Pretectal Neurons Optimized for the Detection of Saccade-Like Movements of the Visual Image

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Price, N.S.C. and M. R. Ibbotson. Pretectal neurons optimized for the detection of saccade-like movements of the visual image. *J Neurophysiol* 85: 1512–1521, 2001. The visual response properties of nondirectional wide-field sensitive neurons in the wallaby pretectum are described. These neurons are called scintillation detectors (SD-neurons) because they respond vigorously to rapid, high contrast visual changes in any part of their receptive fields. SD-neurons are most densely located within a 1- to 2-mm radius from the nucleus of the optic tract, interspersed with direction-selective retinal slip cells. Receptive fields are monocular and cover large areas of the contralateral visual field (30–120°). Response sizes are equal for motion in all directions, and spontaneous activities are similar for all orientations of static sine-wave gratings. Response magnitude increases near linearly with increasing stimulus diameter and contrast. The mean response latency for wide-field, high-contrast motion stimulation was 43.4 ± 9.4 ms (mean ± SD, $n = 28$). The optimum visual stimuli for SD-neurons are wide-field, low spatial frequency (<0.2 cpd) scenes moving at high velocities (75–500°/s). These properties match the visual input during saccades, indicating optimal sensitivity to rapid eye movements. Cells respond to brightness increments and decrements, suggesting inputs from ON and OFF channels. Stimulation with high-speed, low spatial frequency gratings produces oscillatory responses at the input temporal frequency. Conversely, high spatial frequency gratings give oscillations predominantly at the second harmonic of the temporal frequency. Contrast reversing sine-wave gratings elicit transient, phase-independent responses. These responses match the properties of Y retinal ganglion cells, suggesting that they provide inputs to SD-neurons. We discuss the possible role of SD-neurons in suppressing ocular following during saccades and in the blink or saccade-locked modulation of lateral geniculate nucleus activity to control retino-cortical information flow.

INTRODUCTION

The mammalian pretectal nucleus of the optic tract (NOT) contains cells that detect wide-field visual stimuli. The most commonly described neurons in the NOT are direction-selective retinal slip cells, which respond optimally to highly textured, wide-field patterns moving in a tempero-nasal direction over the contralateral eye and are inhibited by naso-temporal motion (rabbit: Collewijn 1975a; cat: Ballas and Hoffmann 1985; opossum: Volchan et al. 1989; primate: Hoffmann and Distler 1989; Mustari and Fuchs 1990; ferret: Klauer et al. 1990; wallaby: Ibbotson et al. 1994). Retinal slip cells control stabilizing eye movements such as optokinetic nystagmus (Collewijn 1975b). In addition to direction-selective cells, wide-field nondirectional neurons have been described in the pretectum of the wallaby (Ibbotson and Mark 1994) and cat (Schoppmann and Hoffmann 1979).

Nondirectional cells in the wallaby have short-latency responses to rapid motion and high-frequency flicker (Ibbotson and Mark 1994). These cells were called scintillation-detectors (SD-neurons) based on their strong responses to rapid movements and also to luminance fluctuations in the absence of motion. Work in awake cats has demonstrated two populations of pretectal nondirectional neurons, labeled "jerk" and "saccade" neurons (Schmidt 1996; Sudkamp and Schmidt 1995). Saccade neurons are responsive to rapid displacements of large visual stimuli and to saccadic eye movements in the light and in darkness (Schmidt 1996). Jerk cells are insensitive to eye movements in the dark but respond strongly to rapid image displacements and saccades in the light (Schweigart and Hoffmann 1992; Sudkamp and Schmidt 1995). Based on the available data, the visual response properties of nondirectional pretectal cells in the wallaby and cat appear similar, suggesting that they have similar functions. Our experiments with anesthetized, paralyzed wallabies did not allow us to distinguish between so-called jerk and saccade neurons, so we use the visual description "SD-neurons" as a general name for both cell types. The term SD-neurons is used in preference to jerk neurons (Schoppmann and Hoffmann 1979) because the cells were found to be sensitive to luminance fluctuations without motion, and the term jerk is usually reserved for the first derivative of acceleration.

Ibbotson and Mark (1994) suggested that SD-neurons may subserve saccadic inhibition of retinal slip cells, but anatomical evidence has not been investigated. Slip cell inhibition could prevent oculomotor compensation for the retinal slip generated by saccades. In cats, it has been proposed that saccade neurons might provide saccade-locked disinhibition of thalamic relay cells (Schmidt 1996). This could reset lateral geniculate nucleus activity after gaze shifts or modulate retinal information flow to the cortex.

Despite the theories outlined above, knowledge of the physiological response properties of pretectal nondirectional neurons is limited in both the wallaby and cat. All that has been reported in the wallaby is that SD-neurons are sensitive to rapid

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motion and flicker. Studies in the cat have used random dot patterns, preventing analysis of the spatiotemporal dependence of motion responses. Furthermore, limited velocity ranges and motion durations have been used: Schweigart and Hoffmann (1992) used angular velocities of 0.1–500°/s but did not specify the stimulus duration; Schmidt and Hoffmann (1992) tested velocities of 0.1–100°/s and >1,000°/s; however, stimuli with velocity >1,000°/s lasted <25 ms. We investigate SD-neuron receptive field properties, contrast sensitivities, velocity tuning, the effects of repetitive motion stimulation, and the responses to contrast reversing gratings and flashed bar stimuli. We speculate on how the neurons may influence visual function during and after saccades.

METHODS

Physiology

Recordings were made from the NOT and nearby pretectal regions in seven anesthetized, paralyzed wallabies (*Macropus eugenii*) weighing 5.0–7.5 kg. All procedures were approved by the animal experimentation ethics committee of the Australian National University and followed the guidelines of the National Health and Medical Research Council of Australia. Anesthesia, surgery, and extracellular recording methods have been described in detail (Ibbotson et al. 1994). The only modification to the previously reported methods was the administration of 1 mg iv vitamin K_1 (Phytomenadione: Konakion, Roche) 1 h prior to surgery to assist blood clotting.

