Computation of Motion Direction by Quail Retinal Ganglion Cells That Have a Nonconcentric Receptive Field

Hiroyuki Uchiyama1,2, Takahide Kanaya1 and Shoichi Sonohata1

1 Department of Information and Computer Science, Faculty of Engineering, Kagoshima University, Kagoshima 890-0065, Japan.
2 Intelligence and Synthesis, PRESTO, Japan Science and Technology Corporation, Tokyo 105-0013, Japan.

Abstract

One type of retinal ganglion cells prefers object motion in a particular direction. Neuronal mechanisms for the computation of motion direction are still unknown. We quantitatively mapped excitatory and inhibitory regions of receptive fields for directionally selective retinal ganglion cells in the Japanese quail, and found that the inhibitory regions are displaced about 1-3 deg. toward the side where the null sweep starts, relative to the excitatory regions. Directional selectivity thus results from delayed transient suppression exerted by the nonconcentrically-arranged inhibitory regions, and not by local directional inhibition as hypothesized by Barlow and Levick (1965).

Keywords: retinal ganglion cells, directional selectivity, motion perception, quail

Introduction

Animals must process dynamic visual information, because they live in dynamic interaction with their environment (Gibson, 1979). Directionally selective (DS) visual neurons prefer object motion in a particular direction and are thought to have an essential role for computation of visual motion information (Marr, 1982; Frost & Nakayama, 1983; Frost & Sun, 1997). While many animals are known to possess a rich population of DS retinal ganglion cells (RGCs) (Maturana & Frenk, 1963; Barlow et al., 1964; Michael, 1968; Lipetz & Hill, 1970; Daw & Beauchamp, 1972; Stone & Fukuda, 1974; Uchiyama & Barlow, 1994), it is still unclear how their directional preference is induced from neuronal activities of distal retinal neurons that show no directional preference. Barlow and Levick (1965) proposed that local directional inhibition gives rise to directional selectivity in the retina, and computational models have been constructed based on this hypothesis (Koch et al., 1986; Hildreth & Koch, 1987). While starburst amacrine cells have been proposed as a possible neural substrate for local directional inhibition (Oyster, 1990; Barlow, 1996), very recently it has been shown that directional selectivity remains unchanged in the rabbit DS RGCs after selective destruction of starburst amacrine cells (He & Masland, 1997). Starburst amacrinines may potentiate the responses of RGCs to moving stimuli, but the potentiation does not appear to have directional bias (Masland et al., 1984; He & Masland, 1997). Thus it remains unknown how local directional inhibition is implemented for DS RGCs. Is local directional inhibition essential for directional selectivity? We report here nonconcentric receptive field (RF) organization of DS RGCs in the Japanese quail, and conclude that this organization is a basis for directional selectivity.

Materials and methods

Sixty-eight Japanese quail (Coturnix japonica) of both sexes were used in the present study. Animals were treated in accordance with the animal usage guideline of the Society for Neuroscience. Animals were anesthetized with a solution of ketamine hydrochloride (4 mg/100 g body weight) and xylazine hydrochloride (0.8 mg/100 g body weight). The anesthetic solution was additionally injected throughout an experimental session if necessary. Tracheotomy was performed and a cannula was inserted. A blunt syringe needle was inserted into an air sac in the lower thorax, and the animal was ventilated unidirectionally by moisturized O2-CO2 gas (95% O2; 5% CO2; 120-150 ml/min) through the inserted cannula. The animal was then immobilized with a solution of tubocurarine chloride (0.15 mg/100 g body weight) and gallamine triethiodide (0.2 mg/100 g body weight). The muscle relaxants were constantly infused during experiment (tubocurarine chloride, 0.075 mg/100 g body weight/hr; gallamine triethiodide, 0.1 mg/100 g body weight/hr). Heart rate was monitored through electrodes inserted into the breast muscle. We then placed the animal in a streo-
tactic head restraining device and anesthetized pressure points with lidocaine jelly. The beak was held 20 deg below from the axis of ear bars. Body temperature was maintained around 40°C by a heating pad during experiments. The left eye was surgically kept open. To avoid drying of the cornea of the stimulation eye, we covered it with a thin layer of high viscosity silicon fluid (60k centistokes). The skin was incised over the skull, and a small hole was made on the dorsal skull with a dental drill. A tungsten electrode (12 MΩ; A-M Systems, Everett, WA) was inserted stereotactically into the optic chiasm through the hole of the skull. Nerve impulses from single optic nerve fibers were isolated, amplified, detected with a time-window discriminator, and fed to an intelligent computer interface (CED 1401plus, Cambridge Electronic Design, England) and an IBM-AT-compatible personal computer for analysis. Upon a successful isolation of single optic nerve fibers, we first made a rough mapping of the RF on a tangent screen using a flash light or a laser pointer. Then, we positioned the face of a monitor scope (Tektronix 608; CRT surface 10 x 12.5 cm) in the region of the RF at a distance of 20-60 cm from the cornea. Presentation of stimuli were controlled by Picasso Image Synthesizer (Innisfree, England), CED-1708 (Cambridge Electronic Design, England) and an IBM-AT-compatible personal computer. Background luminosity of the monitor was less than 0.5 cd/m², and frame rate of the monitor was 200 Hz.

