

## ORIENTATION BIASED EXTENDED SURROUND OF THE RECEPTIVE FIELD OF CAT RETINAL GANGLION CELLS

T. SHOU,\*†‡§ W. WANG† and H. YU\*†

\*Vision Research Lab and Liren Lab, Center for Brain Science Research, School of Life Sciences, Fudan University, Shanghai 200433, PR China

†Vision Research Lab, School of Life Sciences, University of Science and Technology of China, Hefei, Anhui 230027, PR China

‡Laboratory of Visual Information Processing, Institute of Biophysics, Chinese Academy of Sciences, Beijing 100101, PR China

**Abstract**—Here we report that the extended surround outside the classical receptive center (hereafter called the extended surround) of most retinal ganglion cells in the cat exhibit significant orientation bias to grating stimuli, and that the center and the extended surround show different orientation biases at different spatial frequencies.

As a result, some retinal ganglion cells possess a complex receptive field structure, which allows them to detect sophisticated image segmentation (e.g. texture segmentation) in addition to simple luminance edges. This property was previously thought to exist primarily in the visual cortex. Moreover, in about one quarter of 128 cells studied the center did not exhibit an orientation bias. Thus, these surrounds alone may determine the cells' orientation bias.

In conclusion, the extended surround may play an important role in processing more complex pattern in natural scenes since the classical receptive field is too small to describe all the properties of a retinal ganglion cell. © 2000 IBRO. Published by Elsevier Science Ltd. All rights reserved.

*Key words:* orientation, extended surround, receptive field, retinal ganglion cells, cat.

For three decades orientation selectivity, which is essential to the perception of forms, has been considered a unique property of visual cortical cells in the mammal.<sup>5,7–11,29</sup> However, in recent years it has been well documented that most retinal ganglion cells (RGC) and relay cells in the dorsal lateral geniculate nucleus (dLGN) of the cat also exhibit relatively weak, but significant orientation biases.<sup>15–17,23,24,26,28,30,31,35</sup> The orientation biases of these cells are often attributed to the receptive field center since they usually appear when tested with stimulus gratings of relatively high spatial frequencies.<sup>16,17,24,26</sup> A disinhibitory surround beyond the classical receptive field of retinal ganglion cells has been reported.<sup>11,18</sup> Whether the extended surround contributes to the orientation bias of the RGCs remains unknown. In fact, the size of an RGC's classical receptive field is smaller than the area in which the photoreceptors feed signals through the retinal circuits to the cell.<sup>11,12,18,20,22</sup> The extended surround outside the classical receptive field center (hereafter called the extended surround) and the center are often exposed to different features in natural scenes.<sup>1,3</sup>

It is essential to know what the extended surround does in visual information processing. To study this, in the urethane-anesthetized paralysed cats, we separately represented two drifting sinusoidal gratings of different orientations and spatial frequencies on each RGC's classical center and the extended surround, which is about 10 times larger in diameter than the center. The cell's spatial frequency and orientation tuning properties at different stimulus conditions were studied quantitatively. We find that the extended surround of most RGCs receptive fields exhibits significant orientation bias to

grating stimulation, and plays an important role in visual processing of complex patterns.

### EXPERIMENTAL PROCEDURES

#### *Surgical procedures and physiological recording*

The detailed methods for recording single-unit activity from the retinal ganglion cells of anesthetized and paralysed cats have been described elsewhere.<sup>25,26,35,36</sup> All investigations involving animals conformed to the guidelines of the Chinese Association for Physiological Sciences on the Ethical Use of Animals and the ARVO statement on the Use of Animals in Ophthalmic and Vision Research. All efforts were made to minimize the number of animals used and their suffering. Cats were initially anesthetized with ketamine (20 mg/kg). During the rest of the experiment, light anesthesia was maintained with intravenous urethane given at an initial dose of 30 mg/kg followed by an infusion of 20 mg/kg per h. Gallamine triethiodide (Flaxedil, Shanghai Dongfeng Chemicals Factory, China, 8–10 mg/kg per h) was used for immobilization. An indication of the level of the anesthesia was gained from the heart rate and the blood pressure, which were continuously monitored. Pupils were maximally dilated with atropine sulfate (1%), and appropriate contact lenses were used to protect the cornea. Neosynephrine (5%) was administered to retract the nictitating membranes. Since we had found that most eyes of the urethane-anesthetized, gallamine triethiodide-paralysed cats (61% in 44 eyes) had astigmatism ranged from 0.25 to 2.25 diopters with a mean of 0.75 diopters,<sup>26</sup> special care was taken to avoid astigmatism by using a combination of spherical and cylindrical lenses when needed. Optimal optics and optometry of the eyes were confirmed by an ophthalmologist.