Visual stimulation

Computer-generated visual stimuli (AT Vista: True Vision) were presented on a display monitor with 480 lines at 512 pixels/line (CCID 7551: Barco Industries). The refresh rate of the monitor was 97.7 or 100.8 Hz. The monitor could be moved to any location within the animal's visual field. Screen distances from the eye varied from 30 to 65 cm, subtending 65 × 50° to 33 × 25°. Two types of stimuli were used, comprising sine-wave modulated contrast gratings or high contrast bars. The bar stimulus involved the simultaneous presentation of 12 parallel vertical black or white bars, each subtending 34 × 0.8° and separated by 1.6° (Fig. 8, *inset*). The mean background luminance was 42 cd/m^2 before, during, and after the bar presentation. Sine-wave gratings could be presented either moving or stationary, in any orientation, and were presented in rectangular and circular apertures. In addition, the stimulus contrast, grating spatial frequency, temporal frequency of motion, and duration of blank, stationary, and motion periods could be controlled. Averages of 8–32 repetitions of each stimulus were used to assess responses.

RESULTS

We recorded from 28 SD-neurons in detail and from another 22 neurons using hand-held stimuli and a limited number of tests with the stimulus screen. The full range of tests could take over 10 h, which prevented all tests being conducted on all neurons. On average, seven neurons were located per preparation, and recording periods lasted for 20–24 h, so selected experiments were conducted until each experiment had been tested in full on at least six cells in three animals.

Neurons were identified in each preparation because they responded to rapid motion, in any direction, of large hand-held gratings. In all cases, the cells were nondirectional and responded most vigorously to wide-field, high-speed stimulation. These responses distinguished them from retinal slip cells, which are direction selective and prefer slower speeds. SD-neurons were often found in clusters, with up to five cells isolated in the same track, between 11 and 15 mm below the cortical surface. It is unlikely that SD-neurons form a distinct sub-nucleus because they were often found in the same recording track as retinal slip cells, with no obvious vertical segregation. SD-neurons were found in tracks as far as 1 mm lateral and 2 mm medial to the direction-selective neurons that are used as the physiological marker to identify the NOT (Ibbotson et al. 1994).

A peristimulus time histogram (PSTH) for an SD-neuron responding to 5 s of rapid motion [450°/s; 0.055 cycles/degree (cpd)] is shown (Fig. 1*A*). A vigorous increase in firing rate occurs after motion onset, with spiking rates up to 300 spikes/s. As the motion continues, the response declines, usually in an exponential fashion, until a constant, sustained firing rate is attained. Motion cessation causes a rapid decline in firing rate back to the spontaneous level. Latencies measured as the time from motion onset to half-peak firing rate ranged from 30.7 to 59.5 ms (mean 43.4 ± 9.4 ms; median 39.7 ms, $n = 28$) for high contrast gratings (>60%). Responses to visual stimuli will be characterized by Peak and Sustained responses and may be expressed relative to the firing rate when a stationary stimulus is presented (Spontaneous response). Peak responses represent the maximum firing rate in a 40-ms window immediately following the latent period. Sustained responses characterize the mean firing rate during the entire motion period. Including the onset transient in the sustained response did not significantly alter the mean firing rates because of the short duration of the onset response (Fig. 1*A*).

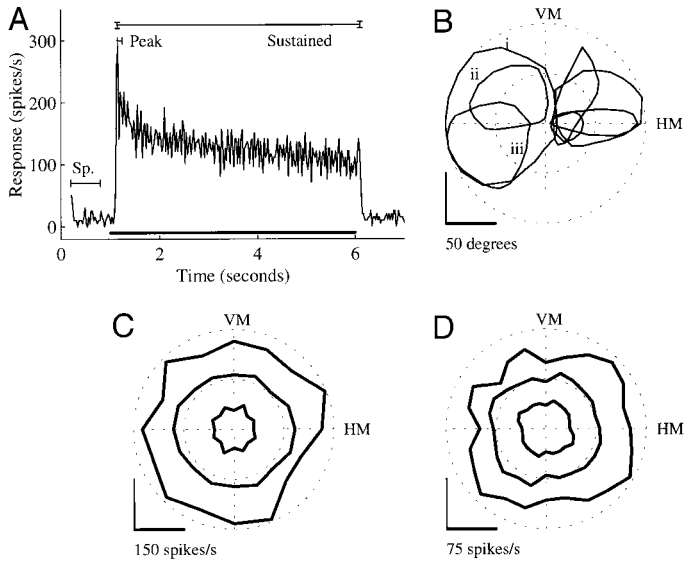

FIG. 1. *A*: peristimulus time histogram (PSTH) of a cell responding to 5 s of motion (450°/s; 0.055 cpd; 8 repetitions). Motion is indicated by the thick lower bar, and the time windows for Peak, Sustained, and Spontaneous (Sp.) responses are indicated by thin horizontal lines. *B*: receptive fields of 7 cells in the left nucleus of the optic tract (NOT). All fields lie in the right visual hemifield and are shown from the animal's perspective, except for *cells i–iii*, which were mirrored about the vertical meridian for ease of presentation. Directional tuning plots for 2 cells are presented, using angular increments of 22.5° (*C*) or 15° (*D*). Mean ($n = 8$) peak, sustained, and spontaneous responses are shown (outer, middle, and inner curves, respectively), for 2-s motion (325°/s; 0.039 cpd) in a circular aperture (36° diam). Error bars were omitted for clarity (maximum SD were 26, 14, and 13%, respectively). HM, horizontal meridian; VM, vertical meridian.

Receptive field sizes

Receptive field sizes for all cells were mapped using a perimeter and by monitoring responses to 2–4° spots of light that were rapidly oscillated or flashed ON and OFF in the animal's visual field. The seven fields shown in Fig. 1*B* were chosen because they represent the full range of field sizes and shapes. The largest field covered nearly the entire visual field of one eye, while the smallest subtended a circular area over 30° in diameter in the frontal visual field.