RFs of the RGCs were quantitatively mapped using brief flashes (100-300 ms) of a small spot of light (0.5-1.2 deg. square; 34 cd/m²). The spots were presented at one of 9 by 11 lattice points on the monitor in a random order. Evoked spikes were counted for 200-500 ms. Counts of all the sampling duration were used for two-dimensional RF mapping (so-called “x-y plot”, Shapley et al., 1991; DeAngelis et al., 1995), and counts of 5- or 10-ms-step durations were used for spatiotemporal mapping (so-called “x-t plot”, Shapley et al., 1991; DeAngelis et al., 1995). Five to 10 responses to each point were averaged. For x-y plots, data sets of responses to the 99 points were interpolated with a cubic convolution method (Keys, 1981) or curvefitted with a two-dimensional Gaussian function.

Directional preference was measured with a light spot (0.5-1 deg. square, 16-25 deg./s) moving across the center of the RF in 12 directions. Responses for every 12 directions were curvefitted with a Gaussian function, and preferred directions were determined by the fitted function.

To measure spatial distribution of inhibition, paired spots of light were presented; one (excitation spot) for the RF center, and another (suppression spot) for the periphery. The suppression stimulus led the excitation stimulus by 100 ms. Both the excitation and suppression spots were presented for 200-300 ms. While the excitation spot was always presented at center of the RFs, the leading suppression spot was presented at one of 9 by 11 lattice points on the monitor in a random order. Each presentation was repeated 10 times. Decreased amounts of on-off transient responses (30-50 ms duration) evoked by the excitation spot at 9 by 11 points were measured, and data sets of the 99 points were curvefitted with a 2-dimensional Gaussian function.

Results

We mapped two-dimensional spatial structures of excitatory regions (ERs) and inhibitory regions (IRs) of the RFs of DS RGCs. Two-dimensional spatial sensitivity distributions of ERs were quantitatively measured in 118 RGCs (Jones & Palmer, 1987; Shapley et al., 1991; DeAngelis et al., 1995), and then their directional preference was examined (Fig. 1). Among them, 33 units (28%) were identified as DS RGCs. Twenty-one units showed transient on and off responses to stationary spots of light (Figs. 2,6C) and 12 units showed only transient off responses, among the 33 DS RGCs. On-off DS RGCs showed responses with twin peaks to light spots moving in intermediate velocities (Figs. 1,5B), indicating that both the leading off-on and the trailing on-off transitions are effective. Off DS RGCs showed single-peak responses to moving stimuli. Although DS RGCs were clearly distinguishable from non-DS RGCs by responses to moving stimuli, responsivity to stimuli moving in the direction opposite to the preferred direction ("null" direction) varied. Some DS RGCs did emit almost no responses to the stimuli moving in the null direction (Fig. 1), but the others showed some modest response to those stimuli (Fig. 5B). Thus non-DS motion sensitivities varied from unit to unit. Although the directional preferences of cells are hard to be predicted just from the 2-dimensional structures of ERs (Fig. 1), some neurons with elongated ERs have a preferred-null axis that is perpendicular to the longer axis of the ER.