The animal's rectal temperature, heart rate, ECG, end-tidal CO<sub>2</sub>, and blood pressure were routinely monitored and kept within normal limits. All pressure points and incisions were infiltrated with local long-acting anesthetic (1% lidocaine HCl). All efforts were made to minimize animal suffering, to reduce the number of animals used, and to utilize alternatives to *in vivo* techniques, if possible.

The action potentials of cat retinal ganglion cells were extracellularly recorded from the optic tract with a tungsten-in-glass microelectrode. The impedance of microelectrodes ranged from 5 to 15 MΩ. Signals were amplified and passed to a window discriminator, whose output was stored in a computer and also fed to an audio-monitor.

§To whom correspondence should be addressed. Fax: +86-21-65340149.  
E-mail address: tdshou@fudan.edu.cn (T. Shou).

Abbreviations: dLGN, dorsal lateral geniculate nucleus; RGC, retinal ganglion cell.

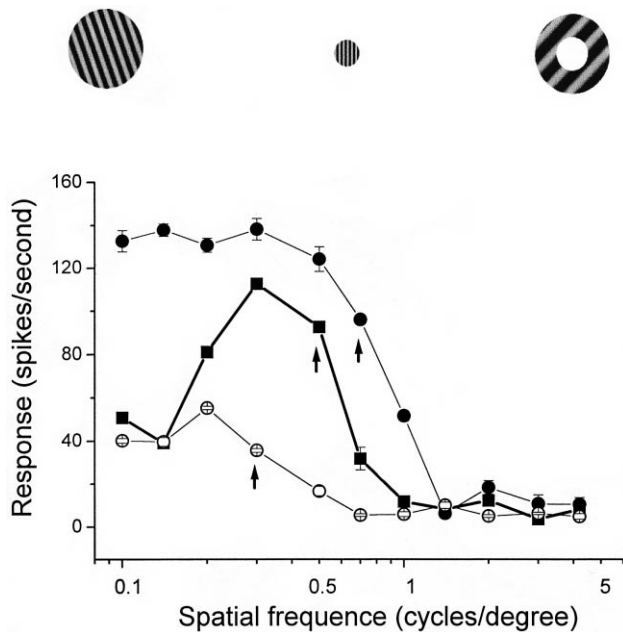


Fig. 1. Spatial frequency tuning curves of a typical RGC (an on-center Y cell) in the cat. The classical receptive field center, the extended surround outside the center and the whole area (the center plus the extended surround) were stimulated, respectively, by drifting sinusoidal gratings of different spatial frequencies at an identical orientation. The schematic visual stimulus patterns employed are listed on the top row. The three arrows indicate the optimal spatial frequencies employed to elicit the cell's best orientation biases of the center, the extended surround and the whole area (0.7, 0.3 and 0.5 cycles/°, respectively). The grating stimuli were identical in mean luminance (19 cd/m<sup>2</sup>), contrast (0.5), and temporal frequency (3 Hz). Note that the tuning curve of the center is like a high cutoff frequency filter (solid dots), the extended surround like a low pass filter (circles), and the whole areas like a band pass filter (solid squares). Moreover, the nonlinear interaction between the center and the extended surround suppressed the responses of the whole area at high frequency, even which the extended surround alone had no response. The vertical short bars denote the 95% confidence level.

#### Visual stimuli

The receptive fields of isolated units were first mapped on a tangent screen 114 cm from the cat's eye. Visual stimulation was generated with a Picasso Image Synthesizer (Innisfree, U.S.A.), an oscilloscope-based optical display (Tetronix 608, U.S.A.) and a computer controlled visual stimulus system (VS System, Cambridge Electronic Design, U.K.). The visual stimulus patterns on a uniform background of mean luminance (19 cd/m<sup>2</sup>) on the display were two drifting sinusoidal gratings independently displayed within an inner patch (diameter 1–1.5°) and an outer annulus (inner diameter 2–2.5°, outer diameter 8–9°). They were carefully centered over the receptive field center of each cell. Within the patch and annulus the two drifting gratings were presented at various orientations and spatial frequencies in a randomized interleaved sequence. The orientation of each grating was orthogonal to the drifting direction. The motions of the two drifting gratings were always kept phase-locked at a constant temporal frequency of 2–4 Hz. Their mean luminance and contrast were 19 cd/m<sup>2</sup> and 0.5, respectively. The diameters and the center positions of the patch and the annulus used for each cell were carefully selected by precise measuring (i) a one-dimensional response distribution using a moving small flash spot; and (ii) an area-response curve using a stationary diameter-increasing flash spot.