Directional properties

Unlike retinal slip cells, SD-neurons showed similar sized responses to rapid motion in all directions. Responses were assessed for both directions of motion along the horizontal and vertical axes ($n = 50$). The sustained firing rates in the four directions never varied by more than 8% of the lowest sustained firing rate. The full directional tuning of eight neurons was assessed with the gratings at orientations separated by 22.5 or 15° intervals (tuning curves for 2 cells are shown in full: Fig. 1, *C* and *D*). The tuning curves were obtained using rapid motion at the cells' preferred spatial frequency and velocity, presented in a circular aperture with a diameter of 36°. The spontaneous activities did not vary significantly for any cells between different orientations of a static grating (inner traces, Fig. 1, *C* and *D*). When tested for their responses to motion in different directions, the peak and sustained responses indicated no significant directional tuning (Fig. 1, *C* and *D*). Circular statistics (Batschelet 1981) were used to confirm the lack of orientation tuning for the spontaneous activities and the directional tuning for the responses to motion. The average of eight cells' mean vector lengths for the spontaneous, sustained and peak responses were 1.7, 4.4, and 8.7 spikes/s, with corresponding averaged standard deviations of (24.8, 24.1), (60.4, 55.8), and (93.2, 88.2) spikes/s, respectively. The standard deviation vectors indicate the response variation in horizontal and vertical directions. The small mean vectors and large standard deviations show that no orientation or motion direction is favored. Hotelling's confidence ellipse at 99% confidence levels always included the origin, indicating no orientation or directional specificity.

Spatial summation and contrast sensitivity

Spatial summation properties were investigated using high contrast moving sine-wave gratings presented in circular apertures with variable diameters (4–58°). For each cell, the receptive field shape was identified, and then the center of the aperture was placed close to the center of the cell's receptive field. Peak and sustained motion responses increased with stimulus diameter but at different rates. Linear fits to the sustained responses of two cells show strong correlation ($R > 0.98$) between response size and stimulus diameter (Fig. 2). The results indicate that the cells respond optimally to wide-field motion stimulation. The minimum aperture diameters required to produce significant responses for the cells shown were 19° (Fig. 2*A*) and 26° (Fig. 2*B;* Student's *t*-test, $P < 0.05$). These aperture diameters were calculated using a cubic spline to interpolate peak and sustained responses at approximately 0.6° aperture increments. The smallest aperture for which all larger apertures gave responses above 95% significance (*t*-test) in both sustained and peak responses was taken as the minimum significant aperture diameter. The minimum significant aperture diameter from seven cells tested in detail ranged from 4 to 26° (mean 18 ± 8°).

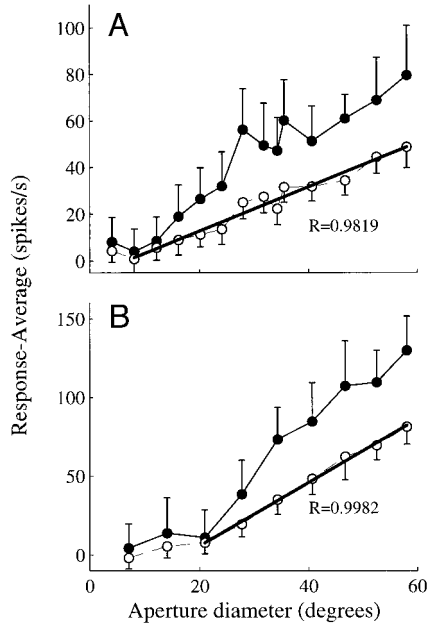

FIG. 2. Spatial summation properties of 2 cells. The corresponding receptive fields are shown in Fig. 1*B* (*A, cell i; B, cell ii*). Peak (●) and sustained (○) firing rates, minus spontaneous firing, are shown for responses to 1-s horizontal sine-wave grating motion (450°/s, 0.055 cpd) presented inside circular apertures. Responses are averages from 32 (*A*) or 16 repetitions (*B*) with error bars indicating 1 SD. The least-squares linear fit to the sustained response and correlation coefficient are shown.

In Fig. 3, peak responses from one cell (Fig. 3, *A–C, receptive field iii* in Fig. 1*B*), and sustained responses from a second cell (Fig. 3, *D–F*) are shown for two neurons tested with contrasts of 10–90% and aperture sizes of 5–41°. Figure 3, *A* and *D*, shows the effects of increasing aperture size with fixed contrast, while Fig. 3, *B* and *E*, shows the effects of increasing contrast for a range of fixed aperture sizes. These results are summarized in surface plots (Fig. 3, *C* and *F*). Peak responses increase quite linearly with contrast, showing no saturation at high contrasts, but a strong dependence on aperture size. Sustained responses show some saturation at contrasts above 30% (Fig. 3*E*). The optimal stimulus for SD-neurons is a rapidly moving image of moderate to high contrast, which covers the entire receptive field. The results demonstrate an interdependence of contrast and stimulus size.

Velocity tuning

To characterize the velocity tuning of SD-neurons, responses were measured across a range of temporal and spatial frequencies (0.39–25.2 Hz; 0.028–1.520 cpd), giving a velocity range of 0.2–900°/s. Spatial frequencies lower than 0.2 cpd were preferred by all cells ($n = 49$) except one, which showed a bimodal spatial frequency preference, giving large responses to spatial frequencies below 0.083 cpd and at 0.66 cpd. PSTHs from a neuron stimulated at its preferred spatial frequency and over a range of temporal frequencies are shown in Fig. 4*A*. The responses at low temporal frequencies are small, but with increasing temporal frequency the peak onset transient and

