

Research report

Effects of bicuculline on direction-sensitive relay cells in the dorsal lateral geniculate nucleus (LGNd) of cats

Bing Hu^a, Xiangrui Li^a, Yifeng Zhou^{a,d,*}, Tiande Shou^{b,c}

^aBeijing Laboratory of Cognitive Science, Vision Research Laboratory, School of Life Science, University of Science and Technology of China, Hefei, Anhui 230027, PR China

^bCenter for Brain Science Research and Liren Lab, School of Life Science, Fudan University, Shanghai 200433, PR China

^cVisual Information Processing Laboratory, Biophysical Institute of the Chinese Academy of Sciences, Beijing 100101, PR China

^dCenter for Brain and Mind Science, Chinese Academy of Sciences, Beijing, PR China

Accepted 12 September 2000

Abstract

The direction sensitivity of relay cells in the cat's dorsal lateral geniculate (LGNd) was measured using sinusoidal grating stimuli before and during local bicuculline administration. One hundred and twenty-eight LGNd relay cells were recorded in laminae A and A1, of which 44 relay cells (34%) were found to be sensitive to direction of stimulus movement. The direction-sensitive LGNd relay cells could be differentiated into two subgroups based on different measures of their response amplitude. Type I cells exhibited their direction sensitivity when the fundamental Fourier component (FFC) of the poststimulus time histograms (PSTHs) was used as response measure, but did not show significant direction sensitivity when mean firing rate was used. Type II cells exhibited their direction sensitivity, no matter whether the FFC or mean firing rate was used as the measure. Of 35 cells analyzed, 27 cells remained direction sensitive during bicuculline administration. At the population level, the direction bias of type I cells did not change systematically, while the direction bias of type II cells decreased significantly during bicuculline administration. These results suggest that the direction bias of these two types of relay cells are mediated by different neural mechanisms. The direction bias of type I cells may involve multiple inputs from spatio-temporally separate subunits within retinal ganglion cells receptive fields. The direction bias of type II cells may involve GABAergic neuronal circuits within the LGNd. © 2000 Elsevier Science B.V. All rights reserved.

Theme: Sensory systems

Topic: Subcortical visual pathways

Keywords: Bicuculline; GABA; Microiontophoresis; Direction sensitivity; LGNd; Cat

1. Introduction

Direction sensitivity is a well-known receptive field property of neurons in mammalian visual cortex [9]. It is widely accepted that this property is generated intracortically although some investigators have noted a weak direction preference in some cells in the LGNd of monkeys [10].

Recently, Leventhal and co-workers reported that about one-third of X and Y type relay cells in the A laminae of the dorsal lateral geniculate (LGNd) exhibited some degree

of direction sensitivity ($DB > 0.1$ see Section 2) in normal cats [24,25], dark-reared cats [33,34], and cats in which the visual cortex had been inactivated [26,34].

Moreover, direction-sensitive cells were also found in the magnocellular and parvocellular layers of the monkey LGNd [24]. These findings raised the possibility that the direction sensitivity of LGNd relay cells may contribute to the development of this property in the visual cortex.

Shou et al. [17] reported that about 26% X- and Y-type retinal ganglion cells (RGCs) of cats exhibit direction biases. It seems likely that the direction sensitivity of most LGNd cells is a reflection of their retinal inputs. However, compared to RGCs, a somewhat greater proportion of LGNd relay cells exhibit direction bias. Thus, one of the purpose of this study was to determine if intrageniculate

*Corresponding author. Tel.: +86-551-360-1436; fax: +86-551-360-7014.

E-mail address: zhouy@ustc.edu.cn (Y. Zhou).

inhibitory mechanisms contribute to the direction-sensitive responses of LGNd relay cells.

