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The temporal impulse response function in infantile nystagmus

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ABSTRACT

Despite rapid to-and-fro motion of the retinal image that results from their incessant involuntary eye movements, persons with infantile nystagmus (IN) rarely report the perception of motion smear. We performed two experiments to determine if the reduction of perceived motion smear in persons with IN is associated with an increase in the speed of the temporal impulse response. In Experiment 1, increment thresholds were determined for pairs of successively presented flashes of a long horizontal line, presented on a 65-cd/m^2 background field. The stimulus-onset asynchrony (SOA) between the first and second flash varied from 5.9 to 234 ms. In experiment 2, temporal contrast sensitivity functions were determined for a 3-cpd horizontal square-wave grating that underwent counterphase flicker at temporal frequencies between 1 and 40 Hz. Data were obtained for 2 subjects with predominantly pendular IN and 8 normal observers in Experiment 1 and for 3 subjects with IN and 4 normal observers in Experiment 2. Temporal impulse response functions (TIRFs) were estimated as the impulse response of a linear second-order system that provided the best fit to the increment threshold data in Experiment 1 and to the temporal contrast sensitivity functions in Experiment 2. Estimated TIRFs of the subjects with pendular IN have natural temporal frequencies that are significantly faster than those of normal observers (*ca.* 13 vs. 9 Hz), indicating an accelerated temporal response to visual stimuli. This increase in response speed is too small to account by itself for the virtual absence of perceived motion smear in subjects with IN, and additional neural mechanisms are considered.

1. Introduction

Infantile nystagmus (IN) is a rhythmic to-and-fro movement of the eyes, usually with the principal component in the horizontal meridian. Typical values for the amplitude and frequency of IN are approximately 4–6° and 3–4 Hz (Bedell & Loshin, 1991; Cesarelli, Bifulco, Loffredo, & Bracale, 2000; Yee, Wong, Baloh, & Honrubia, 1976), resulting in an average velocity of retinal image motion on the order of 12–24°/s. Motion of the retinal image in excess of a few deg/s adversely affects many aspects of normal spatial vision (Chung & Bedell, 1998, 2003; Demer & Amjadi, 1993; Ramamurthy, Bedell, & Patel, 2005; Westheimer & McKee, 1975). Consequently, considerable research has evaluated the influence of the retinal image motion that results from IN on aspects of visual functioning, including visual acuity (e.g., Bedell, 2000; Dickinson & Abadi, 1985; Ukwade & Bedell, 1999). These studies found that visual acuity correlates with the duration of the foveation periods of the nystagmus wave form, during which the eye velocity is relatively slow and the acuity target is imaged on or near the fovea (Abadi & Worfolk, 1989; Cesarelli et al., 2000; Dell'Osso & Daroff, 1975; Sheth, Dell'Osso, Leigh, Van Doren, & Peckham, 1995).

Despite the presence of relatively rapid eye motion, subjects with IN typically do *not* report that stationary objects appear to be smeared (Bedell & Bollenbacher, 1996). In contrast, normal observers report that rapidly moving objects have noticeable motion smear.[1] The perception of motion smear is most extensive for isolated objects in motion, and decreases as the spatial density of moving objects increases, presumably as the result of lateral spatio-temporal interactions (Chen, Bedell, & Ögmen, 1995; Di Lollo & Hogben, 1985; Purushothaman, Ögmen, Chen, & Bedell, 1998). The perception of motion smear in normal observers can be attributed to the sluggish temporal response of the visual system, which results in neural responses that persist at each retinal location after the

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[1] In our previous studies, normal observers reported noticeable motion smear for retinal image velocities ranging from 2 to 80°/s (e.g., Bedell, Chung, & Patel, 2004; Tong, Patel, & Bedell, 2006a).

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image moves elsewhere (Bidwell, 1899; Ganz, 1975; Geisler, 1999; McDougall, 1904).

The temporal impulse response function (TIRF) provides a description of the temporal response of the visual system for a specific set of stimulus conditions. Ikeda (1965) and Rashbass (1970) estimated the normal TIRF by psychophysically determining sensitivity to a pair of visual targets that were flashed briefly on a moderate photopic background and separated in time by various stimulus-onset asynchronies (SOAs). At short SOAs, the sensitivity to two flashes is substantially better than to one flash alone, indicating that the visual response to the second flash adds to the persisting visual excitation from the first. The improvement in sensitivity provided by the second flash decreases gradually as the SOA increases, as would be expected from a gradual decline in the activity from the initial flash. At longer SOAs, both Ikeda and Rashbass found that sensitivity to two flashes is *lower* than to a single flash, which they attributed to a delayed, inhibitory phase of the response to the initial flash. At still longer SOAs, the second flash exerts no effect on visual sensitivity, except for the slight improvement expected on the basis of probability summation.

The temporal contrast sensitivity function (TCSF) also describes the dynamic response of the visual system. As demonstrated by several authors, the shape of the TCSF varies systematically with both the spatial characteristics and the mean luminance of the visual stimulus (e.g., Kelly, 1971, 1979; Robson, 1966; Swanson, Ueno, Smith, & Pokorny, 1987). Specifically, an increase in the spatial frequency of a temporally modulated stimulus results in reduced sensitivity for high temporal frequencies and a change in the TCSF from bandpass to more low pass in shape. Similar changes occur in the TCSF when the mean luminance of the stimulus is reduced.