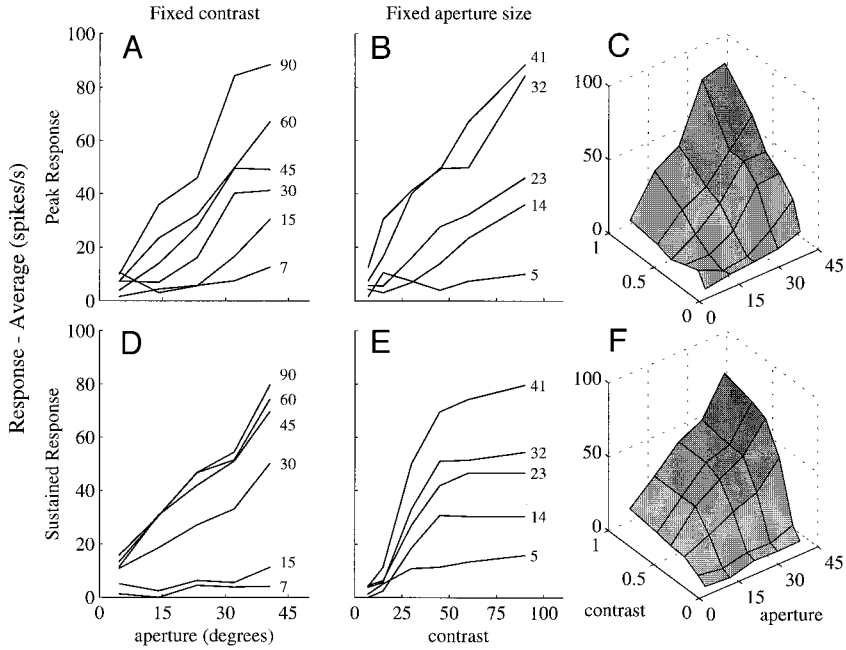

FIG. 3. Peak (*A–C*) and sustained (*D–F*) responses from 2 cells, minus the spontaneous firing rate. The receptive field of the cell whose responses are shown in *A–C* is shown in Fig. 1*B, iii*. Responses were averaged from 12 repetitions of 2-s motion periods (300°/s; 0.084 cpd) with sine-wave gratings of varying contrast presented in circular apertures of varying diameter. *A* and *D*: the responses to stimuli of varying diameter, but fixed contrasts (contrasts indicated on the *right*). *B* and *E*: the same data, plotted with fixed aperture diameters. The results are summarized in surface plots (*C* and *F*). Error bars were ommitted in all plots for clarity, but are of similar size to those shown in Fig. 2.

sustained firing rate increase. The temporal frequency tuning of *sustained* responses are shown for five cells stimulated at their preferred spatial frequencies (Fig. 4*B*). The responses peak at temporal frequencies of 6–15 Hz, with higher frequencies causing a slight reduction in response magnitude. The optimum spatiotemporal response properties of the neurons equate to velocities of 75–500°/s (Fig. 4*C*), which is within the normal range of saccadic velocities (Becker 1989). Velocities are given by temporal frequency/spatial frequency, thus it was necessary to measure the entire spatiotemporal range to determine preferred velocities. Consequently only 18 cells could be included in Fig. 4*C*.

At temporal frequencies of 6 Hz and above, oscillatory responses often arise during long periods of motion stimulation. Figure 5*A* shows the response of one particularly clear oscillation, whose Fourier transform (Fig. 5*B*) shows large amplitude at the fundamental and second harmonic of the stimulus temporal frequency. A small component is also present at the third harmonic of the stimulus. The response component at the fundamental frequency was dominant in all the neurons at low spatial frequencies, as shown in Fig. 5, *B–D*. However, as the spatial frequency increased, the amplitude of the fundamental decreased for frequencies higher than 0.1 cpd, while the second harmonic response persisted until approxi-

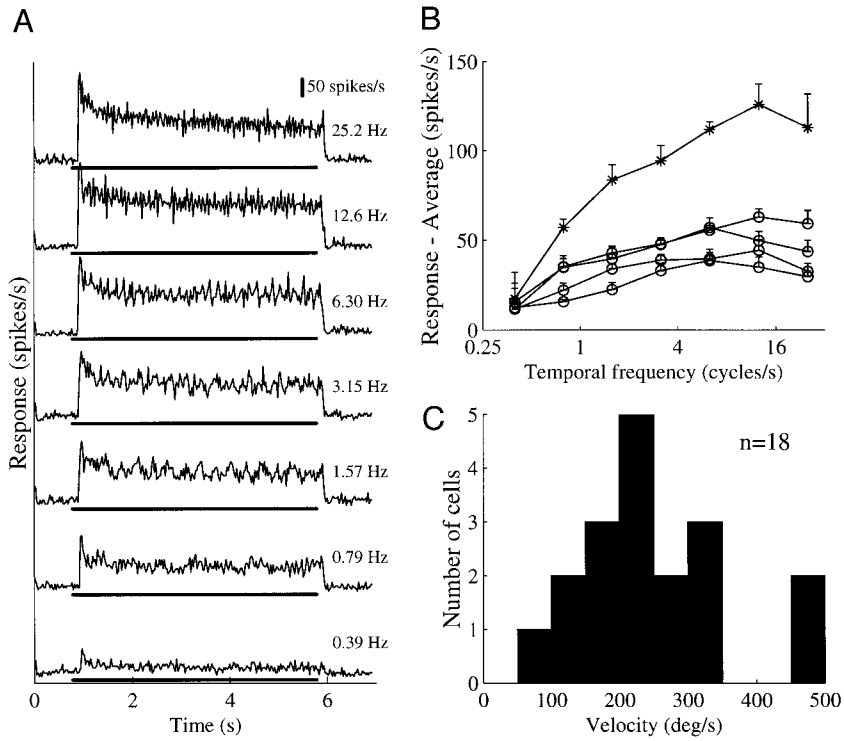

FIG. 4. Temporal frequency and velocity tuning. *A*: responses to 5 s of sine-wave grating motion (0.39–25.2 Hz; 0.055 cpd) averaged from 8 repetitions. The temporal frequency of each stimulus is marked on the *right* of the PSTH. *B*: temporal frequency tuning of sustained responses from 5 cells stimulated with gratings at their preferred spatial frequency are shown. Responses marked with an asterisk correspond to the PSTHs shown in *A*. *C*: distribution of preferred velocities from 18 cells. Velocities were calculated from the preferred spatial and temporal frequencies.

