-linear processing contributes to adaptation (Shapley & Victor, 1978; Victor, 1987; Benardete & Kaplan, 1999; Brown & Masland, 2001). Thus, non-linearity may be one source of the difference in adaptation effects between X- and Y-cells.

Solomon *et al.* (2004) suggested that contrast adaptation is strong in primate M-cells, but is absent in P-cells. Earlier studies also suggested that X-cells in cats correspond to P-cells in primates, while cat Y-cells correspond to primate M-cells, in the time course of the cells' responses (Enroth-Cugell & Robson, 1966; Dreher *et al.*, 1976; Sherman *et al.*, 1976). Studies that focused on the non-linearity of these cells, however, suggested that only about one-third of M-cells were Y-like and the other two-thirds were X-like (Kaplan & Shapley, 1982). Thus, Shapley suggested that cat X-/Y-cells and monkey M-cells were homologous and that the P-cells appeared in primates at higher spatial resolution (Shapley & Hugh Perry, 1986). The data presented here indicate that both X- and Y-cells show a robust contrast adaptation effect, consistent with the idea that X- and Y-cells of cats and M-cells of primates are homologous.

The influence of cortical feedback

Anatomical studies have indicated that cortical afferents from layer 6 of primary visual cortex project to LGN relay cells directly or through interneurons in the LGN and the perigeniculate nucleus (Boyapati & Henry, 1984; Murphy & Sillito, 1996). Furthermore, these feedback connections are topographically organized and can influence the properties of LGN cells (Murphy & Sillito, 1987; Cudeiro & Sillito, 1996). These cortico-geniculate connections are excitatory (Weber *et al.*, 1989; Montero, 1991). It is likely that the excitation is decreased concomitant with adaptation and that this decease acts as a disfacilitation to enhance the strength of contrast adaptation (Ye *et al.*, 2009).

At the physiological level, corticothalamic feedback has a robust influence on the receptive field and the non-linear response properties of LGN neurons (Murphy & Sillito, 1987; Sillito *et al.*, 1993; Jones *et al.*, 2000; Webb *et al.*, 2002). The influence of feedback on non-linearity is also supported by findings in the auditory (Yan & Suga, 1999) and somatosensory systems (Ghazanfar *et al.*, 2001). Presumably, cortical feedback is likely to influence the non-linear subunits of Y-cells, causing Y-cells to show stronger adaptation effects than X-cells.

In summary, we demonstrated that adaptation effects were stronger in Y-cells than in X-cells, suggesting that each channel possesses distinct capacities for processing contrast information. Like a previous study in the macaque monkey (Briggs & Usrey, 2009), our results also provide an example of how corticothalamic feedback can have unique effects on different information channels.

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Abbreviations

LGN, lateral geniculate nucleus; SEM, standard error of the mean.

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