Orientation-specific modulation of rat retinal ganglion cell responses and its dependence on relative orientations of the center and surround gratings.

ABSTRACT.

In the primary visual cortex (V1) it has been shown that the neuronal response elicited by a grating patch in the receptive field (RF) center can be suppressed or facilitated by an annular grating presented in the RF surround area; the effect depends on the relative orientations of the two gratings. The effect is thought to play a role in figure-ground segregation. Here we have found that response modulation similar to that reported in cortical area V1, can also be found in all major classes of retinal ganglion cells (RGCs), including ‘concentric’ cells. Orientation-specific response modulation of this kind cannot result from interactions of independent RF mechanisms; therefore, more complex mechanism, which takes into account the relative orientations of the gratings in the RF center and surround, or sensing the borders between texture regions, has to be present in RFs of RGCs, even of the ‘concentric’ type. This challenges the consensus notion that their responses to visual stimuli are governed entirely by a RF composed of separate mechanisms: center, antagonistic surround and modulatory extra-classical surround. Our findings raise the question of whether initial stages of complex analysis of visual input, normally attributed to the visual cortex, can be achieved within the retina.

INTRODUCTION

A number of studies in the primary visual cortex (V1) in cats and monkey have documented that neuronal responses to a stimulus placed within the cell’s receptive field
(RF) center can be strongly modulated by the simultaneous presentation of stimuli in the ‘silent’ regions which surround the RF center (DeAngelis et al., 1994; Sengpiel et al., 1998; Sceniak et al., 2001; Cavanaugh et al., 2002). The presence of ‘extra-classical’ RF surround has also been suggested in RGCs (Passaglia et al., 2001; Solomon et al., 2006). The most striking feature of center-surround interactions in V1 was revealed by presenting a drifting grating patch in the RF center, and an annular grating in the surround area. This latter stimulus, when presented alone, was ineffective in eliciting the cell’s response, but markedly influenced the neuron’s response when it was presented together with the center patch grating. The response magnitude depended on the relative orientations of these two grating stimuli: the response was maximal when the gratings were orthogonal, and was suppressed when the gratings were collinear, regardless of the orientation of the center grating and the orientation preference of the cell (Sillito et al., 1995; Levitt and Lund, 1997). This character of response modulation reveals contextual dependence of responses in V1: it cannot result from interaction of separate and independent effects elicited by the stimulus in the RF center and surround; rather it implies a mechanism which has to take into account the relative orientations of the center and surround stimuli. This phenomenon has commonly been thought as playing a role in higher-level analysis of visual scenes, such as figure-ground segregation (Albright and Stoner, 2001; Series et al., 2003).

Similar orientation-specific center-surround interactions have also been observed in area V1 in rat (Girman et al., 1999). Furthermore, when recording responses to grating stimuli in the most superficial layer (SGS1) of the rat superior colliculus, we (Girman and Lund, 2007) found that many neurons displayed response modulation very similar to that
found in area V1 as described above. We showed that these responses couldn’t result
from cortical feedback projections to the colliculus. This led us to question whether these
properties were developed de novo in the colliculus in parallel to the cortex, or whether
they reflected properties already developed in the retina. The present study was aimed at
answering this question by exploring whether orientation-specific response modulation
can be seen in the rat retina.

METHODS.

Animal preparation. Long Evans hooded rats (n=18) were used in this study. All
procedures were reviewed and approved by the OHSU Animal Care and Use Committee
and were consistent with NIH and Society for Neurosciences guidelines. Recordings were
made with intraretinal microelectrode penetrations in vivo. Animal anesthesia and general
preparations were described in our previous paper (Girman and Lund, 2007). A neutral
contact lens fixed in a metal ring was placed on the eyeball, with the ring attached to a
stereotaxis frame. A satisfactory level of eye fixation was achieved due to natural
adhesion of the eyeball to the lens. The microelectrode (tungsten-in-glass, tip length and
diameter ~1-2 μm) was inserted obliquely into the eye through the microscopic sclera
incision made ~0.5 mm behind the limbus. We isolated single units within the 40-60 μm
after the microelectrode enters the retina. Our technique allowed stable recordings from
single cells during the time necessary to complete up to 10 -15 tests, which could take up
to five hours. At the end of the recording session, the animal was recovered from the
anesthesia, and the eye was treated with antibiotic ointment. The animal was rested for 5-
10 days between subsequent, up to five, recording sessions. In subsequent sessions no
signs of deterioration of the eye state or RGC responses were observed: the eye could not
be distinguished by its appearance from an intact one (no inflammation, healed conjunctiva, normal pupil reflex); the multiunit activity, recorded when microelectrode approached the retina, was strongly modulated by visual stimuli; the maintained activity and responsiveness of isolated RGCs appeared normal.