Spatiotemporal structures of the ERs (or "x-t plot") were also examined (Fig. 2). Latency of responses was slightly shorter (< 5 ms) in the null side than in the preferred side of the ER in some units. (After He and Masland (1997), the null side is defined as the side where stimulus movement in the null direction starts, and vice versa.) Response duration was also short in the null side, possibly reflecting delayed activation of IR shifted toward the null side, as described below. Spatial distributions of on-responses were coincident with those of off-responses in all the on-off DS RGCs.

For 17 DS RGCs (12 on-off units, 5 off units), precise directional tuning curves were successfully measured. Directional preferences of the 17 DS RGCs were not evenly distributed in polar coordinate (Fig. 3). Preferred directions of the 12 on-off units were separated into three discrete preference groups: forward-preferred, upward-preferred and back-downward-preferred groups, whose average preferences are approximately 120 deg. apart (~10, 109 and -134 deg. from the horizon, respectively) (Fig. 3). In contrast to the preferred directions of the quail DS RGCs, preferred directions of the rabbit on-off DS RGCs have been reported to be segregated into 4 orthogonal directions (Oyster & Barlow, 1967). Spatial distribution bias of the preferred directions of the quail DS RGCs was not observed.
Fig. 1  ER of a quail on-off DS RGC (#5127) (center figure), and its responses to a light spot moving across the center of ER in 12 different directions (surrounding PST histograms). The ER was mapped with a stationary spot of light, and represented with gradations of 10%-step of the maximal response. The maximal response point is indicated by +. Diameters of gray circles in the center figure indicate relative response intensities at each lattice point. The raw data were interpolated with a cubic convolution method. Black arrows indicate directions of motion. The preferred direction (-125 deg. from the horizon) was determined by curvefitting of the responses using a Gaussian function. PST histograms: 10-ms bin, 5 sweeps.

Fig. 2  Spatio-temporal structure of the ER of an on-off DS RGC. The same unit (#5127) as the Fig. 1. The spatial axis (-135 deg. from the horizon) that is the closest to the preferred-null axis (-125 deg. from the horizon) of the cell was chosen. Asterisks indicate dimples, probably caused by delayed activation of the IR.
Fig. 3  Distribution of preferred directions of the examined quail DS RGCs. On-off (solid arrow; n = 12) and off (dotted arrow; n = 5) DS RGCs. Note that on-off DS RGCs are separated into three discrete groups according to their directional preferences. The thick arrow stands for 2 overlapped RGCs, whose preferred directions are 0 deg.

Fig. 4  Responsivity of two quail DS RGCs (#5116, thin line and #5176, thick line) to stimuli moving at various velocities in the preferred and null directions. a: Peak discharge rate normalized by the highest value. Preferred (solid lines) and null (dotted lines) direction. b: Preferred/null responsivity ratios of peak discharge rates normalized by the highest value.

Velocity tunings of the DS RGCs were examined along preferred-null axes using light spots moving at 1-100 deg/s. Maximal discharge rates at various velocity were measured (Fig. 4A). Responsivity to spots moving in the null direction was minimal at the velocity of 3-8 deg/s, and preferred/null responsivity ratio was the highest at the same velocity range (Fig. 4B). The velocity tuning for the preferred direction is the highest at more higher range than the range.
Responses evoked by a stationary stimulus applied to the ERs were strongly suppressed by a stationary stimulus applied to the null side, but not strongly suppressed by a stimulus applied to the preferred side (Figs. 5,6). The suppression was transient, and the suppression spot, when turned on 50-100 ms before the excitation spot, maximally suppressed the response to the excitation spot (Fig. 5C). DS suppression was measured as differences between suppressions by stimuli applied to two sides of the RF along the preferred-null axis, and was transient and the largest at 100-ms time lag (Fig. 5D).