As pointed out by Kelly and others (e.g., Kelly, 1971; Roufs, 1972), the TIRF is the inverse Fourier transformation of the TCSF, as long as linearity of visual responses can be assumed under the conditions of visual stimulation. Based on this relationship, the changes that occur in the TCSF with the spatial frequency and mean luminance of the stimulus are expected to produce systematic and predictable changes in the time course and shape of the TIRF. Specifically, reduced sensitivity to high temporal frequencies should extend the duration of the TIRF in time and a change in the shape of the TCSF from bandpass to low pass should attenuate the secondary inhibitory phase of the TIRF. Increasing the spatial frequency or decreasing the mean luminance of two-flash targets produces these expected changes in the duration and shape of estimated TIRFs (Georgeson, 1987; Ikeda, 1965; Watson & Nachmias, 1977).

Burr and Morrone (1996) presented data from two-flash detection experiments indicating that the shape of the TIRF also is affected during saccadic eye movements. During saccades, the peak amplitude of the estimated TIRF decreases, consistent with the reduction in sensitivity that is expected from saccadic suppression, and the time course of the TIRF speeds up. Specifically, in the study by Burr and Morrone (1996), the peak of the first positive lobe of the TIRF shifted in time from approximately 20 ms during fixation to approximately 12 ms during saccades. Concomitantly, the trough of the second, inhibitory phase shifted from approximately 60 to 40 ms. The results shown for the two observers in this study suggest also that the depth of the inhibitory second phase of the TIRF is *relatively* less during a saccade than during fixation. We reported that a similar but less pronounced speeding up of normal observers' TIRFs occurs during smooth pursuit compared to fixation, although with little or no change in the amplitude of the response (Bedell, Ramamurthy, Patel, & Vu-Yu, 2003; Tong, Patel, & Bedell, 2006b).

Reppas, Usrey, and Reid (2002) determined the impulse responses of individual primate LGN neurons from spike trains recorded in response to a full-field flickering stimulus. In addition to a saccade-dependent modulation of the overall level of responsiveness, they found that the impulse responses of magno-cellular LGN neurons speed up just after the end of a saccade, when compared to the responses obtained during intervals of fixation. The post-saccadic acceleration was more pronounced for the secondary inhibitory phase of the magno-cellular impulse response than for initial excitatory component.

If temporal processing speeds up also during the involuntary eye movements of individuals with IN, then we would expect the duration of visual persistence to be reduced, compared to that measured during normal fixation. A reduced duration of visual persistence would be expected to translate into a smaller extent of perceived motion smear. Consequently, we sought to evaluate whether an increase in the speed of temporal processing could contribute to the minimal perception of motion smear by individuals with IN. Previously, Waugh and Bedell (1992) measured TCSFs for normal observers and subjects with IN using a 35° uniform flickering field. The resulting functions were similar except for slightly higher contrast sensitivity among the subjects with IN at low rates of flicker. These temporal contrast sensitivity data would suggest that the speed of the TIRF differs little between normal observers and subjects with IN. However, the perception of motion smear occurs only for visual stimuli that include local spatial structure, which is absent from the uniform flickering field used by Waugh and Bedell (1992). Consequently, in this study, we estimated and compared TIRFs derived from 2-pulse thresholds and from TCSFs using spatially structured targets in normal observers and subjects with IN.

2. Methods

2.1. Experiment

Stimuli were presented on a gamma-corrected, Image Systems M21L monchromatic monitor, running at 171 Hz. This monitor is equipped with DP104 phosphor, which has peak output at a wavelength of 565 nm and a spectral bandwidth of approximately 90 nm. After excitation, screen luminance decays to less than 1% of its peak value within 250 μs. Increment sensitivity was determined for *pairs* of successively presented flashes (one frame or 5.85 ms each) of a 15° long, 10 min-arc high horizontal line. Long horizontal lines were used to maximize the overlap between the retinal images of stimuli presented before and after the SOA in observers with IN. Each pair of lines was superimposed on a 65-cd/m^2 homogeneous background field and was presented 0.9° above or below a continuously visible fixation cross (Fig. 1). Each observer viewed the stimuli monocularly from a distance of 114 cm, using his or her preferred eye. The observer initiated each trial by pressing a button on a joystick, and subsequently used the joystick to report whether the flashed lines appeared above or below the fixation cross. The stimulus-onset asynchrony (SOA) between the first and second flash varied randomly among blocks of 70 trials from 5.85 to 234 ms. Increment sensitivity for each SOA corresponds to 75% correct responses, determined from 30 to 60 trials at each of seven contrast levels using the method of constant stimuli.

Increment sensitivity was measured as a function of the SOA for 8 normal observers with 20/20 or better corrected visual acuity and for 2 subjects with predominantly pendular IN. For this study, we specifically included subjects with predominantly pendular IN, to minimize the contribution of nystagmus fast phases (saccades) to any speeding up of the TIRF (Burr & Morrone, 1996). The clinical characteristics of the two subjects with IN, along with those of a third subject who participated only in Experiment 2, are provided in Table 1. The horizontal position of the left viewing eye was monitored by infra-red limbal tracking during Experiment 1 for the two subjects with IN. An experimenter rejected trials in which a nystagmus fast phase occurred during the presentation of the target lines. Rejected trials were repeated on the immediately following trial. A sample wave form for each subject with IN is presented in Fig. 2. As the nystagmus of neither of the observers who participated in Experiment 1 has a latent component, their eye movements are highly similar during monocular and binocular viewing.