Visual stimulation, data acquisition and analysis. We used the same technique of visual stimulation and data acquisition as described previously. In short, the visual stimuli were created with Neurophysiology software (Vision Research Graphics, Durham, NH) and presented in black and white mode on NEC FE 950 monitor (the screen size 360 x 270 mm, frame rate 120 Hz, resolution 800 x 600 pixels) positioned 40 cm from the animal’s eye. The monitor was windowed by a circular aperture (270 mm in diameter) in a wide black shield. The stimuli were the flashing circular spots or annuli centered on the RF, or drifting sinusoidal grating patches and annuli of varying orientations and diameters. The grating spatial and temporal frequencies were set to optimal (typical values 0.1 c/deg and 5 Hz respectively), the mean grating brightness was 26 cd/m², same as background illumination, and Michelson contrast was around 80%. The brightness of flashing stimuli alternated from the background level to Black (1.5 cd/m²) or White (50 cd/m²) for 0.67 s, and then switched back; the inter-stimulus intervals were 1.2 s.

Ambient illumination was kept at ~0.5 cd/m².

The RF location, in most of the recorded RGCs, was invariantly (due to roughly the same orientation of the microelectrode relative to the eye coordinates) within an area ~30° in diameter with the center located around 30° above the horizontal plane and 45° lateral to the median plane. This helped positioning the display in register with the RF. The RF was precisely centered on the display by adjusting the display position until the
response to a circular, concentric with the display screen, contrast-reversing bipartite field, oriented horizontally and then vertically, contained no or minimal component at the frequency of reversal. If the cell did not respond to this stimulus (only a minority of cells did not respond), the RF center was located by a maximal response to a flashing spot of a minimal diameter producing reliable responses. In a great majority of recordings there was no need to correct the stimulus position during the whole experiment, but at any sign of RF displacement we re-mapped its position.

In all cases the recordings were made from well isolated single cells, achieving the spike amplitude to noise ratio (the discharges of neighbor cells have been considered as a noise component) no less than 5, in order to accommodate the spike amplitude decrease often occurring during the phase of high-frequency responses, and to avoid interference from the background noise. We periodically recorded the digitized samples of spike discharges and stored them together with the main experimental data, so that almost all recorded cells (except for those showing very short responses and no spontaneous activity, SA) could be characterized by spike shape. To assure further that recordings were made from single units, we programmed the software controlling the data acquisition to send a warning message if the interval between two consecutive spikes was less than the pre-set value, usually 1.5 ms. We made sure that no such events occurred before starting an experiment, and discarded any data contaminated in such a way.

Neuronal activity was amplified, filtered (150 – 3000 Hz bandwidth) and played over a loudspeaker. The spikes transformed into standard impulses by window discriminator were passed, together with stimulus IDs from the stimulus presentation software, to a CED 1401 data acquisition device under control of Spike2 software (CED
Data analysis, firstly on-line and then more detailed off-line, was performed with the Spike2 script language program. With stimuli composed of drifting gratings, the response was expressed as F0, F1 and F2 coefficients of the Fourier transform of the response peri-stimulus time histogram (PSTH), whose time span was equal to the period of the grating; each histogram accumulated ten grating periods presented in a trial.