#### Data analysis

The amplitude of the fundamental Fourier component of averaged post-stimulus time histogram (PSTH) of a cell's response to grating stimuli was defined as response (spikes/s). The retinal ganglion cells were categorized as on- and off-center, X and Y type cells according to criteria commonly used.<sup>6,8</sup> The circular statistics was employed to quantify the preferred orientation and orientation bias as previously

reported.<sup>2,24,32,33,35</sup> The responses of each cell to the different orientations of stimuli presented were measured as a series of vectors. The vectors were added and divided by the sum of the absolute values of the vectors. The polar angle of the resultant vector is the cell's preferred orientation. The length of the resultant summed vector provides a quantitative measure of orientation bias of each cell. A cell's bias over 0.1 means that the cell showed statistically significant orientation bias at the level of 0.005.<sup>15,23,24,30,32,35</sup>

## RESULTS

One hundred and twenty-eight retinal ganglion cells including 97 Y cells and 31 X cells (70 on-center and 58 off-center cells) were studied in seven adult cats. Each cell's spatial frequency tuning and orientation tuning curves were separately measured with respective stimulating on the center, the extended surround, and the whole area covering the center and the extended surround (hereafter called the whole area).

#### Spatial frequency tuning property

The spatial frequency tuning curves of the center, the extended surround, and the whole area for a typical cell are shown in Fig. 1. The curve of the center (solid dots) always shows the highest cutoff spatial frequencies, and that of the extended surround (circles) shows the lowest. Between them is the curve of the whole area (solid squares). The bell-shaped curve of the whole area indicates that the simultaneous stimulation of the extended surround produced a strong inhibitory effect on the center response, especially at both low and high parts of spatial frequency. In contrast to the classical linear model of the difference of Gaussians,<sup>6,8</sup> the response decline of the whole area at high spatial frequency, to which the extended surround alone responded silently, indicates a nonlinear interaction between the center and the extended surround.

#### Orientation tuning property

Based on the circular statistical criteria,<sup>2,33</sup> we found surprisingly that most cells (75.8%, 97 in 128 cells, 70 Y cells, and 27 X cells) studied showed significant orientation biases (bias > 0.1,  $P < 0.005$ ) when their extended surrounds were stimulated alone with gratings mostly at relatively low spatial frequencies. In contrast, only about half of the cells (48.4%, 62 in 128 cells, 44 Y cells and 18 X cells) studied did so when the centers were stimulated alone with gratings mostly at relatively high spatial frequency. It is noticeable that these orientation biases were spatial frequency dependent. As shown in Fig. 1, the three arrows indicate the optimal spatial frequencies, to which the center, the surround and the whole area exhibited the best orientation bias, respectively. In fact, there was no significant difference in mean orientation bias between the biased center and the biased extended surround, whose mean biases were  $0.199 \pm 0.093$  (S.D.) and  $0.202 \pm 0.078$  (S.D.), respectively ( $t$ -test,  $P > 0.10$ ). There was also no significant difference in mean orientation bias among the center [ $0.127 \pm 0.102$  (S.D.)], the extended surround [ $0.170 \pm 0.093$  (S.D.)] and the whole area [ $0.165 \pm 0.097$  (S.D.)] ( $t$ -test,  $P > 0.05$  for all) of total 128 cells, as shown in Fig. 2. This does not seem to agree with the previous view that the orientation bias of ganglion cells is only a reflection of an elliptical receptive field center.<sup>17,15,28</sup>