There has been some evidence suggesting that more than

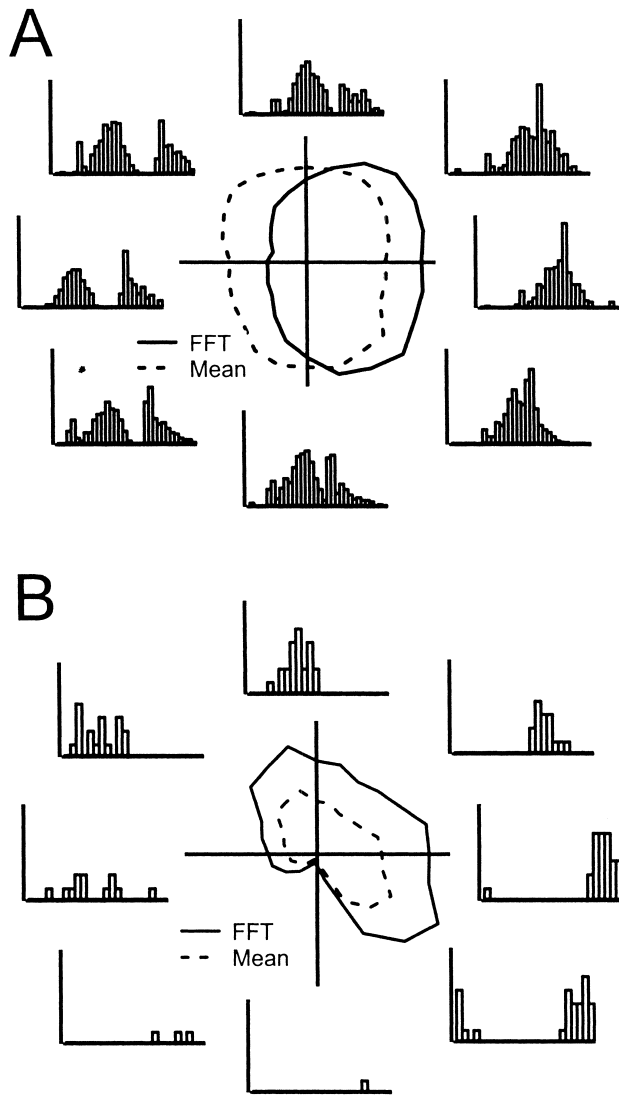


Fig. 1. Poststimulus time histograms (PSTHs) showing the two different types of neuronal activity elicited by drifting sinusoidal gratings that result in direction sensitivity in LGNd cells. The polar plots in the center of the PSTHs were direction tuning curve of the cell. PSTHs are shown for the two horizontal directions, the two vertical directions, and the four oblique directions (separated by 45°), respectively. (A) An On-center X cell, whose direction sensitivity was presumably mediated by a spatio-temporally separate subunit structure within the excitatory center, is classified as type I cell; stimuli spatial frequency 0.4 cycle/deg., temporal frequency 1 Hz, repeat 15 cycles, DB was 0.272 for FFC and 0.015 for Mean, respectively. (B) An off-center Y cell, whose direction sensitivity was presumably mediated by an asymmetric inhibition in the nonpreferred direction which cause poor response (see left bottom two PSTHs), is classified as type II cell; stimuli spatial frequency 0.4 cycle/deg., temporal frequency 2 Hz, repeat 10 cycles, DB was 0.291 for FFC and 0.282 for mean, respectively. The response scales represented by axes of abscissa and ordinate are 42 spike/s in (A) and 16 spike/s in (B), respectively.

one mechanism may be involved in the generation of the direction sensitivity of the LGNd neurons. One may be determined by the asymmetric inhibitory surround of the receptive field, and another may involve the excitatory center of the receptive field receiving inputs from many subunits with different latencies [20–22,25]. As shown in Fig. 1A,B, the poststimulus time histograms (PSTHs) show the two different types of neuronal activities, elicited by drifting sinusoidal gratings, that result in direction sensitivity in LGNd cells. This phenomenon suggested that we could differentiate these direction-sensitive cells into subgroups based on different measures of their response amplitude. Type I cells (Fig. 1A as an example) exhibited their direction sensitivity (DB=0.272) when the fundamental Fourier component (FFC) of the PSTHs was used as response measure, but did not show significant direction sensitivity (DB=0.015) when mean firing rate was used. Type II cells (Fig. 1B as an example) exhibited their direction sensitivity, no matter whether the FFC (DB=0.291) or mean firing rate (DB=0.282) was used as the measure [32,34]. Another purpose of this investigation is to test whether there are different mechanisms involving the generation of direction sensitivity of cells with different shapes of PSTHs, including intrageniculate inhibitory mechanism.

2. Materials and methods

2.1. Physiological recording procedures

Seventeen adult cats were prepared for electrophysiological recording as described previously [15,34]. Animals were anesthetized with urethane (20 mg/kg per h) and paralyzed with gallamine triethiodide (10 mg/kg per h) intravenously during the duration of the experiments. Body temperature was maintained at 38°C . The ECG and EEG were monitored throughout the experiment. Expired CO_2 was maintained at approximately 4%.

The eyes were protected from desiccation with proper contact lenses. The cat's optic disks were projected upon a white screen positioned 114 cm from the eye repeatedly during the course of recording. These projections were used to determine the positions of the area centralis conventionally [5,14]. The clarity of the optics was checked often during all experiments.