Presenting moving or stationary flashing spots and annuli we characterized the cell’s type (as ON, OFF or ON-OFF, ‘concentric’, directional selective, ‘local edge detector’), defined the ‘size’ of the RF center (as the diameter of the spot eliciting maximal response), the extent of the RF ‘classical’ surround (as the maximal inner diameter of the annulus still eliciting the cell’s responses; in this test the outer annulus diameter was 270 mm). Applying the grating patch stimulus, we defined the optimal grating parameters (spatial and temporal frequencies, patch diameter, grating orientation). To evaluate the cell’s tuning for orientation, we calculated the orientation selectivity index (OSI):

$$OSI = \frac{\sqrt{\sum_{i}^{N} R(\Theta_i) \sin(2\Theta_i)^2 + R(\Theta_i) \cos(2\Theta_i)^2}}{\sum_{i}^{N} R(\Theta_i)}$$

Eq. 1

where R(\Theta_i) is the response (F1 component) at the orientation \(\Theta_i\) of the grating patch.

To evaluate the effect of the annular grating of varying orientation on the response elicited from the RF center by the grating patch whose orientation was constant, we calculated the orientation selectivity index of modulation (mOSI) with Eq. 1, where R(\Theta_i) is the response magnitude at the orientation \(\Theta_i\) of the annular grating.

The magnitude of the modulation was evaluated by two indices
where $R(\Theta)$ is as indicated above, and Rc is the response to the center grating patch presented alone; $m_{\text{Max}} > 1$ indicates response facilitation.

After recording the area response curve presenting the center grating patch of varying diameter, we computed response suppression index (RSI). This was defined as:

$$RSI = 1 - \frac{R_{\text{max diam}}}{R_{\text{pref diam}}}$$

Eq. 3

where $R_{\text{(pref diam)}}$ is a peak value of the area response curve, and $R_{\text{(max diam)}}$ is the response at the maximum size (20º). In the case of response asymptotic increase with the diameter, $RSI = 0$.

RESULTS.

Applying stimuli and criteria commonly used to classify RGCs in other mammalian species we identified all the main RGC types in the rat retina, as specified below. The cell’s types identified and the percentage of cells in each class is shown in Table. 1. When stimulated with flashing spots centered on the cell’s RF, each cell class shows characteristic responses; their examples are presented in Fig. 1.

In each class, many cells responded well to a patch of drifting grating placed in the center of their RFs. We tested these cells further to see how the grating annuli presented in the RF periphery affected the center response. The results are presented separately for each cell type.

a. ‘Concentric’ RGCs. These cells were identified as those responding with spike bursts to brightness changes in their receptive field center and periphery in an antagonistic manner. They were typified further as belonging to ON- or OFF-subclasses according to the brightness transition of the center spot eliciting the cell’s response. All
these cells responded with spike bursts to the circular patch of drifting grating centered on the RF, and a majority of them showed some degree of response orientation tuning (OSI > 0.05).

We tested the ‘concentric’ cells for center-surround interactions by presenting the following grating stimuli: circular grating patch concentric with the RF, and grating annuli with the inner diameter equal to the diameter of the patch, and with an outer diameter of 20º; during the test, the orientation of the center grating was constant, while the orientation of the grating annulus varied. About 40% of the cells (74 of 184) showed significant orientation-dependent modulation of the center response by the surround stimulation. We observed such modulation in ON- and OFF-cells, of both brisk-sustained and brisk-transient cell subclasses.

The strongest effects of the annulus grating on center responses were observed in cells, which, when tested with center grating patches of increasing diameter, displayed considerable response suppression (RSI > 0.3; 22 of 59 cells). Typical examples of responses recorded in these cells are illustrated in Figs. 2 and 3. The diameter of the center grating patch (in a range of 6 – 9º) was set to elicit a maximal response. A striking characteristic of the center response modulation by the annular grating was the response dependence on relative orientations of the center and surround stimuli. When the annular grating was collinear with the grating of the center patch, the center response was most suppressed; in case of orthogonal orientations of the gratings, the response suppression was absent or much weaker. Often, response facilitation was even observed. Rotation of the center grating by 90º resulted in the 90º shift of the surround modulation pattern. The absolute orientation of the center grating affected to some degree the magnitude of the
effect, but in every case the response modulation depended on the relative orientations of the center and surround gratings as described.