The majority of cells studied (71.1%, 91 in 128 cells, 68 Y

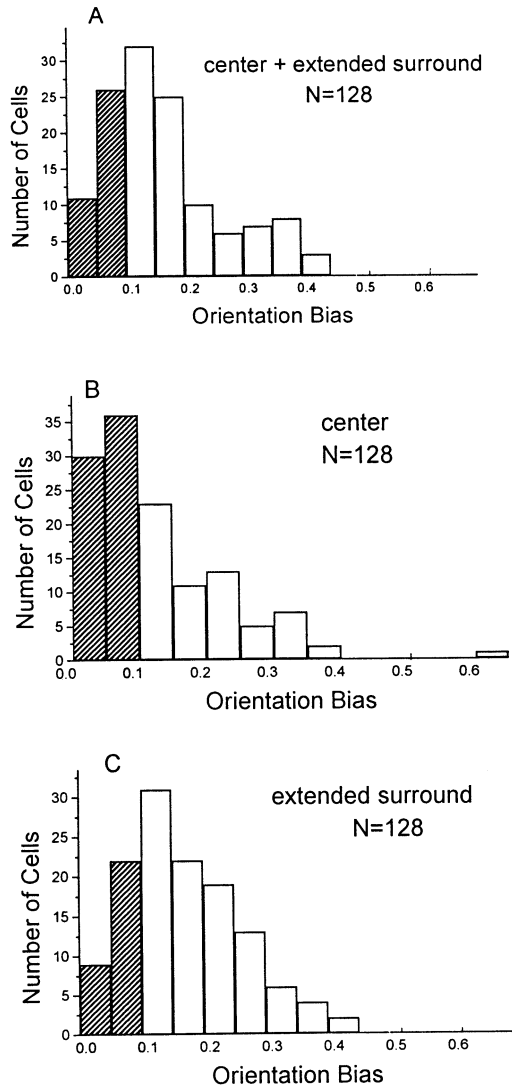


Fig. 2. Distribution of orientation biases of 128 retinal ganglion cells when both the classical center and the extended surround (A), the classical center only (B) and the extended surround only (C) were separately stimulated with gratings of different optimal spatial frequencies. The shaded columns represent numbers of cells showed no orientation bias ( $<0.1$ ) according to the circular statistics. Note that there is no significant difference in mean orientation bias either among them ( $t$ -test, all  $P > 0.05$ ) or among those cells with biases greater than 0.10 ( $t$ -test,  $P > 0.10$ ).

cells and 23 X cells) exhibited statistically significant orientation biases [mean bias  $0.205 \pm 0.090$  (S.D.)] when the whole areas were stimulated with gratings of medium spatial frequencies. Therefore, the extended surround must have something to do with the cell's orientation bias. As in the cells shown in Fig. 2B, interestingly, in 51.6% (66/128) of the cells studied, the grating stimuli of the centers alone did not elicit significant orientation biases, while stimulation of the extended surrounds and the whole areas did so. Obviously, the extended surrounds of these cells are dominantly responsible for the orientation bias of these cells.

Figure 3 shows typical samples of the orientation tuning curves for three cells. The curves in Fig. 3A exhibit a difference of  $90^\circ$  in preferred orientation between the center (solid dots, orientation bias 0.22) and the extended surround (circles, bias 0.27). As a result, the orientation bias of the whole area (triangles, bias 0.43) increased indicating an