Action potentials of LGNd cells were recorded with an extra/intra-cellular preamplifier (Nihon Konden, Japan) and an AC/DC amplifier (FZG-IA, Liuhe, China) through the recording micropipette of a trimicrocapillary electrode. The recording micropipette contained 3 M NaCl with high-impedance ranging from 2 to 10 $\text{M}\Omega$. The electrode was advanced using an electrohydraulic microdrive (Narishige, Japan) and was moved at least 100 μm between units to reduce sampling bias.

2.2. Receptive field mapping procedures

For each cell, the receptive field was mapped on the tangent screen 114 cm away from the cat's eye by hand-held targets. The retinal eccentricity of each cell's receptive field was defined as the distance in visual degree from the center of the receptive field to the projection of the area centralis of that eye.

The responses of single units to visual stimulation were studied quantitatively with an image synthesizer (Innisfree, USA), an oscilloscope-based (Tektronix 608) optical display, and a Compaq 386/20e computer (USA) controlled visual stimulus system (VS System, Cambridge Electronic Design, UK). We developed an apparatus that allows the oscilloscope display to be tangentially moved to any point in the animal's visual field while maintaining a fixed distance of 57 cm between the display and the cat's eye. Thus, we can study cells' receptive field properties at different parts of the visual field without distortion.

The responses of single cells to drifting sinusoidal gratings as well as to contrast alternating gratings were used to determine the cell's linearity and frequency doubling. The spatial resolution, receptive field size, time course of response, response to rapid stimulus motion, and sluggishness of response were also studied. Units were identified as X- and Y-types [3,4,6,23].

2.3. Direction sensitivity measurement

Drifting sinusoidal gratings across the receptive field were used to determine the direction sensitivity of cells in the A and A1 layers of the LGNd. The stimulus gratings were displayed on a $10^\circ \times 12.5^\circ$ oscilloscope screen with mean luminance of 5.9 Cd/m^2 . The temporal frequency and contrast of the gratings were generally kept at 2 Hz and 50%, respectively. Two definitions of response amplitude were used in this study. One was the amplitude of the fundamental Fourier component (FFC) of the PSTH in spikes/s. The other was the mean firing rate in spikes/s, which was used only for classification of cells. Direction sensitivity is usually most pronounced when relay cells are tested with low spatial frequency sinusoidal gratings, and orientation sensitivity is most distinct for relay cells and retinal ganglion cells when using a high spatial frequency (close to its cutoff frequency) [11,12,16]. Thus, the spatial frequency tuning curves were routinely first tested at certain orientations (for example, vertical or horizontal), then several appropriate spatial frequencies were selected from the resultant spatial frequency tuning curves to measure the direction tuning curves.

In general, when at least three to five direction tuning curves at various spatial frequencies were measured, the maximal direction bias can be clearly shown. Fifteen presentations of drifting gratings (temporal frequency of 2 Hz) at each of 24 randomly generated directions with 15° intervals were used to compile the direction tuning curves

for the cells studied. The stimulus area used was at least three times larger than the receptive field center of the cell tested. These procedures are similar to those employed by Levick and Thibos [12] and Soodak et al. [21] in their studies of retinal ganglion cells and LGNd cells.

Direction preferences and sensitivities were calculated for each cell using statistical methods described in detail by Zar [31]. These methods have been previously used in the calculation of orientation sensitivity of retinal ganglion cells [11,12] and LGNd relay cells [16], also in the calculation of the direction sensitivity of LGNd relay cells [25] and the orientation and direction sensitivity of cortical cells to moving stimuli [29]. Briefly, the responses of each cell to the different directions presented were stored in the computer as a series of vectors for later analysis. The angle of each vector was defined relative to the meridian of the retina with horizontal as 0 or 180° and vertical defined as 90 and 270° counterclockwise. The sum of the vectors was divided by the sum of the absolute values of the vectors. The angle of the resultant vector gives the preferred direction of the cell. The length of the resultant vector, termed the direction bias (DB), provides a quantitative measure of the direction sensitivity of the cell.

$$\vec{b} = \frac{\sum \vec{R}_i}{\sum R_i} = \sum R_i \cdot \exp(j \cdot \theta_i) / \sum R_i = b \cdot \exp(j \cdot \theta_p)$$

where b is direction bias (DB); θ_p is preferred direction; $j = \sqrt{-1}$; R_i is response amplitude to the i th stimulus direction; θ_i is direction angle of the i th stimulus.