This orientation-specific modulation was also observed in cells not tuned to the grating size. Their responses steadily rose and saturated with increasing diameter of the center patch, or declined mildly after reaching the maximum (these cells are characterized by RSI < 0.15, cell number N = 19). We tested the response modulation in these cells by applying a center patch of optimal diameter, or of a diameter eliciting ~95% of the saturated response; typical values of diameters were in a range of 6 – 9°. The center responses were almost unaffected when the orientation of the annular grating was collinear to that of the center patch, in accord with the cell’s area-response curve. But many of these cells showed significant response facilitation when the grating orientations were orthogonal, as illustrated in the examples in Fig. 4. Again, the modulation profile depended on the relative grating orientations: rotation of the center grating by some angle resulted in a shift of the modulation pattern by the same angle, though the magnitude of modulation varied somewhat. An annular grating presented alone evoked no response or only a weak response.

The orientation-specific modulation was independent of how robustly the cell’s response was tuned to grating orientation: even the cells showing no orientation tuning, displayed strong orientation-specific modulation of the center response, as illustrated in Fig. 3.

All the cells in which orientation-specific modulation was observed were further tested by presenting flashing center spots of light of varying diameter, and flashing annuli with varying inner diameter (the outer diameter of the annuli being equal to the diameter...
of the aperture windowing the screen, ~36°). The goal was to check whether the grating annuli used in two-grating tests were located outside the ‘classical’ RF outlined with flashing stimuli. We found that responses, antagonistic to those elicited by the center spot, were present in all cases when the inner diameter of the flashing annulus was considerably larger than the inner diameter of the grating annulus used in two-grating tests. Frequently, the inner diameter of the flashing annulus was even larger than the outer diameter of the annular grating (as shown in examples in Fig. 2). Thus, the annular gratings lay entirely within the limits of the ‘classical’ RF surround, or extended beyond it; the gratings were never entirely outside the ‘classical’ RF surround.

A summary of quantitative characterization of the center response modulation by the annular gratings presented in the RF surround is presented in Fig. 5. We characterized the strength of modulation by two indices, mMax and mMin (Eq. 2). The plot of indices calculated for 74 cells in which the modulation was significant (by a criterion mMax – mMin > 0.2), and the histogram of modulation depth (mMax – mMin) in these cells show that, in a majority of these cells a facilitation of the center response by a simultaneous presentation of the annular grating occurs; the effect of the annular grating was strong: modulation depth exceeded 0.6 in 56 of 74 cells (Fig. 5, A, B). We calculated the correlation between the orientation selectivity indices OSI and mOSI in 59 ‘concentric’ RGCs which displayed the modulatory effect of the surround stimulation, and in which both indices were measured. Results are presented in Fig. 5, C; the two indices show rather weak correlation. Analysis of correlation between the degree of the cell’s area response tuning (RSI) and the mOSI index show that they correlate strongly (Fig. 5, D).
b. ON-OFF and ON-directional RGCs. These cells showed responses to the spot of light moving in the preferred direction, and no or very weak responses to movement in the opposite direction. Occasionally we also encountered bi-directional units (of ON-type) showing optimal responses for movement in both directions along the axis of the preferred orientation. The direction-tuned cells of both types displayed also strong increase in the mean spike rate and a robust modulated response at the fundamental grating frequency (F1) when stimulated with the center patch of the drifting grating. The cell responses were tuned for the patch size and for the drift direction, but not, in case of uni-directional cells, for the grating orientation: the grating drifting in the preferred direction elicited maximal response, while the grating of the same orientation but drifting in opposite direction (i.e., whose orientation differed by 180º with respect to the first) elicited no or minimal response, as shown in the examples in Figs. 6 and 7. When tested with a center grating patch and grating annuli placed in the RF surround, all cells tested (ON-OFF: N = 8; ON: N = 6) displayed strong modulation of the center response by the peripheral annular grating, which itself was ineffective in eliciting the cell’s response. The orientation dependence of modulation was very similar to that reported in the previous section: regardless of absolute orientations of the center grating patch and of the grating annulus, the strongest response suppression was observed when the gratings presented in the RF center and surround were collinear; the maximal response corresponded to the orthogonal grating orientations, and, frequently, this response was stronger than those elicited by the center stimulation alone.