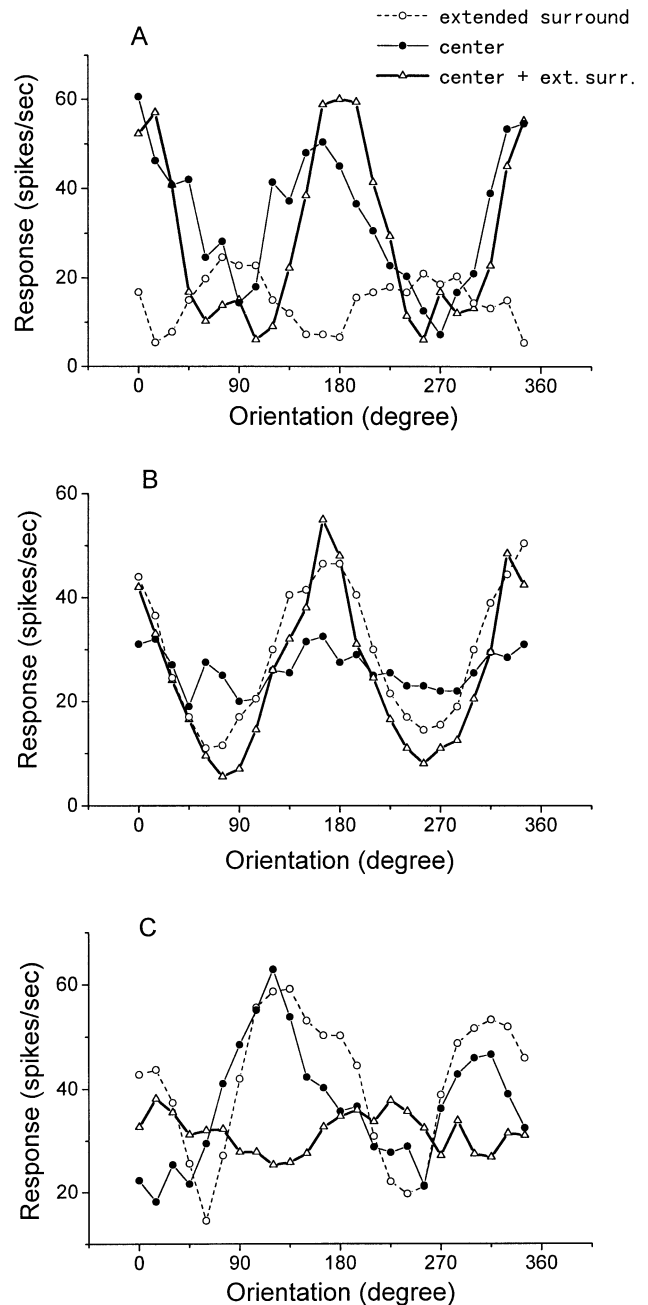


Fig. 3. The orientation tuning curves of three retinal ganglion cells when the center (solid dots), the extended surround (circles) and the whole area (triangles) were separately stimulated by drifting gratings at different orientations and optimal spatial frequencies. (A) The preferred orientation of the whole area of an on-center Y cell was parallel to that of the center, but orthogonal to that of the extended surround, indicating a cross-orientation-inhibition. (B) The center of an on-center X cell showed no orientation bias ( $<0.1$ ), while the extended surround showed a strong bias of 0.22. The cell's extended surround determines the preferred orientation of the whole area through a sign inverse mechanism such as disinhibition. (C) Both the center and the extended surround exhibited clear orientation bias, but the whole area had no bias at all. The spatial frequencies used for the center, the surround and the whole area are in turn in A, 1.0, 0.5 and  $0.7\ c^\circ$ ; B, 0.8, 0.3 and  $0.5\ c^\circ$ ; 1.0, 0.5 and  $0.7\ c^\circ$ , respectively.

orientation cross-inhibition mechanism involved. For the cell in Fig. 3B, the extended surround (circles, bias 0.22) dominated the cell's orientation bias (triangles, bias 0.31) because the center alone (solid dots, bias 0.07) lacked orientation sensitivity.