Direction biases range from 0 to 1, with 0 being completely insensitive to direction and 1 respondent to only one direction. The measure of direction bias used in this study is analogous to that used by Levick and Thibos [12] in their study of the physiological orientation sensitivity of retinal ganglion cells, but with a difference in the ranges for direction from 0 to 360° and for orientation from 0 to 180° . It has been argued that these methods are more accurate than others (i.e., half-width-at-half-height and direction index) in describing the orientation and direction sensitivity of visual neurons [29,30]. A direction bias of 0.1 or greater indicates that the bias is statistically significant at the $P < 0.005$ level (Rayleigh test) [31]. In this study, a cell exhibiting a bias of 0.1 or greater (on the basis of FFC) was considered to be direction sensitive; cells with biases less than 0.1 were defined as being non-direction sensitive. The reliability of LGNd cells direction determination has been discussed in detail previously [25].

2.4. Microiontophoretic injection of bicuculline

Bicuculline (bicuculline methobromide (Sigma, USA), molecular weight, 462) was injected into the LGNd by using a microiontophoresis micropipette filled with 0.5 mM bicuculline in physiological saline (pH 3.0). The

microiontophoretic electrode (the second micropipette) was for local microiontophoresis in the LGNd, and the balance electrode (the third micropipette) containing 3 M NaCl was used to balance the current. Both were connected to a microiontophoresis current programmer (WPI 260, USA). Bicuculline was injected using currents of 20–80 nA for about 10 min, and then reduced to 10 nA for the remainder of the time. The direction tuning curves of each cell were obtained before, during and after the microiontophoresis of bicuculline.

2.5. Histological identification of location of the cell studied

At the end of each experiment, animals were deeply anesthetized and perfused. The brains were removed, and the portions containing the electrode tracts were frozen and sectioned at 75 μm . The Nissl-stained coronal sections through the LGNd were used to identify the exact location of the cells studied in the brain.

3. Results

One hundred and twenty-eight LGNd relay cells were recorded in laminae A and A1. Forty-four relay cells (34%) were found to be sensitive to moving direction ($\text{DB} > 0.1$). This agrees well with the earlier reports [25,32]. In general, their direction sensitivity was most significant when relay cells were tested with low spatial frequency of sinusoidal gratings (close to the optimal spatial frequency of the cell). However, some, but not many cells were direction sensitive over a wide range of spatial frequencies. Cells subserving the vertical, oblique, and horizontal retinal meridians were included in the sample.

Bicuculline was applied to the 44 direction-sensitive relay cells. Of these cells, only 35 were studied quantitatively. This was due to that the local microiontophoresis of bicuculline increased the spontaneous discharge rate and evoked response of these 35 cells. The other nine cells seemed not affected by bicuculline, so these nine cells were not included in the present study. Of 35 cells studied, 27 cells remained direction sensitive ($\text{DB} > 0.1$) during bicuculline administration. The effects of bicuculline lasted 15–30 min, and then the cells' response returned to the normal level.

Two different types of LGNd cells (type I and type II cells) were found. This classification is based upon the cells' responses to moving gratings [32,34]. Our results support the classification mentioned above. Quantitative measures of 35 direction-sensitive LGNd cells showed that 24 cells were classified as type I cells (11 X cells and 13 Y cells, 17 on-center cells and seven off-center cells), 11 as type II cells (eight X cells and three Y cells, five on-center cells and six off-center cells). This classification was

independent of the classification of X and Y type, or on- and off-center of cells. The results presented below indicate that bicuculline has apparently different effects on these two types of direction-sensitive cells.

Of 24 type I cells studied, 23 cells still remained direction sensitive during bicuculline administration. A typical sample in Fig. 2 shows the effect of bicuculline on a type I direction-sensitive cell. The type I cell exhibited direction sensitivity only when FFC of PSTHs was used as the response measure (solid curve in Fig. 2A, $\text{DB} = 0.27$). This cell did not show significant direction sensitivity when mean firing rate was used (Fig. 2B, $\text{DB} = 0.013$, far less than 0.1). During bicuculline injection, the cell's response increased strikingly (compare the solid curve and dash curve in Fig. 2A), but exhibited almost no change in direction bias from 0.27 to 0.28.

The data from 24 type I direction-sensitive relay cells are plotted in Fig. 4 (open triangles). Most data for type I relay cells distributed around the line with a slope of one. The mean ratio between direction biases during and before bicuculline injection was 1.16 ± 0.49 (S.D.). This was slightly higher than 1, but showed no statistical difference (*t*-test, $P > 0.1$, $n = 24$).