c. Local edge detectors. These cells were encountered infrequently and were characterized by ON-OFF responses and small RF size (typically in a range of 3-5º);
overall we encountered five cells of this type. The cells responded moderately but reliably to the center grating patch, and showed some response dependence on the grating orientation. They also showed responses to moving spots, but no directional selectivity. When tested in two-grating experiments, these cells showed very strong modulation of the center response by the annular grating which, when presented alone, induced no responses. Representative examples of their responses are shown in Fig. 8. The magnitudes of the center response suppression or facilitation by the annular grating varied somewhat depending on its absolute orientation, but in every case the center response modulation profile was dependent on the relative orientations of the center grating patch and the annular grating in the RF surround: the center response was maximally suppressed when the gratings were collinear, and the response was maximal when the gratings were orthogonal. When the orientation of the center grating was changed, the modulation pattern shifted correspondingly. In some cells, the center response was strongly facilitated by the annular grating orthogonal to the center grating (example of Fig. 8, Cell 2).

DISCUSSION.

Our data show that the properties of rat RGCs, described using traditional analysis, conform to standard classifications, including the classical center-surround relationship in ‘concentric’ RGCs. However, we have uncovered evidence of more complex RF properties. We showed that in a majority of rat RGCs a modulation of the center response by the surround depends on the relative orientations of the two grating stimuli. The effect was observed in all major RGC types, but was strongest in ‘non-standard’ cells, directional RGCs and the local edge detectors. Around 40% of ‘concentric’ RGCs also
showed this kind of response modulation. The RGCs of ‘concentric’ type are the most common RGCs in the mammalian retina, and were most frequently encountered in our recordings; the properties of orientation-specific modulation in these cells are the main focus of our study.

It is well documented in the literature that ‘concentric’ RGCs display many effects which cannot be simply attributed to their ‘classical’ RFs. Examples are: (i) the ‘shift-effect’ elicited by a sudden change in contrast or by a continuously moving texture in the far periphery of the receptive field (McIlwain, 1966; Barlow et al., 1977; Fischer and Kruger, 1980); (ii) an increase or decrease, depending on the spatial and temporal structure of the stimulus, induced in the continuous discharge rate by remote moving patterns (Passaglia et al., 2001); (iii) suppression of responses to brief probes by simultaneous changes in surrounding patterns (Solomon et al., 2006). These effects are attributed to a separate RF mechanism, termed the ‘far’ (‘extra-classical’, ‘modulatory’) surround.

Novel in our study is a demonstration that modulation of the center responses by surround in RGCs is orientation-specific and depends on the relative orientations of the center and surround gratings. The common notion is that the response modulation dependent on relative grating orientations described above is a context-dependent phenomenon that cannot be explained in the terms of the ‘classical’ RF (Sillito et al., 1995; Levitt and Lund, 1997; Albrigth and Stoner, 2002; Series et al., 2001; Series et al., 2003). First discovered in the VI, the phenomenon is considered as revealing an initial stage of context-dependent transformation of image into perception which starts in the
visual cortex. Thus, it is surprising to find such a complexity of response properties at the retinal level.