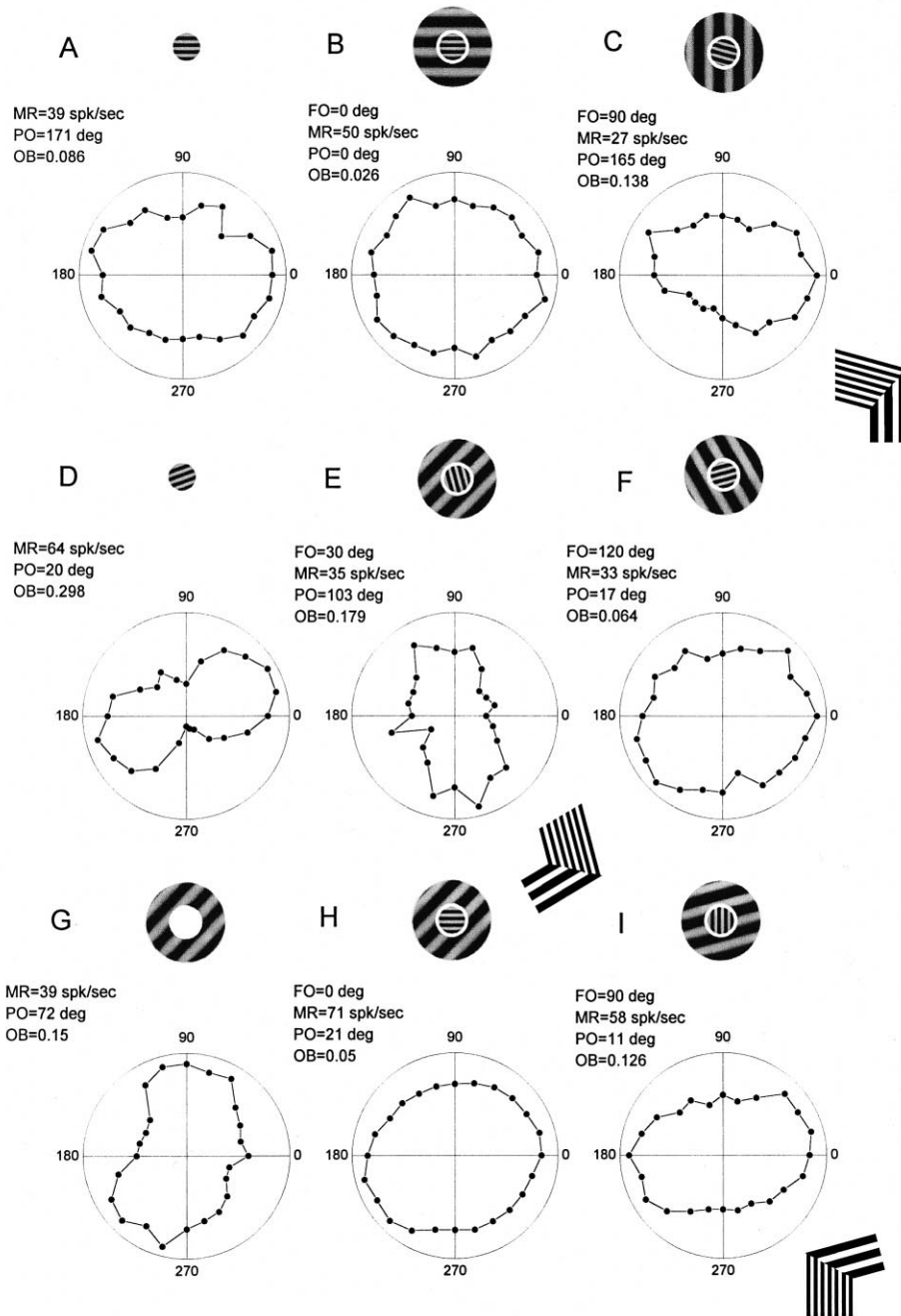


Fig. 4. Influence of drifting grating stimulation of the extended surround (or the center) on the orientation tuning curves of the center (or the extended surround). The grating was fixed at orientations parallel or orthogonal to the cells' preferred orientations of the extended surround (or the center). (A, D), Polar plots of orientation tuning curves of the center (or the extended surround in G) when the cell's receptive field center (of the extended surround in G) alone was stimulated with a drifting grating at the optimal spatial frequency. (B, E), Polar plots of orientation tuning curves of the center (or the extended surround in H) when the extended surround (or the center in H) was simultaneously stimulated with a drifting grating fixed in the preferred orientation of the extended surround (or the center in H). (C, F), Polar plots of orientation tuning curves of the center (or the extended surround in I) when the extended surround (or center in I) was stimulated with a grating fixed at the orientation orthogonal to the preferred one of the extended surround (or the center in I). The schematic stimulus patterns are shown on the top row for each tuning curve. The patterns at the right bottom of some tuning curves (shown in C, E and I) represent the presumable texture segmentations that the cells tend to detect preferentially. FO, fixed orientation; MR, maximum response; PO, preferred orientation; OB, orientation bias.

The cell's preferred orientation of the whole area is exactly identical to that of the extended surround, suggesting a possible disinhibitory mechanism is involved. In addition, in a few cells (e.g. the cell in Fig. 3C) the center and the extended surround with similar orientation bias (solid dots and circles, bias 0.18 and 0.20, respectively) and preferred orientation seemed to antagonize each other. Thus, the orientation tuning curve of the whole area turns out to be flat (triangles, bias 0.07).