In contrast to type I cells, most type II direction-sensitive cells exhibited declining direction bias during bicuculline injection. Of 11 type II cells studied, only four cells remained direction sensitive during bicuculline application. A sample of type II cell is shown in Fig. 3. Regardless of whether the FFC or mean firing rate was used, the cell exhibited significant direction sensitive. Using these two measures, the DBs were 0.25 and 0.18,

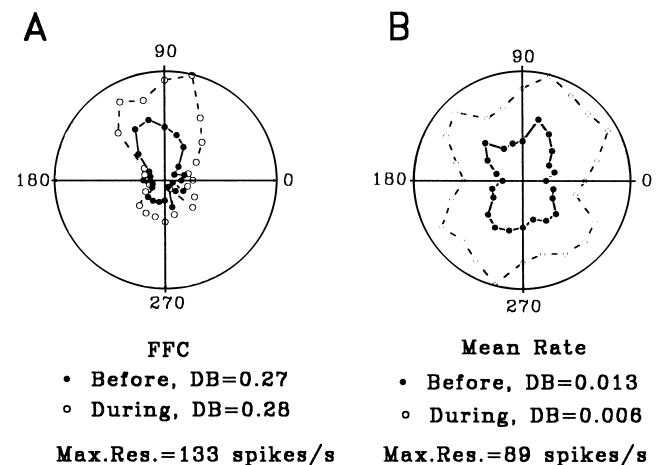


Fig. 2. Direction tuning curves of a type I direction-sensitive LGNd relay cell (on-center, Y). The angles in polar curves represent the moving direction and the magnitudes represent the responses at the corresponding directions. The direction bias (DB) before and during bicuculline injection was almost the same (see text for details). The grating spatial frequency was 0.2 cycle/deg.; temporal frequency, 2 Hz. The response scales represented by radii are 133 spike/s in (A) and 89 spike/s in (B), respectively.

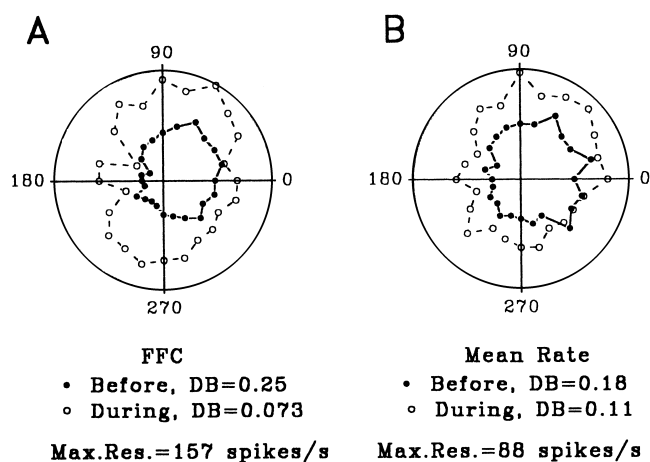


Fig. 3. Direction tuning curves of a type II direction-sensitive LGN relay cell (on-center, X). During bicuculline application, the direction bias of the cell dramatically declined (see text in detail). The grating spatial frequency was 0.09 cycles/deg., temporal frequency, 2 Hz. The response scales represented by radii are 157 spike/s in (A) and 88 spike/s in (B), respectively.

respectively (solid curve in Fig. 3A,B). The shape of cell's direction tuning curves changed dramatically due to bicuculline administration. During bicuculline injection, the cell's direction bias decreased significantly from 0.25 to 0.073 (solid and dashed curves in Fig. 3A) when FFC was used as response amplitude, and from 0.18 to 0.11 (solid and dashed curves in Fig. 3B) when mean firing rate was used. Notice that the cell's response was increased by bicuculline no matter whether the FFC or mean firing rate was used (compare the solid curve and dashed curve in each figure).

The solid circles in Fig. 4 show the data from 11 type II direction-sensitive cells. It is noteworthy that all points are located below the line with a slope of one. This result indicates a clear decrease in direction sensitivity during bicuculline injection. The mean ratio between direction bias during and before bicuculline injection was 0.52 ± 0.25 (S.D.). This is significantly lower than 1 (*t*-test, $P < 0.0002$). The different effects of bicuculline on the two types of direction-sensitive relay cells were statistically pronounced (*t*-test, $P < 0.0001$).