In the cortex, the contextual effects are thought to be mediated by cortico-cortical feedback from higher cortical areas, and by long-range horizontal connections within V1; network model of the center-surround modulation based on interconnections between neurons at different locations in the cortical orientation map has been proposed (Series et al., 2001). Orientation tuning of cortical neuronal responses is their major property, and is suggested to play an important role in mechanisms underlying the orientation-specific modulation of the center responses from the RF ‘far’ surround (for review see Series et al., 2003). In the retina, there is no evidence that neuronal mechanisms specifically tuned for grating orientation are present (but see Shou et al. 2000). Orientation bias of responses demonstrated in many RGCs is thought as reflecting elongated profiles of their RFs (Soodak et al., 1987; Passaglia et al., 2002). Moreover, orientation selectivity plays perhaps no role in the orientation-specific modulation we have uncovered in the retina: (i) the modulation was well expressed even in cells showing no orientation tuning of the center response; (ii) population data shows that the mOSI correlates weakly with the OSI. Perhaps, the modulation effect of the RF surround we described in the retina may have more in common with the cortical mechanism related to the perceptual ‘pop-out’ effect of the borders between texture regions.

Response modulation dependent on relative orientations of the grating patch and annulus, besides VI, have previously been seen in the rat superior colliculus (Girman and Lund, 2007). There are controversial data on whether the effect of the surround stimulation in the lateral geniculate nucleus is tuned for grating orientation: while some
studies found no preference for orientation of the surround effects (Solomon et al., 2002; Bonin et al., 2005; Camp et al., 2009), other showed its dependence on the relative orientations of the two gratings (Naito et al., 2007) or more complex relations (Sun et al., 2004).

In the cortical literature, orientation-specific center-surround response modulation is considered to arise from the ‘salient’ ‘far’ surround, spatially separated from the neuron’s ‘classical’ RF. Our data cast doubts on whether the same notion can be applied to RGCs. First, we found strong correlation of mOSI with the degree of response tuning to the stimulus size (Fig. 5). The descending branch of the area response curve in RGCs is commonly attributed to response suppression form the ‘classical’ RF surround, whose involvement increases with the stimulus diameter increase. Second, in our experiments the annular gratings were not in the ‘far’, but in the ‘classical’ RF surround. This was demonstrated by presenting a uniform flashing annulus even in the more remote RF periphery: the annulus elicited a ‘classical’ surround response, antagonistic to those elicited from the RF center. Thus, geometrically, the annulus gratings were within the limits of the ‘classical’ RF, but the stimulus strength was subthreshold for eliciting significant, if any, spike responses. Our results suggest that the ‘classical’ RF mechanism and the mechanism underlying the orientation-specific modulation may originate from the same RF area. Similar conclusion was made regarding the extent of the ‘extra-classical’ RF surround in LGN of cat and monkey (Bonin et al., 2005; Camp et al., 2009).

A majority of the cells that show orientation-specific modulation, exhibits marked response facilitation when the center and surround gratings are orthogonal. In RGCs tuned to grating orientation, we observed a facilitation of the center response even in
cases when the center grating patch was in a non-preferred orientation. A similar type of
response facilitation was reported previously in V1 (Sillito, 1995), although this finding
was not confirmed in other laboratories. One explanation for the facilitatory effect noted
in this study is that facilitation was observed in tests where the surround grating abutted
the center grating, and thereby partly stimulated the center mechanism, so that the
excitation of the ‘classical’ RF center by the optimally oriented grating annulus summed
with the response to the center grating patch (Cavanaugh et al., 2002; Angelucci and
Bressloff, 2006). Our data do not support this ‘classical’ explanation of facilitation of
responses to the center grating patch of non-preferred orientation: (i) in some RGCs
tuned for orientation, we observed facilitation of the response (to the center grating patch
of an optimal diameter) with both, preferred and orthogonal to that (non-preferred),
orientations of the annular grating, when the latter was orthogonal to the center grating;
(ii) facilitation was observed even in the cells showing none orientation selectivity at all.
Obviously, the facilitatory effect of modulation in these cases cannot be explained in
terms of the ‘classical’ RF mechanism, and have to result from the orientation-specific
center-surround modulation whose mechanism remains to be identified.