For 11 DS RGCs (9 on-off units, 2 off unit), two-dimensional spatial distributions of the DS suppression were measured with paired stationary stimuli for excitation and suppression (Fig. 6). Although the suppression spot near the ER activated responses by themselves, the responses were transient and easily distinguishable from responses to the excitation spot. Fig. 6E shows one example of the Gaussian-fitted ER and IR. Although both the ERs and IRs were well fitted with a two-dimensional Gaussian function, the IRs were slightly asymmetrical along the preferred-null axis in some units: measured peaks shifted to a lesser extent toward the ERs, relative to fitted peaks. Contours of 1-standard-deviation from the fitted centers of ERs and IRs were $3.4 \pm 1.0$ (mean $\pm$ S.D., $n = 11$) and $3.4 \pm 0.8$ (mean $\pm$ S.D., $n = 11$) deg. in diameter, respectively. Centers of the ERs and IRs were not aligned, and the distances between the centers were $1.2-3.2$ deg. ($2.0 \pm 0.6$ deg., $n = 11$). IRs were always shifted toward the null side of the cells (Figs. 6,7). Estimation of displacements of the IRs based on the Gaussian-fitted ERs and IRs were significantly smaller in non-DS RGCs (0.4-0.8 deg.; $0.6 \pm 0.2$ deg. mean $\pm$ S.D., $n = 3$) than in DS RGCs.
Fig. 6  IR of a quail DS RGC (#5116) measured by paired stationary spots for excitation and suppression.  A: Gaussian-fitted ER and locations of an excitation spot (e) and four examples of suppression spots (s_{2,2}, s_{1,1}, s_{-1,-1}, s_{-2,-2}).  Indexes of the suppression spots indicate their coordinates.  The preferred and null directions are indicated.  B: Excitatory responses to the center spot (upper row; e in A) and the four peripheral spots (middle row; s_{2,2}, s_{1,1}, s_{-1,-1}, s_{-2,-2} in A), and suppressive effects of the four stationary suppression spots (bottom row; s_{2,2}, s_{1,1}, s_{-1,-1}, s_{-2,-2} in A) on the response evoked by the stationary excitation spot (e in A).  The suppression spots (s_{-1,-1} and s_{-2,-2}) in the null side strongly suppressed the on and off responses.  Those light spots were 1.2 deg. square (300 ms in duration, 10 cd/m²), and both the peripheral spots led the center spot by 100 ms.  PST histograms: 10-ms bin, 10 sweeps.  C, D: Excitation (C) and suppression (D) by a spot presented at the 99 locations.  Two-dimensional array of PST histograms.  Numbers indicate coordinates indexes of the suppression sites.  The excitation spot for suppression measurements was presented at [0, 0].  E: ER (solid line) and IR (gradation and dotted line).  Thick contour lines indicate the contours of 1-standard-deviation from the Gaussian-fitted centers.  Other contour lines indicate 10%-step lines of the maximal response.  Center of the IR is indicated by a white +.  Compass plot indicates the directional tunings to a light spot moving in 12 directions.  Length of the arrows is proportional to the responses.
Fig. 7  Relationship between the preferred directions and directions of displacements of IRs. On-off DS RGCs (filled circles) and off DS RGCs (open circles). Solid line is the line of "$y = x$", and dotted line is the regression line ($y = 0.77x - 14.05$) of the data.

Fig. 8  Effect of excitation spot location on mappings of the IR. A, B: Predictions from the unidirectional inhibitory conduction model (A) and nonconcentric receptive field model (B). Solid contour line indicates the ER, dotted contour lines indicate the IRs, and solid squares indicate three different excitation spots. C, D: Experimental data of a quail DS RGCs (C, #5176; D, #5142). The solid contour lines indicate the ER (1-standard-deviation area). The dotted contour lines indicate the IRs (1-standard-deviation area), measured with three different excitation spots (solid squares, $e_c$, $e_a$, $e_b$). Light spots were 1 deg. square in C and 0.8 deg. square in D. Three excitation spot locations in D were overlapped, and dotted lines in a solid box indicate upper/lower edges of the spots.
For a few DS RGCs, measurements of the IRs were repeated using three different locations of the excitation spot (Fig. 8). The hypothesis by Barlow and Levick (1965) assumes that there are many local directional inhibitory conductors distributed throughout the RFs (Fig. 9A), and that their directions of conduction are all the same. Based on these assumptions, it may be expected that measured IRs are to be shifted according to excitation sites, if the excitation spot is relocated (Fig. 8A). But, that is not the case, as shown in Fig. 8C, D. Size and location of the IRs were not much affected by location of the excitation spots (Fig. 8C, D), and thus presence of local directional inhibition was not supported.