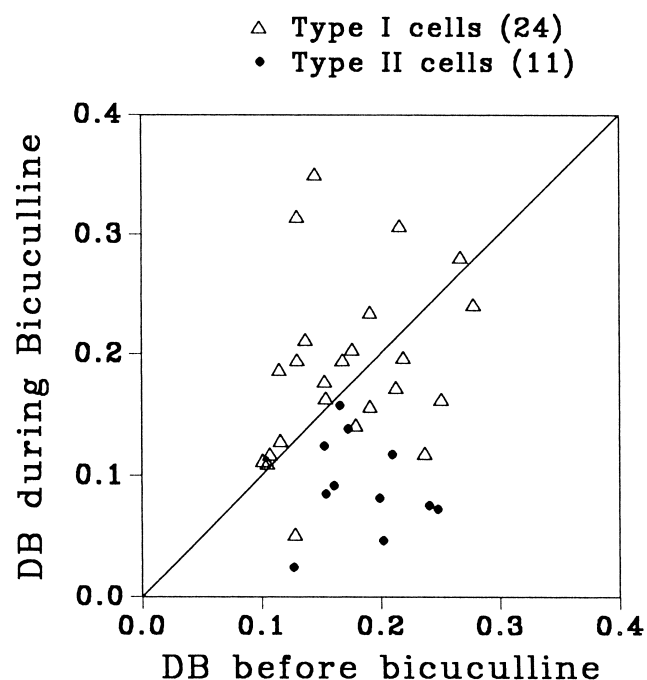


Fig. 4. Changes in direction bias of 24 type I (hollow triangles) and 11 type II (solid circles) direction-sensitive relay cells before and during bicuculline injection. The horizontal and vertical axes represent the DB (obtained by FFC) values before and during bicuculline injection, respectively. Data above and below the line of slope 1 show the cells whose direction biases increased and decreased during bicuculline administration respectively. For type I cells, the data are scattered around the line of slope 1, except three points. For type II cells, however, data are all located below the line of slope 1 without exception.

4. Discussion

Direction sensitivity of X and Y cells in the cat's LGNd has been reported [24–26,33,34]. This study confirms that direction sensitivity is a common property of the receptive fields of LGNd neurons in the cat. Moreover, the results provide the first demonstration that there are two types of direction-sensitive LGNd cells, which are affected differently by bicuculline, an antagonist to GABA_A receptors.

It is very important in microiontophoretic work to be certain that the drugs applied really affect the neurons studied without injection artifacts. It should be emphasized that several controlled experiments, in which 3 M NaCl were used instead of bicuculline were conducted. The comparison showed that there was no obvious change in cells' responsivity and direction bias before and after 'microiontophoresis' of saline. Also, we studied each cell for more than 1 h and the direction bias of single units was stable before bicuculline administration. Some cells (five type I and six type II relay cells) were studied repeatedly and exhibited similar effects during microiontophoresis of bicuculline.

Approximately 25% of the cells in the LGNd are immunoreactive for GABA [27]. GABA is an intrageniculate inhibitory neurotransmitter [1,2,7,8,13,19,28]. Blocking GABA_A receptors appears, at the population level, to decrease the direction bias of type II direction-sensitive cells significantly, but to show no systematic effect on type I cells. The different influences of bicuculline on the two types of direction-sensitive relay cells were statistically pronounced (*t*-test, $P < 0.0001$). This study presents pharmacological evidence supporting the physiological differ-

ence between the two types of direction-sensitive LGNd cells.

Significant numbers of RGCs in the cat are sensitive to direction [17]. The distribution of their direction bias, the spatial frequency dependence of their direction sensitivity, the relationship between their preferred orientations and preferred directions are similar to those of the LGNd relay cells to which they project. It seems likely, thus, that the direction-biased responses of many LGNd relay cells originate from excitatory inputs of direction-sensitive RGCs. Our finding that the direction bias of many LGNd cells like those type I cells in Figs. 2 and 4, changed little during bicuculline administration is consistent with this idea. However, we could not rule out the possibility of some type I cells involving the intra-geniculate GABAergic mechanisms due to the great changes in DB during bicuculline administration (Fig. 4).

In fact, 26% of RGCs (22% of X and 34% of Y) were reported to be sensitive to direction in the cat [17]. The proportion is a little lower than that of direction-sensitive cells in the LGNd (about one-third) [25,32,33]. This suggests that the intrageniculate mechanism may enhance the direction sensitivity of some LGNd cells. Our finding that bicuculline injection decreased direction sensitivity of type II cells is a support to this idea. During bicuculline administration, the proportion of direction-sensitive cells in the LGNd was reduced to 26%, the same as previously reported for cat retinal ganglion cells.