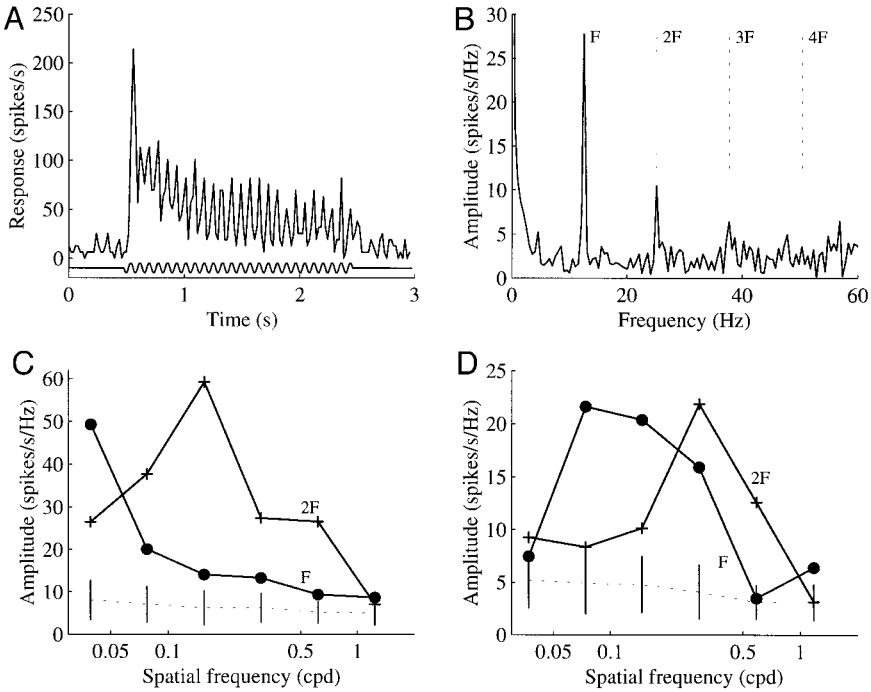

FIG. 5. *A*: oscillatory response of a scintillation detector neuron (SD-neuron), stimulated with sine-wave grating motion (19°/s; 0.662 cpd; 8 repetitions). The period of motion and its temporal frequency are indicated by the sine wave. *B*: Fourier transform amplitude spectrum of the response in *A*, with the fundamental frequency ($F = 12.6$ Hz) and its harmonics indicated. *C* and *D*: the amplitude spectra of the fundamental and 2nd harmonic for 2 cells, plotted as functions of stimulus spatial frequency (motion temporal frequency: 12.6 Hz). For comparison, the dashed line and errorbars represent the mean ± SD amplitude of Fourier transform components for frequencies between 0 and 100 Hz, excluding those frequencies falling within a 3-Hz window centered on each harmonic of the fundamental frequency.

mately 0.6 cpd in the four cells tested in four animals (e.g., Fig. 5, *C* and *D*). This result indicates that at higher spatial frequencies, the dominant input to SD-neurons is nonlinear and produces frequency doubling, sustaining the oscillatory response at the second harmonic. This phenomenon is seen in Y retinal ganglion and Y lateral geniculate nucleus (LGN) cells, and is known as the Y-cell signature (Hochstein and Shapley 1976; Shapley and Perry 1986).

Responses to repetitive stimuli

A stimulus mimicking the visual inputs that occur during optokinetic nystagmus (OKN) was used to investigate the responses of the neurons to repetitive stimulation. The stimulus consisted of 56 stationary rest periods (20–320 ms) interspersed by saccade-like periods of rapid motion (>170°/s; 10–80 ms). It was found that SD-neurons respond with similar magnitude to each saccade-like period, provided they are given an adequate rest period between the "saccades." Figure 6*A* shows one cell responding to a series of 80-ms periods of rapid motion (saccades) interspersed with 320-ms rest periods (no motion). The motion responses show little sign of response attenuation even after 27 saccade-like movements over a period of 11 s.

Reducing the duration of the stationary rest periods relative to the motion periods made the cells less responsive to motion.

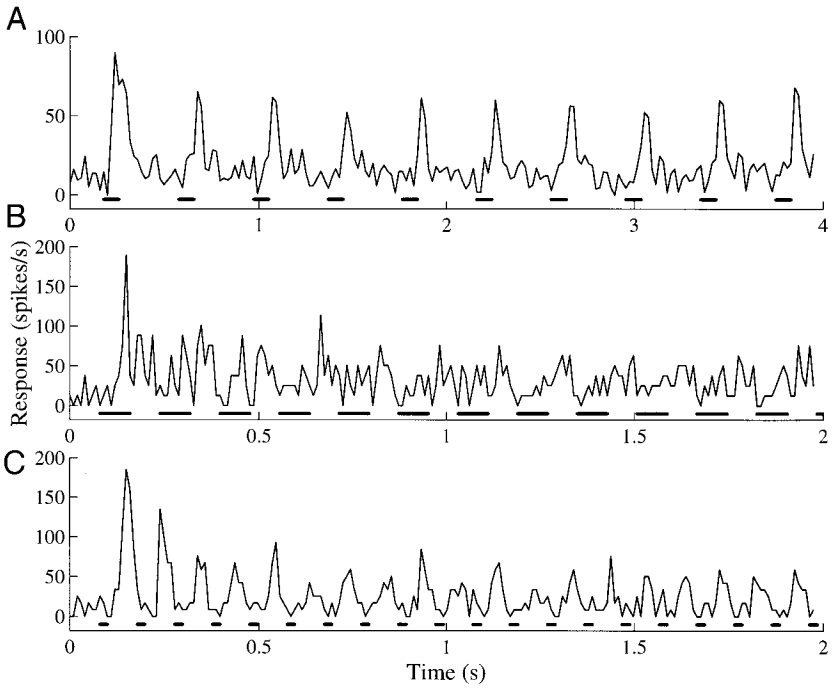

FIG. 6. Responses to repetitive saccade-like motion of sine-wave gratings (300°/s; 0.083 cpd). Motion periods are marked by the underlying bars. *A*: 80-ms motion periods alternated with a 320-ms stationary rest period. *B*: 80-ms motion, 80-ms stationary. *C*: 20-ms motion, 80-ms stationary. Responses are averages from 8 (*B*) or 12 repetitions (*A* and *C*).