2.2. Analysis of 2-pulse data

The temporal impulse response function of the visual system was modeled as an impulse response of a linear second-order low-pass system. The form of the equation that describes a second-order linear system depends on a variable called the damping ratio, D:

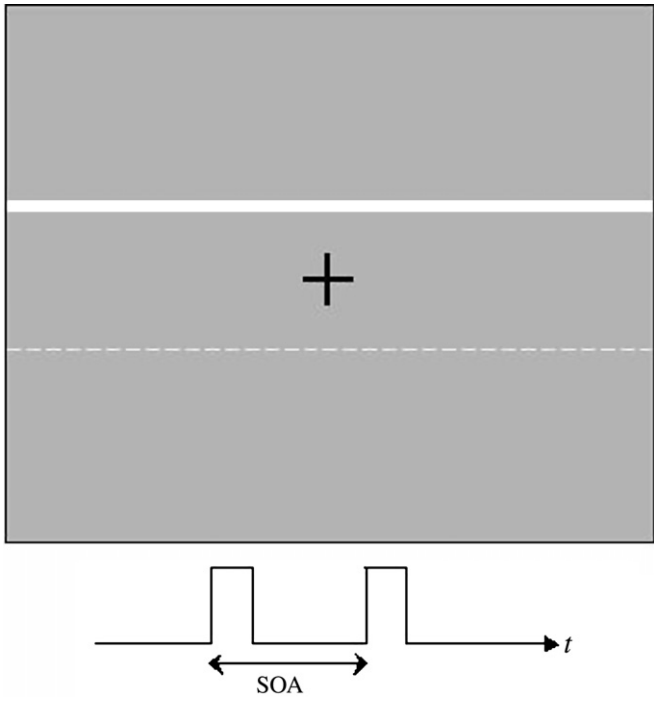

Fig. 1. The top drawing depicts the stimulus used to measure 2-pulse increment sensitivity. On each trial, the long horizontal line was flashed twice either 0.9° above (as shown here) or below (dotted line) the fixation cross. The diagram below indicates the timing of the two bright pulses on each trial.

If $0 \leqslant D < 1$ (an underdamped system), then

$$R(t) = \left(A * W/\mathrm{Sqrt}\left[1 - D^2\right]\right) * \exp(-D * W * t) * \sin\left(W * \mathrm{Sqrt}\left[1 - D^2\right] * t\right).$$

If $D = 1$ (a critically damped system), then

$$R(t) = \left(A * W^2\right) * \exp\left(-D * W * t\right) * t.$$

If $D > 1$ (an overdamped system), then

$$R(t) = \left(A * W/2 * \mathrm{Sqrt}\left[D^2 - 1\right]\right) * \exp\left(-(D - \mathrm{Sqrt}\left[D^2 - 1\right]) * W * t\right) - \left(\mathrm{A} * \mathrm{W}/2 * \mathrm{Sqrt}\left[D^2 - 1\right]\right) * \exp\left(-\left(D + \mathrm{Sqrt}\left[D^2 - 1\right]\right) * W * t\right). \quad (1)$$

In the equations above, R is the response of the visual system at time (t) to a brief pulse, A is the response amplitude, and W is the natural temporal frequency of the system in radians/s. It is assumed that $R(t) = 0$ for $t \leqslant 0$. In contrast to a first-order, low-pass system, a *second-order* low-pass system does not necessarily have a uniphasic TIRF. Rather, a second order linear low-pass system can exhibit either a uniphasic or a biphasic temporal impulse response, depending on the value of the damping ratio, D. When D is less than 1, the system is under-damped and exhibits a biphasic impulse response. Other values of D (i.e., when $D \geqslant 1$) yield a uniphasic impulse response.

The response of the visual system to two pulses that are separated in time by a SOA is given by:

$$R_2(t, \mathrm{SOA}) = R(t) + R(t - \mathrm{SOA}).$$

A simplex optimization procedure in MatLab (fmins) was used to estimate the values of A, W, and D that provided the best fit to each subject's increment contrast sensitivity data when summed at the various SOAs. Each iteration of the optimization procedure included the following steps at each SOA:

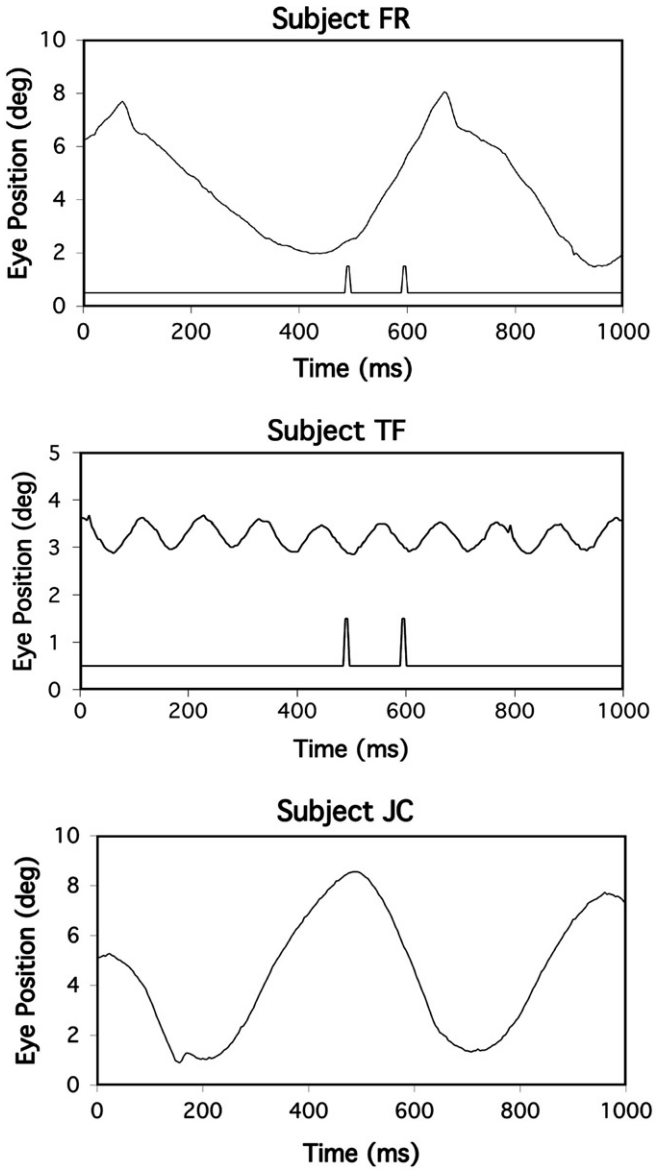

Fig. 2. Sample horizontal IN wave forms are shown for subjects F.R., T.F. and J.C. Upward deflections correspond to leftward eye movements. The pair of pulses near the bottom of the upper two panels indicates the times that the horizontal line was flashed on these trials in Experiment 1. Pulses are not shown for subject J.C. because he participated only in Experiment 2.

(a) R_2 was evaluated with a temporal resolution (Δt) of 0.5 ms.
(b) Assuming that the visual system uses information up to 250 ms after the first pulse, an estimate of increment sensitivity was determined from R_2 using the criterion function (Burr & Morrone, 1993):

$$\mathrm{CS}(\mathrm{SOA}) = \left[\sum_{i=0}^{500} |R_2(\mathrm{i}\Delta t, \mathrm{SOA})|^{3.5}\right]^{1/3.5}$$

(c) The residual error was computed by subtracting CS(SOA) from the psychophysically measured increment sensitivity, $\mathrm{CS}_{\mathrm{data}}(\mathrm{SOA})$.

Table 1
Characteristics of the observers with IN

Observer	Refractive error	Visual acuity (logMAR)	Predominant wave form	Amplitude (°)	Frequency (Hz)	Foveation duration (ms)
F.R.	RE: +5.50 − 3.75 × 180; LE: +5.75 − 4.50 × 168	0.803	Pendular + foveating sac	7.3	3.2	36
T.F.	RE: −0.50 sph; LE: −0.25 − 0.50 × 0.90	0.396	Pendular	1.1	9.4	27
J.C.	RE: +0.50 − 3.00 × 145; LE: −0.50 − 0.75 × 005	0.369	Pendular	5.5	2.1	78

The optimization procedure adjusted the values of *A*, *W*, and *D* to minimize the squared residual errors, summed across SOAs.

2.3. Experiment 2

Temporal impulse response functions were estimated from the TCSFs (e.g., Kelly, 1971; Roufs, 1972) determined for four of the normal observers who participated also in Experiment 1, and for 3 subjects with IN (Table 1). Stimuli were presented at a mean luminance of 65 cd/m^2 on the same Image Systems monitor that was used in Experiment 1. For this experiment, the refresh rate of the monitor was increased to 239 Hz. Contrast sensitivity was determined using a two-alternative temporal forced choice, combined with a one-up, one-down staircase procedure. On each trial, the observer indicated whether a 3 c/°horizontal square-wave grating was presented in one of two 2-s intervals, before and after a 500-ms inter-stimulus interval. The spatial half-period of this grating subtends 10 min arc, which is equal to the vertical dimension of the flashed horizontal lines that were used to measure 2-pulse increment sensitivity in Experiment 1. The field that contained the grating had a diameter of 16°and underwent sinusoidal counterphase flicker at one of eight temporal frequencies, ranging from 1 to 40 Hz. Temporal frequencies were presented in random order, using the "Psycho" software included with the VSG2/3 software package (Cambridge Research Systems). During the 2-s interval on each trial that contained the flickering grating, its contrast ramped linearly on and off during the first and last 250 ms. Maximum contrast of the flickering grating decreased by 15% following correct responses and increased by 30% following incorrect responses. Viewing was binocular and, because of the 4.5-s duration of each trial, it was not plausible to reject trials that included saccadic eye movements. Consequently, the subjects' eye movements were not recorded during the experiment. Each staircase terminated after 30 trials and the threshold contrast for each temporal frequency was defined as the mean of the accumulated reversals. Except for observer J.C. with IN who completed only 1 run, temporal contrast sensitivities represent the average of 2 or more runs for each observer.

2.4. Analysis of temporal contrast sensitivity data

The temporal impulse response function for a second-order linear system (see Section 2.2) was determined iteratively from the measured temporal contrast sensitivity function using MatLab. Each iteration of the optimization procedure included the following steps:

(a) The Fourier transform of the impulse response function was computed with a temporal frequency resolution of 1 Hz.
(b) For each temporal frequency tested experimentally, the residual error was computed by subtracting the measured log contrast sensitivity from the amplitude of the corresponding Fourier component computed in step (a)

The optimization procedure (see Section 2.2) adjusted the values of *A*, *W*, and *D* to minimize the squared residual errors, summed across the temporal frequencies that were tested in the experiment.