There has been some evidence suggesting that more than one mechanism may be involved in the generation of the direction sensitivity of the LGNd neurons. The first possible mechanism may involve the excitatory center of the LGNd cell's receptive field receiving inputs from many spatially separated retinal subunits with different temporal properties [25,32,34]. Another possible mechanism is that type I LGNd relay cells receive excitatory input from type I retinal ganglion cells [18]. For these direction-sensitive cells, the responses in some stimulus directions are separated into at least two peaks in PSTHs in a complicated manner (see Fig. 1A). Their mean firing rates in any two opposite directions are almost the same (not sensitive to direction), but they may respond differently in different directions when the FFC is used as measure. The second possible mechanism underlying direction sensitivity in the LGNd may involve an asymmetric inhibitory surround of the receptive fields [25,32,34]. For direction sensitivity involving this mechanism, responses of cells to different directions of moving stimulus are different, no matter whether the FFC or mean firing rate is used as a measure (see Fig. 1B). Our results show that direction sensitivity of most type I and type II cells can be explained by the first and second mechanisms, respectively. In summary, our results show that at least two possible mechanisms are involved in the generation of direction sensitivity of LGNd cells. It remains to be determined whether the direction sensitivity of some LGNd cells is exclusively mediated by

one of these mechanisms, while the sensitivity of others is mediated by two or more mechanisms.

Acknowledgements

This investigation was supported by grants (No. 97908003, No. 39893340-03 and No. 30070257) from the National Natural Science Foundation of China, and the Foundation of the Chinese Academy of Sciences. We are grateful to Dr. A.G. Leventhal in Department of Neurobiology and Anatomy, University of Utah, School of Medicine, USA, for his critical review and comments.

References

- [1] N. Berardi, M.C. Morrone, The role of gamma-aminobutyric acid mediated inhibition in the response properties of cat lateral geniculate nucleus neurones, *J. Physiol. (London)* 357 (1984) 505–523.
- [2] N. Berardi, M.C. Morrone, Development of gamma-aminobutyric acid mediated inhibition of X cells of the cat lateral geniculate nucleus, *J. Physiol. (London)* 357 (1984) 525–537.
- [3] B.G. Cleland, W.R. Levick, Properties of rarely encountered types of ganglion cells in the cat's retina and an overall classification, *J. Physiol. (London)* 240 (1974) 457–492.
- [4] C. Enroth-Cugell, J.G. Robson, The contrast sensitivity of retinal ganglion cells of the cat, *J. Physiol. (London)* 187 (1966) 517–552.
- [5] R. Fernald, R. Chase, An improved method for plotting retinal landmarks and focusing the eyes, *Vision Res.* 11 (1971) 95–96.
- [6] S. Hochstein, R.M. Shapeley, Quantitative analysis of retinal ganglion cell classification, *J. Physiol. (London)* 262 (1976) 237–264.
- [7] R.N. Holdefer, T.T. Norton, R.R. Mize, Laminar organization and ultrastructure of GABA-immunoreactive neurons and processes in the dorsal lateral geniculate nucleus of the tree shrew (*Tupaia belangeri*), *Vis. Neurosci.* 1 (1988) 189–204.
- [8] R.N. Holdefer, T.T. Norton, D.W. Godwin, Effects of bicuculline on signal detectability in lateral geniculate nucleus relay cells, *Brain Res.* 488 (1989) 341–347.
- [9] D.H. Hubel, T.N. Wiesel, Receptive fields and functional architecture of monkey striate cortex, *J. Physiol. (London)* 202 (1968) 251–260.
- [10] B.B. Lee, O.D. Creutzfeldt, A. Elepfandt, The responses of magnocellular and parvocellular cells of the monkey's lateral geniculate body to moving stimuli, *Exp. Brain Res.* 35 (1979) 547–557.
- [11] W.R. Levick, L.N. Thibos, Orientation bias of cat retinal ganglion cells, *Nature* 286 (1980) 389–390.
- [12] W.R. Levick, L.N. Thibos, Analysis of orientation bias in cat retina, *J. Physiol. (London)* 329 (1982) 243–261.
- [13] T.T. Norton, R.N. Holdefer, D.W. Godwin, Effects of bicuculline on receptive field center sensitivity of relay cells in the lateral geniculate nucleus, *Brain Res.* 488 (1989) 348–352.
- [14] J.D. Pettigrew, M. L. Cooper, G.G. Blasdel, Improved use of tapetal reflection for eye-position monitoring, *Invest. Ophthalmol. Vis. Sci.* 18 (1979) 490–495.
- [15] T. Shou, D. Ruan, Y. Zhou, The orientation bias of LGN neurons shows topographic relation to area centralis in the cat retina, *Exp. Brain Res.* 64 (1986) 233–236.
- [16] T. Shou, A.G. Leventhal, Organized arrangement of orientation sensitive relay cells in the cat's dorsal lateral geniculate nucleus, *J. Neurosci.* 9 (1989) 4287–4302.
- [17] T. Shou, A.G. Leventhal, K.G. Thompson, Y. Zhou, Direction biases