Fig. 9 Barlow-Levick model, or local directional inhibition model (A) and nonconcentric receptive field model (B) for retinal directional selectivity.

Discussion

Thus quail DS RGCs have nonconcentrically arranged RFs (Fig. 9B). Inhibition was quantified with decreased amounts of transient on-off responses (30-50 ms durations). The suppression spots themselves caused some amounts of excitation, if they were applied to the central part of ER (Fig. 6B, middle row). In the most cases, transient responses to the excitation and suppression spots were easily distinguishable (Fig. 6B, bottom row), because of their response time lags (, 100 ms). Thus, the present measurements of spatial distribution of inhibition were not much affected by excitation evoked by the suppression spots, although insignificant underestimation of inhibition could not be denied. Holden (1977) similarly supposed that the IRs are displaced toward the null side in pigeon DS RGCs, judging from responses evoked by stimuli applied separately to the preferred and null sides. For a RGC with a nonconcentric RF, a moving object that stimulates the IR before the ER evoked a smaller response than an object moving on any other trajectory through the RF (Fig. 9B). This trajectory defines the null direction. Stimulation in the opposite direction evokes a maximal response and defines the preferred direction. Thus, displaced IRs may generate directional selectivity. Barlow and Levick (1965) hypothesized that directional selectivity results from local directional inhibitory conduction distributed throughout the RF, based on their experiments on rabbit DS RGCs (Fig. 9A). Wyatt and Daw (1975) extended the Barlow-Levick model into two-dimensional space. However, when the IRs are displaced, as shown in the present study, such local directional inhibitory mechanisms may not be needed for directional selectivity. Furthermore, independence of the IR from excitation sites, as shown in Fig. 8, does not support the hypotheses of local directional inhibition. However, Amthor and Grzywacz did not find such nonconcentric receptive field organization in rabbit DS RGCs by means of paired stationary stimuli (Amthor & Grzywacz, 1993; Grzywacz & Amthor, 1993). Thus it should be further studied whether there are species differences in RF organization between the avian and mammalian DS RGCs. Our model predicts local directional preferences that are varied within the RF, depending on a relative position to the IR center (Figs. 8B, 9B). In order to examine this possibility, careful measurements of local directional preferences must be performed. RF structures of DS neurons have been extensively studied in the mammalian primary visual cortex (see Emerson et al., 1987; Shapley et al., 1991; Gaska et al., 1994; DeAngelis et al., 1995). The 2nd order kernel measurement used for monkey V1 complex cells (Gaska et al., 1994) would more precisely describe spatiotemporal structures of RFs of the quail DS RGCs. Then motion mechanisms could be compared in detail between the quail DS RGCs and cortical DS neurons.

Although structural bases for the displacement of the IRs are unknown, the displacement of dendritic fields of rabbit DS RGCs reported by Yang and Masland (1994) seems suggestive. They reported that dendritic fields were displaced toward the null side, relative to their RFs, in some rabbit DS RGCs. If distribution and density of inhibitory inputs on dendrites of DS RGCs are spatially biased toward the null side, relative to the distribution of excitatory inputs,
displaced IRs could be achieved. Thus directional selectivity may be implemented as nonconcentrically-arranged distributions of excitatory and inhibitory inputs on the dendritic fields of DS RGCs. Biophysical mechanisms for delayed suppression maximally at around 100-ms-delay are also unknown. A GABA\(_B\) agonist, baclofen, enhances directional selectivity of DS RGCs in a salamander (Pan & Slaughter, 1991), and G-protein-coupled GABA\(_B\) receptors mediate slow increase in potassium conductance, or late IPSPs (see McCormick, 1990; Mody et al., 1994). Thus it may be possible that GABA\(_B\) receptors participate in the delayed suppression mechanism for directional selectivity, although only GABA\(_A\) blockers have so far been reported to be effective in diminishing the directional selectivity (Wyatt & Daw, 1976; Caldwell et al., 1978; Ariel & Daw, 1982; Massey et al., 1997).

**Acknowledgements**

We thank Drs. Robert Barlow, Erik Herzog, James Albert and Andrew Ishida for comments on the manuscript. This study was supported partly by grants from Japan Science and Technology Corporation to H.U.

**References**