Like the temporal impulse response, the temporal frequency response of a linear second-order low-pass system also depends on the value of the damping ratio, *D*. When the damping ratio is less than 1/Sqrt(2), a second-order low-pass system exhibits a higher response in the region of the corner temporal frequency than at lower (and higher) frequencies. The magnitude of this peak increases as the value of *D* decreases. Nevertheless, the system is low-pass and not band-pass because (1) the response drops monotonically for frequencies that are higher than the corner frequency and (2) the response is relatively flat for temporal frequencies that are lower than some critical frequency, which is below the corner temporal frequency. If the value of *D* is greater than 1/Sqrt(2), the temporal frequency response is relatively flat up to the corner temporal frequency and then drops monotonically at higher frequencies. Regardless of whether a peak exists, the rate at which the frequency response drops above the corner temporal frequency is greater in a second-order low-pass system (12 dB/octave) than in a first-order low-pass system (6 dB/octave).

3. Results

3.1. Experiment 1

Average 2-pulse increment sensitivity for the eight normal observers decreases to a minimum at a SOA between 50 and 60 ms, and increases slightly at longer SOAs (Fig. 3, top). As shown in the bottom of the figure, the fitted TIRF is biphasic, with a peak at approximately 20 ms and a trough at approximately 75 ms. The natural temporal frequency (*W*) of the system that provides the best fit to the normal observers' 2-pulse data is 9.8 ± 0.47 (SE) Hz. This fit, which is shown in the top of Fig. 3,

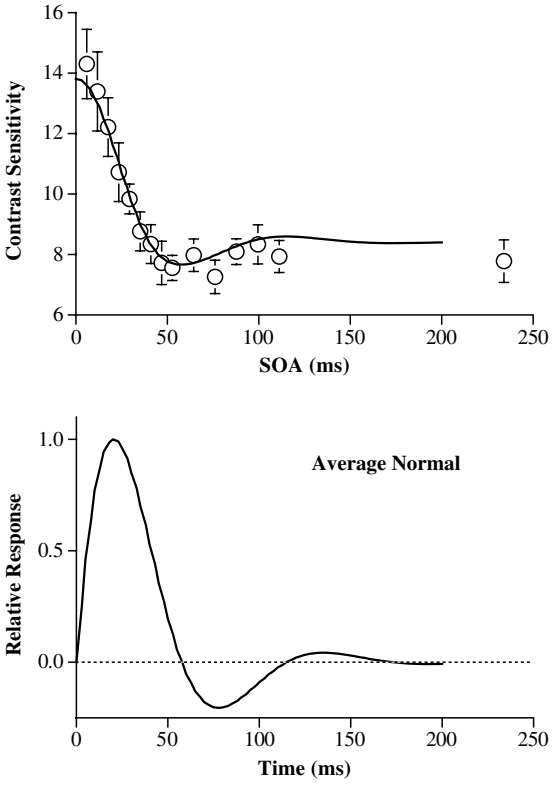

Fig. 3. The top panel shows the average 2-pulse increment sensitivity data for eight normal observers, as a function of SOA. Error bars are ±1 standard error of the mean, across the eight observers. The solid line is the fit to the 2-pulse increment sensitivity, based on the temporal impulse response function shown underneath.

has a coefficient of determination equal to 0.97, indicating that the second-order linear model accounts for 97% of the variance of the average contrast sensitivities measured in the normal subjects. To facilitate comparison with the TIRFs determined for subjects with IN (Fig. 4, bottom), the amplitudes of the TIRFs in Figs. 3 and 4 are normalized to a maximum relative response of 1. The parameters of the estimated TIRFs prior to normalization are listed in Table 2.

Two-pulse increment sensitivities and the estimated TIRFs are presented separately for the 2 subjects with IN in Fig. 4. Although the estimated TIRFs have essentially the same biphasic shape as the average normal function, both the peak and trough occur at earlier SOAs (peak approximately 5 ms earlier; trough between 7 and 17 ms earlier) for the subjects with IN. In addition, the TIRFs estimated for the subjects with IN are narrower than the normal TIRF, as indicated by the half-widths at half-height given in the legend for Fig. 4.[2] Accordingly, the TIRFs for the 2 subjects with IN have natural temporal frequencies that are significantly higher (11.8 and 13.1 Hz) than the average normal value ($t_{[df=8]} = 2.62$, $p = 0.031$). On the other hand, neither the amplitudes ($p = 0.90$) nor the damping ratios ($p = 0.17$) of the fitted TIRFs differ significantly between the 8 normal observers and the 2 subjects with IN (Table 2). Model fits for the 2-pulse contrast-sensitivity data have coefficients of determination of 0.62 and 0.84 for the two subjects with IN.

[2] Similar differences between the TIRFs of the subjects with IN and normal observers were found using other criteria, such as the widths of the functions at 10% and 1/e of the maximum response.