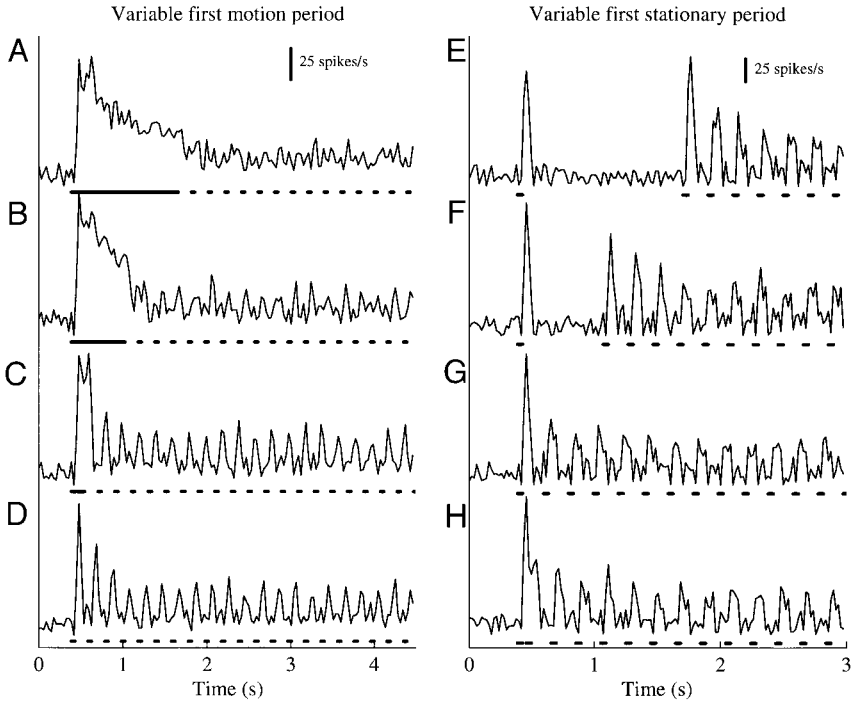

FIG. 7. Responses of a cell to 40-ms periods of rapid saccade-like grating motion alternating with 160 ms of stationary grating presentation (mean of 12 repetitions). The repetitive motion phase occurs subsequent to an initial motion period of variable duration (*A–D*: 1,280, 640, 160, and 40 ms) or subsequent to a stationary, variable duration, 1st inter-stimulus period (*E–H*: 1,280, 640, 160, and 20 ms). Bars mark the periods of motion.

This is demonstrated in the PSTHs of a cell to 80-ms (Fig. 6*B*) or 20-ms (Fig. 6*C*) periods of motion, alternating with 80-ms rest periods. The cell gave distinct responses to the 20-ms motion periods and therefore should have been able to resolve the 80-ms periods of motion. Despite this, the responses with 80-ms motion periods are quite variable, and it is often difficult to distinguish individual saccade-generated responses (Fig. 6*B*). Across the six cells tested, for relatively short rest periods and long motion periods, the cells did not have sufficient time to recover from the previous stimulus, so the cells were unable to resolve the simulated saccades.

Adaptation tests

To investigate the effects of motion adaptation, a stimulus was devised incorporating a stationary grating presented for 160 ms alternating with 40 ms of rapid motion. The first period of motion was varied between 40 and 1,280 ms (Fig. 7, *A–D*). The six cells tested were unable to resolve any short periods of motion during a 5-s period after an initial 1,280-ms period of rapid motion (e.g., Fig. 7*A*). As the length of the initial period of motion was reduced, the cells became more responsive to subsequent short motion periods (Fig. 7, *B–D*). It is noticeable, however, that the responses to the stimulus with the shortest initial rest period declined during the first four saccade-like movements, which was a consistent feature from the neurons (also see Fig. 6*C*). This is in contrast to the highly repeatable responses observed when 80-ms motion periods were alternated with long rest periods (Fig. 6*A*).

A similar stimulus was employed to investigate the effects of the rest period durations. This stimulus incorporated an initial 40-ms motion period, a variable rest period (40–1,280 ms), then 50 alternating periods of 40 ms of rapid motion interspersed with 160 ms of a stationary grating. As the length of the rest period declined, the cells became less responsive to subsequent motion periods (Fig. 7, *E–H*). Rest periods of 640–1,280 ms were required in all the neurons to allow full recovery between short motion periods. This suggests some form of response suppression acts for over half a second following the initial saccade, since fatigue is unlikely to occur after only 40 ms of stimulation, and our previous responses show sustained firing in response to continuous motion.

Responses to bar stimuli

All 50 cells showed strong responses to brightness increments and decrements, showing that they receive input from ON

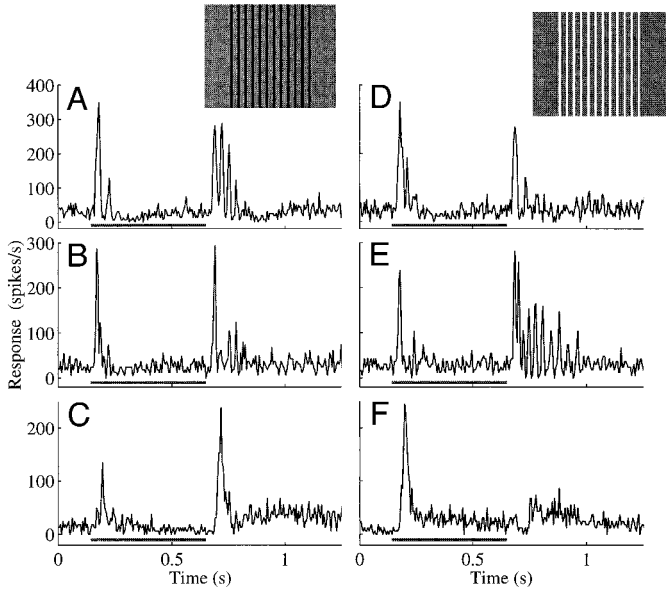

FIG. 8. PSTHs showing 3 cells' responses (3 rows) to 500-ms presentation of 12 vertical black (*A–C*) and white (*D–F*) bars (mean of 32 repetitions). The *insets* show the 2 types of stimulus, and the period of presentation is indicated by the horizontal bars.

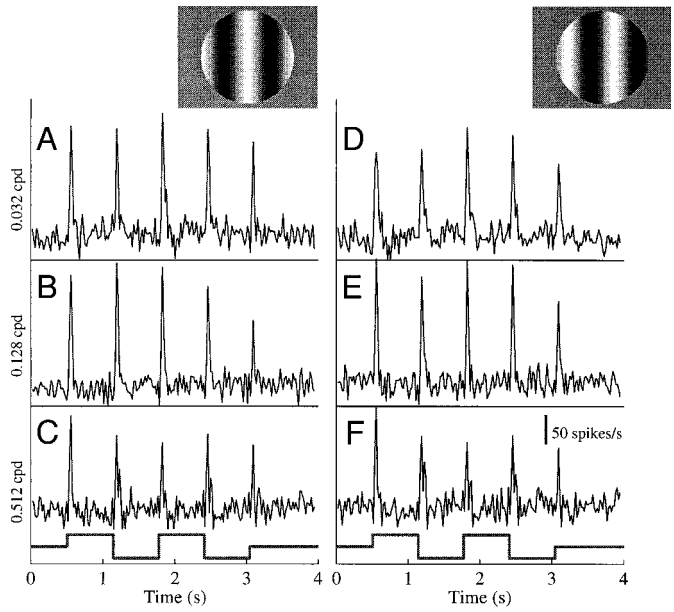

FIG. 9. Responses of a cell to 1.56-Hz contrast reversal of a sine-wave contrast grating presented in a circular aperture (30° diam). PSTHs from 3 spatial frequencies are shown (mean of 12 repetitions): 0.032 cpd (*A* and *D*); 0.128 cpd (*B* and *E*), and 0.512 cpd (*C* and *F*), with the sine-wave grating stimulus used in *D–F* displaced by 90° from its position in *A–C*. The gratings above *A* and *D* indicate the 90° relative phase shift between stimuli. Contrast changes are marked by the square-wave traces: the mean level represents a blank screen; upper and lower levels correspond to the 2 phases of contrast reversal.