Whether the orientation-dependent surround effect in the retina is specific to rat is
not clear: it has not been examined in the retinas of more heavily studied animals, such as
rabbit, cat and monkey. However, a study in monkey retina (Solomon et al., 2006)
showed a modulatory effect (while its orientation specificity has not been examined) of
surround on center response, where stimulation of the surround alone had little effect on
the cell’s response. This effect was mainly observed in magnocellular cells, characteristic
of which is a strong tuning to the size of the center grating. In line with this finding, our
data show very reliable correlation between the orientation selectivity of modulation (mOSI) and the degree of the response tuning to the size of the center grating (RSI index). It should be noted however that the monkey studies were using a different stimulation condition and were not specifically addressing the issue of orientation-specific surround effects on responses to center stimulation.

While, following the cortical literature, we interpret our data as indicating that high-order visual processing can start in the retina, we cannot rule out that response dependence on relative orientations of the center and surround gratings might simply be a property of the ‘classical’ RF described by the Difference-of-Gaussians (DOG) model. From general considerations only, that seems improbable, but that has to be proved. We can refer to a mathematical solution of response of the DOG model to circular grating patches concentric with the RF (Einevoll and Plesser, 2005). Results demonstrate that, in some conditions, expansion of the patch into the strong classical antagonistic surround results not in response suppression, but in its facilitation; that seems very unexpected. With the use of mathematical tools described in the cited paper, it is possible to find response of the DOG model to grating patches and annuli presented together. But finding the solution is not a trivial task, which can constitute a goal of a separate study and is beyond the scope of our paper.

In conclusion, our findings suggest that initial stages of complex analysis of visual input, normally attributed to the visual cortex, can be achieved within the retina.

ACKNOWLEDGMENTS.

This work was supported by Foundation Fighting Blindness. We thank Drs.
REFERENCES:


Table 1. The cell’s types identified and the percentage of cells of each class.

<table>
<thead>
<tr>
<th>Cell type</th>
<th>Number</th>
<th>(%)</th>
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<tbody>
<tr>
<td>OFF BT</td>
<td>59</td>
<td>26.9</td>
</tr>
<tr>
<td>OFF BS</td>
<td>42</td>
<td>19.2</td>
</tr>
<tr>
<td>ON BT</td>
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<td>21.9</td>
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<td>ON BS</td>
<td>35</td>
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<tr>
<td>ON DS</td>
<td>6</td>
<td>2.7</td>
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<tr>
<td>LED</td>
<td>7</td>
<td>3.2</td>
</tr>
<tr>
<td>Unclassified</td>
<td>14</td>
<td>6.4</td>
</tr>
</tbody>
</table>

Abbreviations: BT – brisk transient; BS – brisk sustained; DS – directionally selective; LED – local edge detector.

FIGURE LEGENDS

Figure 1. Examples of PSTHs recorded in different RGC types in response to flashing spot of light centered on the RF. The traces below the histograms here and in the following figures indicate the spot brightness changes. Stimulus ON or OFF duration was 0.67 s followed by 1.2 s inter-trial interval during which a blank Gray screen was displayed. Bin width is 5.68 ms.
Figure 2. Examples recorded in two ‘concentric’ RGCs showing orientation-specific modulation of the center response by an annular grating placed in the RF surround. The charts A - D in each example show responses (here and in all figures below: solid curves – F1, dotted gray curves, when present – F0 Fourier components, mean ±SE) to drifting grating patches and annuli; SA – spontaneous activity. Charts A and B: the plots of responses to the center grating patch and annulus presented together; orientation of the grating annulus varied (indicated at X-axis) while the orientation of the center patch was permanent; response to the center patch presented alone is shown at right (dashed line), its diameter and orientation are as indicated. Charts A and B only differ by the orientation of the center grating patch. Note that changing its orientation results in the shift of modulation pattern by the same angle. Charts C: responses to the annular grating of varying orientation presented alone (no responses in Cell 1 example); the Y-axis scale is the same as in the chart above. Charts D: responses to the center grating patch of varying orientation presented alone; arrows indicated the center responses corresponding to these shown in charts A and B. Charts E: area response curves plotted versus the grating patch diameter; right to the curve: the response to the center patch of 20° in diameter is shown. Note that in these examples the cells displayed strong response decrease when the diameter of the grating patch exceeded an optimal value. Gratings spatial frequency (here and in all figures below) was 0.1c/deg, temporal frequency 5 Hz. In columns F the charts show responses (500-ms average ±SE) to the flashing stimuli; responses are plotted against the diameter of the flashing center spots (solid curves, OFF-responses) or against the inner diameter of the annulus (dashed curves, ON-responses); annulus outer diameter
was equal to the diameter of visible screen. PSTH below each chart corresponds to the peak response in the chart.