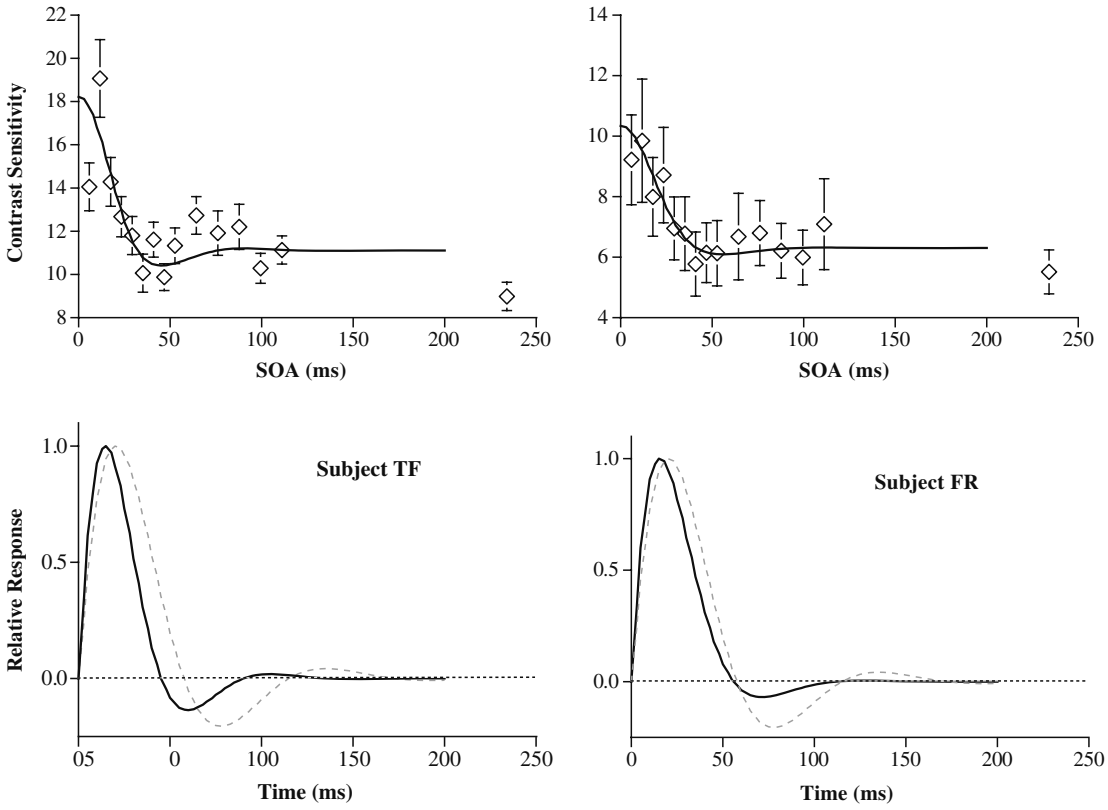

Fig. 4. The top panels present 2-pulse increment sensitivity data for two subjects with IN, F.R. and T.F. Error bars are ±1 standard error of estimate, based on the contrast sensitivity determined at each SOA. As in Fig. 3, the solid line is the fit to the 2-pulse increment sensitivity, based on the estimated temporal impulse response function (TIRF) for each observer (bottom). Full-widths of the estimated TIRFs at half-height are 30 ms for subject FR and 26 ms for subject T.F. For comparison, the TIRF that was fit to the average results of eight normal observers has a full-width at half-height of 35 ms, and is replotted from Fig. 3 in each lower panel (dashed lines).

Table 2
Parameters of fitted temporal impulse response functions (2-pulse data)

	Amplitude	Natural TF	Damping
Normal observers			
H.B.	0.071	8.3	0.51
J.T.	0.066	10.1	0.57
L.V.	0.089	7.9	0.28
M.M.	0.063	11.6	0.56
M.R.	0.061	11.2	0.31
S.O.	0.069	10.1	0.39
S.S.	0.063	10.4	0.59
V.H.	0.051	8.8	0.32
Means ± SE	0.064 ± 0.002	9.80 ± 0.47	0.44 ± 0.05
Subjects with IN			
F.R.	0.053	11.8	0.65
T.F.	0.078	13.1	0.54
Means ± SE	0.065 ± 0.02	12.47 ± 0.56	0.59 ± 0.05

3.2. Experiment 2

The TCSFs determined for counterphase flickering 3 c/°horizontal square-wave gratings are approximately low pass, both for normal observers and for the subjects with IN (Fig. 5). For normal observers, this outcome is consistent with the results of several previous studies (e.g., Kelly, 1979; Robson, 1966). The maximum value of contrast sensitivity varies considerably among the 3 observers with IN. Nevertheless, compared to the normal observers, the subjects with IN exhibit *relatively* better contrast sensitivity at high temporal frequencies. The TIRFs (of the form described above in Section 2.2, but with the maximum response normalized to a value of 1) that best fit the temporal contrast sensitivity data are compared for normal observers and the observers with IN in Fig. 6. Model fits for the temporal contrast sensitivity data have coefficients of determination that range from 0.91 (subject J.C.) to 0.99 (average normal data). Consistent with the results of Experiment 1, the first excitatory peak occurs approximately 7–10 ms earlier in the TIRFs of the subjects with IN than in the function determined from the normal observers' temporal contrast sensitivity data. The fitted parameters of the temporal impulse response functions of normal observers and the subjects with IN (before normalization) are listed in Table 3 and half-widths at half-height are reported in the legend for Fig. 6. The TIRFs of the 3 subjects with IN have natural temporal frequencies that are significantly higher than the natural temporal frequency of the average normal function ($t_{[df=5]} = 3.89$, $p = 0.012$). Although the magnitude of damping is generally greater for the TIRFs of the subjects with IN, neither the difference in the tabulated damping constant ($p = 0.180$) nor in the amplitude ($p = 0.131$) of the fitted TIRFs reach statistical significance.