and OFF cells earlier in the visual system. To quantitatively characterize the brightness polarity sensitivity of the SD-neuron inputs, we measured the responses to 12 vertical black or white bars (width 0.8°, separation 1.6°) simultaneously presented for 10–1,000 ms against a gray background. Using this stimulus, the response latencies for OFF responses were shorter than for ON responses (OFF: 27.9 ± 2.6 ms, mean ± SD; ON: 34.8 ± 3.8 ms, $n = 7$). The size of the ON and OFF responses were not always equal, but in all cells both types of stimulation produced highly significant responses.

Irrespective of the polarity of the brightness change, the return to the blank screen at the end of the stimulus generated longer lasting responses than the appearance of the bars (Fig. 8). The response to the stimulus disappearance increased while the response to stimulus appearance remained constant with increasing stimulus duration. Therefore when the appearance and disappearance were close in time, the response to the latter was suppressed. As the separation between appearance and disappearance increased, the effects of suppression were diminished.

An interesting phenomenon associated with the bar stimuli was the oscillatory nature of the response to bar disappearance, referred to here as ringing (most prominent in Fig. 8, *A* and *E*). The poststimulus oscillations typically contained 6–10 peaks, lasting up to 300 ms. Spacing of the peaks was variable (e.g., from 26.6 ± 9.2 ms to 30.2 ± 8.7 ms) and tended to increase as the ringing continued. Prolonged ringing was never observed after bar appearance in the seven cells tested. If the bars stayed visible, spiking rates would fall rapidly to the spontaneous level after the initial transient peak.

Contrast reversing stimulus

Contrast reversing sine-wave gratings of variable spatial frequency (0.032–1.024 cpd) were presented in circular apertures subtending 4, 12, and 30° of the visual field. Contrast reversal occurred every 640 ms. Before and after the appearance of each grating, the screen was kept at the grating's mean luminance. Responses to the appearance, disappearance, and contrast reversal of the gratings were of similar size, latency, and duration for the eight cells tested. To assess the phase dependence of the response, two runs with the sine-wave grating spatially displaced by 90° were used. The relative spatial phase of the grating had no significant effect on the responses of the neurons (Fig. 9). Contrast reversing stimulation within the 30° aperture produced highly repeatable, transient responses reaching over 200 spikes/s and lasting 50–150 ms. Stimulation within the 12° aperture produced similar, but smaller responses that were still independent of spatial phase. As expected, stimulation within the 4° aperture did not produce significant responses (see Fig. 2). Response sizes decreased with increasing spatial frequency (Fig. 9), in accordance with the spatial tuning of the neurons (Ibbotson and Mark 1994).

DISCUSSION

Are SD-neurons tuned to detect saccades?

Pretectal SD-neurons are particularly sensitive to rapid flicker or motion of a wide-field stimulus, suggesting a role in the visual detection of saccades or blinks. During saccades, the visual scene sweeps across the retina at high velocities (>100°/s), blurring the image and removing high spatial frequencies (Becker 1989). Since SD-neurons are tuned to low spatial frequencies and high velocities, their spatiotemporal tuning matches the image during saccades (Ibbotson and Mark 1994). Visual detection of saccades necessitates cells with large receptive fields that are optimally sensitive to wide-field stimuli. All SD-neurons have large receptive fields covering up to the entire visual field of one eye (Fig. 1*B*), and cell responses increase almost linearly with increasing stimulus aperture diameter (Fig. 2). Importantly, large stimuli (mean: >18° diam) were necessary to evoke significant responses. Since saccades produce motion of the entire visual field, they will stimulate the entire receptive field of all SD-neurons. Thus cell responses should depend primarily on stimulus contrast and speed. While SD-neurons were maximally stimulated by wide-field, high-contrast images (Fig. 3), they cannot distinguish small, high-contrast stimuli from large, low-contrast stimuli. Spatial pooling of outputs from SD-neurons with distinct receptive fields could compensate for the interdependence of stimulus contrast and size.

It has been proposed that pretectal nondirectional jerk cells in the cat may help drive eye movements compensating for rapid image displacements (Schweigart and Hoffmann 1992). This suggestion was based on the finding that pretectal electrical stimulation could elicit saccades; however, these saccades were typically directed only contralaterally or upward (Fig. 6B in Schweigart and Hoffmann 1992). Given the nondirectional nature of SD-neurons (Fig. 1, *C* and *D*) and the analogous cat jerk cells, it is unclear how they could be used to align eye movements with rapid image slip.

Possible inputs to SD-neurons

With high-contrast moving stimuli, SD-neuron spiking rates saturate at levels dependent on the stimulus size (Fig. 3*E*), suggesting that they summate outputs from units with smaller receptive fields. Sensitivity to rapid contrast change, rather than specifically motion sensitivity, could be mediated by spatial summation of Y-retinal ganglion cell inputs. In the cat, indirect and direct Y-cell inputs have been proposed for saccade and jerk neurons, respectively, from studies of optic chiasm stimulation latencies (Ballas and Hoffmann 1985; Schmidt and Hoffmann 1992). Our results suggest that SD-neurons receive phasic inputs from ON- and OFF-channels because the cells respond transiently to stepped increases or decreases in luminance and to contrast reversing gratings, independent of the grating's spatial phase. This is consistent with inputs from retinal Y-cells, which give transient responses to luminance increments and decrements (Fukuda et al. 1984; Victor 1988). Our results also demonstrate the "Y-cell signature" (Hochstein and Shapley 1976; Shapley and Perry 1986).