- of X and Y type retinal ganglion cells in the cat, *J. Neurophysiol.* 73 (1995) 1414–1421.
- [18] T. Shou, Y. Zhou, B. Hu, Two types of directional sensitive X and Y cells in the cat retina, *Chin. J. Neurosci.* 2 (1996) 29–36.
- [19] A.M. Sillito, J.A. Kemp, The influence of GABAergic inhibitory processes on the receptive field structure of X and Y cells in the cat dorsal lateral geniculate nucleus (LGNd), *Brain Res.* 277 (1983) 63–77.
- [20] R.E. Soodak, Two-dimensional modeling of visual receptive fields using gaussian subunits, *Proc. Natl. Acad. Sci. USA* 83 (1986) 9259–9263.
- [21] R.E. Soodak, R.M. Sharpley, E. Kaplan, Linear mechanism of orientation tuning in the retina and lateral geniculate nucleus of the cat, *J. Neurosci.* 58 (1987) 267–275.
- [22] R.E. Soodak, R.M. Sharpley, E. Kaplan, Fine structure of receptive-field centers of X and Y cells of the cat, *Vis. Neurosci.* 6 (1991) 621–628.
- [23] J. Stone, Y. Fukuda, Properties of cat retinal ganglion cells: a comparison of W-cells with X- and Y-cells, *J. Neurophysiol.* 37 (1974) 722–748.
- [24] K.G. Thompson, Y. Zhou, A.G. Leventhal, S.J. Ault, Direction sensitive relay cells in the LGNd of cats and monkeys, *Soc. Neurosci. Abstr.* 16 (1990) 158.
- [25] K.G. Thompson, Y. Zhou, A.G. Leventhal, Direction sensitive X and Y cells within the A laminae of the cat's LGNd, *Vis. Neurosci.* 11 (1994) 927–938.
- [26] K.G. Thompson, A.G. Leventhal, Y. Zhou, D. Liu, Stimulus dependence of orientation and direction sensitivity of cat LGNd relay cells without cortical inputs: a comparison with area 17 cells, *Vis. Neurosci.* 11 (1994) 939–951.
- [27] D.J. Uhrlich, J.B. Cucchiaro, GABAergic circuits in the lateral geniculate nucleus of the cat, in: R.R. Mize, R.E. Mare, A.M. Sillito (Eds.), *Progress in Brain Research*, Vol. 90, Elsevier, New York, 1992, pp. 171–192.
- [28] T.R. Vidyasagar, Contribution of inhibitory mechanisms to the orientation sensitivity of LGN neurons, *Exp. Brain Res.* 55 (1984) 192–195.
- [29] F. Wörgötter, O. Grundel, U.T. Eysel, Quantification and comparison of cell properties in cat's striate cortex determined by different types of stimuli, *Eur. J. Neurosci.* 2 (1990) 928–944.
- [30] F. Wörgötter, G. Holt, Spatiotemporal mechanisms in receptive fields of visual cortical simple cells: a model, *J. Neurophysiol.* 65 (1991) 494–510.
- [31] J.H. Zar, in: *Circular Distribution in Biostatistical Analysis*, Prentice-Hall, Englewood Cliffs, NJ, 1974.
- [32] Y. Zhou, T. Shou, B. Hu, Two types of direction sensitivity of the cat's lateral geniculate nucleus (LGN) and their possible models, *Chin. Sci. Bull.* 37 (1992) 2093–2096.
- [33] Y. Zhou, A.G. Leventhal, K.G. Thompson, Visual deprivation does not affect the orientation and direction sensitivity of relay cells in the lateral geniculate nucleus of the cat, *J. Neurosci.* 15 (1995) 689–698.
- [34] Y. Zhou, T. Shou, Decortication and visual deprivation does not affect two types of directional properties of LGNd relay cells in the cat, *Chin. Sci. Bull.* 41 (1996) 1986–1990.