The amplitude of the TIRF derived from the average normal TCSF data is much higher than the amplitude determined in Experiment 1 from 2-flash data (compare values in Tables 2 and 3; $t_{[df=10]} = 14.60$, $p = 4.54 \times 10^{-8}$). This difference reflects the observers' substantially higher contrast sensitivity for a temporally and spatially extended sinusoidal flickering grating than for a briefly flashed pair of lines. Although the natural temporal frequency of the average normal TIRF obtained from the TCSF data in Experiment 2 is lower than for the 2-flash condition in Experiment 1 (8.66 vs. 9.80 Hz), this difference is not statistically significant ($t_{[df=10]} = 1.41$, $p = 0.188$). Similarly, the higher damping ratio of

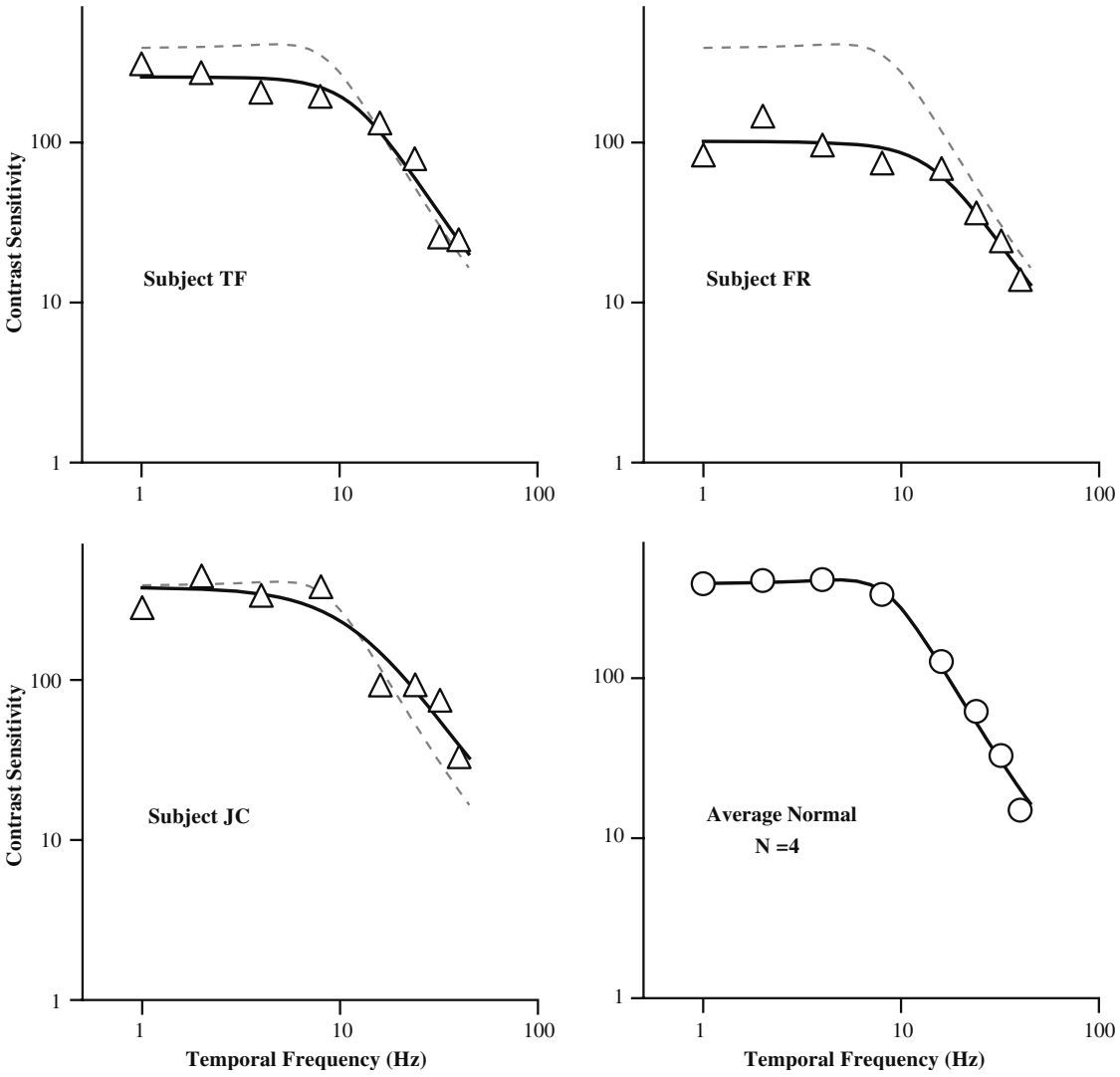

Fig. 5. The lower right panel shows the average temporal contrast sensitivity function (TCSF) for four normal observers (H.B., M.R., S.O. and S.S.). The other three panels show individual TCSFs for subjects with IN (F.R., T.F. and J.C.). The average normal TCSF is shown for comparison as a dashed line. Temporal contrast sensitivity was determined for temporally-windowed 2-s trials of a 3 c/°square-wave grating that was modulated temporally by sinusoidal counterphase flicker between 1 and 40 Hz. Note that the half period of a 3 c/°square-wave grating corresponds to 10 minarc, which is the height of the lines used to measure 2-pulse increment sensitivity (Figs. 3 and 4). The solid line in each panel is the Fourier transform of the best-fitting temporal impulse response function, shown in Fig. 6, below.

the normal TIRF obtained from TCSF data in Experiment 2 does not differ significantly from the damping ratio determined from the 2-flash data in Experiment 1 (0.63 vs. 0.44, $t_{[df=10]} = 1.89$, $p = 0.088$).