Figure 3. Another example of orientation-specific center-surround modulation. In Column A, the responses are calculated and plotted in the same way as in Fig. 2. Note that the RF center shows no orientation tuning (chart C), and the annular grating presented in the RF surround (eliciting no significant responses when presented alone) strongly modulated the center responses in an orientation-specific way. Chart B: area response curve. Histograms D, showing responses recorded to flashing stimuli described in Fig. 2, prove that the cells was of the ‘concentric’ ON-BS type.

Figure 4. Examples of orientation-specific modulation of the center response by an annular grating presented in the RF surround. The charts A in each example shows, in the same way as in Fig. 2, the center response modulation by annular gratings presented in the RF surround. Note the shift of the modulation pattern when the orientation of the center patch grating is changed. The upper charts in columns B: the area response curves; note that responses of these cells increased monotonically or decreased only slightly after reaching the maximum. Below are plotted responses versus the orientation of the center patch of grating. The PSTHs show responses to the flashing stimuli as described in Fig 2.

Figure 5. A. Diagram of modulation indices mMax and mMin (Eq. 2) calculated for 74 RGCs (which show significant response modulation, mMax – mMin > 0.2) of ‘concentric’ type. Note that a great majority of dots representing the cell response modulation lies above mMax = 1 i.e. shows response facilitation by the annular grating presented in the RF surround. B. Histogram of the depth of modulation calculated as mMax – mMin (for the same cells included in panel A). C. Diagram of mOSI plotted
versus OSI; D Diagram of mOSI plotted versus RSI; in each diagram a regression line is shown (dashed). Note much stronger correlation between mOSI and RSI than between mOSI and OSI (ANOVA test).

Figure 6. Examples of responses of ON-OFF directional cells to different stimuli. Charts A – C: responses to grating stimuli presented in the same way as in Fig. 2 (responses to the annulus grating alone are shown below the chart C or B). Charts D: responses to the spot of 4º in diameter brighter than background plotted versus the direction of its movement through the RF center. Charts E: responses to the center patch of drifting grating plotted versus the grating orientation. The PSTHs show responses to the center flashing spot; the time scales are the same as in the histograms of Fig. 1 and elsewhere.

Figure 7. Examples of responses of ON directional cells to different stimuli. Charts A - B: responses to grating patches and annuli are shown in the same way as in the previous figures. Charts C: responses to the moving 5º spot plotted versus the movement direction. Chart D: responses to the center patch of drifting grating plotted versus the grating orientation. The PSTHs show, in the same way as in Fig. 6, responses to the center flashing spot.

Figure 8. Examples of responses recorded in ON-OFF local edge detectors. Charts A and B shows, in the same way as in previous figures, the center response modulation by the annular grating presented in the RF surround. Charts C: responses to the spot of light moving through RF center; chart D – responses to the center patch of drifting grating plotted versus the grating orientation. The PSTHs show responses to the center flashing spot of light similar to those shown in the previous figures.
Figure 1

- ON BS
- ON BT
- OFF BS
- OFF BT
- ON DS
- ON-OFF DS
- ON-OFF LED

Imp/s
Figure 2
Figure 3
Figure 4

Cell 1 (OFF-BS)

Cell 2 (OFF-BS)
Figure 5

A

B

C

\[ r^2 = 0.12 \quad P = 0.006 \]

\[ r^2 = 0.514 \quad P = 1.7 \times 10^{-10} \]
Cell 1 (ON-OFF-DS)

Figure 6
Figure 7

Cell 1 (ON-DS)

Cell 2 (ON-biDS)
Cell 1 (LED)

Cell 2 (LED)

Figure 8