We demonstrated the phase independence of SD-neuron responses to contrast reversing gratings with a range of spatial frequencies (Fig. 9). This could arise with phase-independent inputs or the spatial summation of sufficient linear, phase-dependent inputs to cancel the phase dependence. The phase independence of SD-neuron responses stimulated in apertures of 12 and 30° diameter suggests nonlinear inputs such as Y-cells synapse onto SD-neurons. With the smaller stimulus aperture, no phase-dependent responses were observed even though relatively few inputs would be spatially summated to cancel any inherent phase dependence. Although Y-cells and some W-cells display nonlinear, phase-independent processing (Enroth-Cugell and Robson 1966; Levick and Thibos 1983; Victor and Shapley 1979), the long latencies of W-cells to contrast changes suggests they could not support the rapid responses of SD-neurons (Stone and Fukuda 1974).

Habituation and adaptation

In behaving animals, the eyes are rarely stationary for extended periods because saccades regularly change the point of gaze between objects of interest. Thus the retinal input is characterized by stationary images during fixation alternating with saccade-related motion. SD-neurons were capable of responding to repetitive and closely spaced saccade-like image displacements; however, the minimum stationary rest period necessary to allow distinct motion responses was dependent on the duration of motion. This suggests fatigue or suppression limits responses to closely timed saccades, with the size of fatigue or suppression dependent on saccade length. Long recovery times are required for SD-neurons to give similar responses to repeated motion periods: Fig. 7*E* shows that over half a second of rest was required for complete recovery following only 40 ms of saccade-like motion. Similarly, following a large response to an initial period of motion, responses to subsequent saccade-like image displacements are attenuated (Fig. 7*A*). This suppression may represent a refractory state that occurs after a saccade or during nystagmus.

Our data indicate that the response and recovery times of SD-neurons fit with the metrics of the mammalian saccadic system. Saccade durations are proportional to their amplitude, ranging from 50 to 200 ms in humans (Becker 1989), with 7.5° saccades in cats lasting ~90 ms (Lee and Malpeli 1998). In monkeys, the closest possible spacing of electrically stimulated saccades was 30 ms (Becker 1989), while measurements of OKN indicate intersaccadic intervals of 150–500 ms in wallabies (unpublished observations) and 300 ms or longer in humans (Cheng and Outerbridge 1974). Based on the saccade durations and frequencies in a range of mammals, it is likely that SD-neurons could respond distinctly to closely timed saccades during visual search or OKN. The highly repetitive motion periods of our OKN-like stimulus were possibly more demanding of the cells than natural stimuli, but demonstrated that the SD-neurons would not be fatigued or saturated by the continual saccadic eye movements performed by awake animals. Since nondirectional pretectal cells in cats differ in responses to saccades and saccade-like visual stimuli, it is likely that eye movements may influence SD-neuron responses and their susceptibility to fatigue or habituation. To further characterize the nature of SD-neuron visual responses, it is necessary to better understand the size, duration, and frequency of eye movements in normally behaving animals and to investigate cell responses in awake behaving animals.

Functional considerations

Our results have demonstrated that SD-neurons are well adapted to detect wide-field, rapid contrast changes: the visual disturbances associated with saccades and blinks. We will speculate on how SD-neurons may help overcome visual processing problems associated with the need to prevent ocular following of saccades and the need to modulate visual processing during and after saccades or blinks.

The first of these problems arises because wide-field retinal slip normally stimulates ocular following to stabilize the retinal image (e.g., Carpenter 1977). Pretectal retinal slip cells, which help generate eye movements compensating for retinal slip, are suppressed by the optimal stimuli for SD-neurons (Hoffmann and Schoppmann 1981; Ibbotson and Mark 1994). This suppression is tightly coupled to the onset and cessation of motion and matches the response latencies of SD-neurons to rapid motion. The close anatomical proximity of retinal slip cells and SD-neurons, and the presence of GABAergic interneurons in the pretectum support the possibility that SD-neurons suppress slip cells during saccades (Cucchiaro et al. 1991; Ibbotson and Mark 1994). Findings of postsaccadic enhancement of pursuit suggest that the motion sensitivity of retinal slip cells is facilitated after saccades (Kawano and Miles 1986; Lewis et al. 1999; Lisberger 1998). This does not contradict the proposed saccadic suppression of retinal slip cells by SD-neurons, since suppression is only evident during the saccade and could give way to facilitation following the detection of a stable image at saccade end.

Second, to prevent conscious awareness of the rapid motion during saccades or image darkening during blinks, it is desirable to suppress visual perception during these movements. Further, it is desirable to facilitate visual processing after these events to rapidly analyze the new scene. Since blinks and large saccades regularly occur in conjunction (Evinger et al. 1994),

SD-neuron responses to the associated large contrast changes would be strong. Studies of saccadic and blink suppression have demonstrated that visual perception is modulated before the onset of eye or eyelid movements, necessitating a motor corollary signal (Lee and Malpeli 1998; Volkmann et al. 1968). Although we did not investigate SD-neuron responses to eye movements, studies of the analogous saccade neurons in awake cats indicated that they do not respond until after saccade onset (Schmidt 1996). Thus pretectal nondirectional cells would be unable to mediate presaccadic or preblink suppression of visual perception.

In the cat, LGN-projecting pretectal cells are sensitive to saccadic eye movements (Schmidt 1996) and possibly have GABAergic synapses on inhibitory interneurons, which subsequently synapse on thalamic relay cells (Cucchiaro et al. 1991; Wahle et al. 1994). Given that saccadic suppression and postsaccadic facilitation has been reported in the cat LGN (Lee and Malpeli 1998), SD-neurons may modulate thalamic relay cell activity during saccades or blinks. Since relay cells are part of a retino-cortical circuit, the pretectum could affect cortical visual processing. Schmidt (1996) proposed that postsaccadic facilitation of relay cells was mediated by pretectal nondirectional cells, a mechanism supported by the pretectum's disinhibitory effect on thalamic relay cells during saccades (Fischer et al. 1996, 1998).

We found an average half-peak response latency of 41 ms in wallaby SD-neurons stimulated with rapid motion. Accounting for synaptic delays and the effects of anesthesia, this correlates well with latencies of 30–60 ms for LGN facilitation measured in awake behaving cats responding to rapid movements (Fischer et al. 1996). The temporal relationship between saccade onset and LGN facilitation has not been studied but could be tested by examining the onset of facilitation associated with saccades or saccade-like motion of varying durations. This could also determine whether saccadic facilitation of the LGN is linked to the start or end of eye movements. To extend our understanding of SD-neuron function, experiments investigating the modulation of LGN activity mediated by SD-neurons in response to a range of electrical, visual and behavioral stimuli are underway.

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