#### *Interaction of the center and the extended surround*

The non-linear interaction of the center and the extended surround having different orientation bias at different spatial frequencies makes it possible for some cells to be sensitive to some image segmentation. In Fig. 4A–F, the two cells were sensitive to certain combinations of two gratings with different spatial frequencies and orientations that stimulated

separately on the center and the extended surround (as shown at the right bottom in Fig. 4C and E). The cell's orientation bias reached to the maximum when the extended surround was simultaneously stimulated with a grating which was fixed at an orientation orthogonal to (Fig. 4C), but not parallel to (Fig. 4B) the preferred one of the surround. For the cell in Fig. 4D–F, the additional stimulating grating of the extended surround, which was fixed at an orientation parallel (Fig. 4E), but not orthogonal (Fig. 4F) to the preferred one of the surround, made the cell's preferred orientation change to about  $90^\circ$ , indicating a strong non-linear action of the extended surround on the orientation tuning of the cell. In contrast, the differently oriented grating stimulation of the extended surround completely eliminated the center's orientation bias (shown in Fig. 4B and F) because of the different fixed orientations used. A similar non-linear interaction was observed when we measured the orientation tuning property of the extended surround simultaneously with fixed grating stimuli on the center (Fig. 4H, I). This finding suggests that a complex receptive field structure larger than the classical receptive field of some ganglion cells may extract information of image segmentation (e.g. texture segmentation), which is a property often found in visual cortical cells.

#### DISCUSSION

This study provides the first demonstration that the extended surround of most cat ganglion cells exhibits significant orientation bias. This orientation bias can contribute greatly to the orientation tuning property of the cell's whole receptive field, including enhancement or decrease of the cell's orientation bias, determine the cell's orientation bias when the center exhibits no bias, and so on. Interestingly, this contribution seems to be of non-linear mechanism because the grating stimulation of the extended surround at different fixed orientations can vary the orientation tuning of the center differently, and vice versa. On the other hand, the contribution of the extended surround to the spatial frequency tuning of the whole receptive field also demonstrates non-linearity. This non-linear interaction between the classical center and the extended surround enables some cells to process more sophisticated visual patterns, such as image segmentation. From the results above there emerges a new concept that the large-scale extended surround outside the classic receptive center plays an important role in visual information processing in addition to the classical one. Thus, the function of RGCs is not only in extracting luminance contrast, but also in detecting complex patterns in a non-linear manner at the first stage of the visual pathway.

The classical receptive field, which was discovered by Kuffler with flashing light spots, consists of a concentric antagonistic center/surround structure.<sup>13</sup> Through the classical receptive field, the main function of the RGCs is to detect visual boundary contrast, either in luminance or in wavelength.<sup>6,8,13</sup> However, the size of a RGC's classical receptive

field is much smaller than the area in which the photo-receptors feed signals through the retinal circuits to the cell.<sup>11,12,18,20,22</sup> Under natural conditions, both the extended surround and the center of each RGC are usually exposed to different features simultaneously. Thus, the classical receptive field is not enough in describing a retinal ganglion cell's function in nature, and our study on the extended surround does demonstrate its important contribution to the function of visual processing on a large scale in addition to the classical one. The results we reported here are somehow in conflict with prior work on orientation tuning in retinal ganglion cells and dLGN cells<sup>15,17,28</sup> because of different stimuli used. Previous studies have never studied the orientation tuning property of such a large extended surround area with grating stimuli of different spatial frequencies systematically.

Recently, the region beyond the classical receptive field of the visual cortical cells and its function in modulating cell responses, even detecting focal orientation discontinuities were reported.<sup>19,27</sup> The function of the extended surround reported here may provide a neural basis of these cortical properties at retinal level. The ganglion cells' receptive fields can do more than we expected due to the surprising new property of the extended surround. In fact, it has been shown that ganglion cells respond to natural scenes more strongly and precisely than simple laboratory stimuli on the classical receptive field.<sup>1,3</sup> The powerful action of the extended surround may supply a reasonable explanation of this phenomenon.

There are several lines of evidence to indicate that the RGCs receive inputs from linear and non-linear subunits in the inner and outer plexiform layers of the retina. These subunits can be horizontal cells, amacrine cells, or bipolar cells.<sup>4,12,14,21,22,34</sup> Furthermore, two types of orientation-sensitive and orientation-biased amacrine cells with different functional mechanisms and morphological features have been found in rabbit retinae.<sup>4</sup> If amacrine cells like those also exist in cat retina, they may contribute greatly to the orientation bias of the extended surround and the center observed here. The heterogeneity of various subunits in the neural network of the extended surround might result in a receptive field structure more complex than the classic one, and the surround is able to have a powerful influence on the center due to its large area. It has been shown here that both the center and the extended surround consist of linear and non-linear subunits that exhibit different preferred orientations at different spatial frequencies. This may enable the cell to be sensitive to some types of image segmentation.

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