4. Discussion

4.1. The influence of eye movements on the TIRF

Burr and Morrone (1996) considered two possible explanations for the speeding up of the TIRF that they estimated for luminance-defined targets during normal saccadic eye movements. One mechanism is a relative loss of sensitivity in magno-cellular compared to parvo-cellular neurons, which is consistent with the selective loss of sensitivity for luminance-defined, low-spatial frequency stimuli that occurs during saccades (Burr, Morrone, & Ross, 1994; Uchikawa & Sato, 1995; Volkmann, Riggs, White, & Moore, 1978). However, as Burr and Morrone point out, an explanation based on a reduction of magno-cellular sensitivity requires the *unsuppressed* parvo-cellular responses to be more transient than the suppressed magno-cellular responses, which is not in agreement with the usual conceptualization of these two pathways, especially for the structured spatial stimuli that we used here (e.g., Derrington & Lennie, 1984; Merigan & Maunsell, 1990).[3] Further, the speeding up of the TIRF that occurs in subjects with IN is accompanied by no significant loss of contrast sensitivity during nystagmus slow phases (Tables 2 and 3; see also Jin, Goldstein, & Reinecke, 1989). The retention of approximately normal sensitivity during the slow phases of IN would tend to exclude an explanation for an acceleration of the TIRF based on the suppression of magno-cellular activity.

The second explanation considered by Burr and Morrone is that a gain control mechanism reduces sensitivity preferentially for luminance-defined targets of low compared to high temporal frequency (Shapley & Victor, 1981). In addition to speeding up the TIRF, the preferential reduction of response gain at lower temporal frequencies would account for saccadic suppression. Although Burr

[3] On the other hand, the second, inhibitory phase of the TIRFs estimated by Burr and Morrone (1996) is relatively smaller during saccades than during fixation. In the context of the model that we used to fit the TIRF data, this difference is indicative of increased damping, which would *by itself* be consistent with a shift from magno- to parvo-cellular pathway responses during a saccadic eye movement. Comparison of the TIRFs for observers with IN to those of normal observers reveals a similar, although statistically non-significant increase in damping.

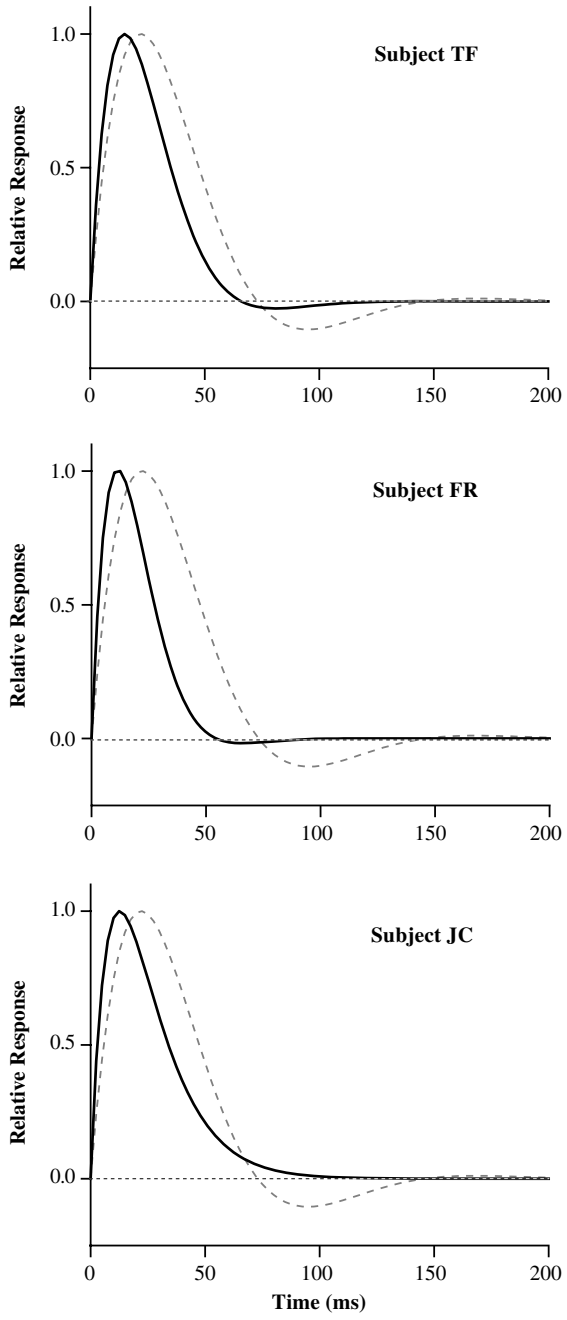

Fig. 6. Temporal impulse response functions (TIRFs) estimated from the TCSFs shown in Fig. 5 are plotted for three observers with IN. An estimate of the TIRF based on the average TCSF data of four normal observers is provided also in each panel for comparison (dashed line). Full widths of the estimated TIRFs at half height are 25, 31, and 31 ms, respectively, for subjects F.R., T.F., and J.C., compared to 42 ms for the normal function.

Table 3
Parameters of fitted temporal impulse response functions from TCSF data

	Amplitude	Natural TF	Damping
Normal observers ($N = 4$)			
H.B.	1.88	7.75	0.36
M.R.	1.49	8.18	0.55
S.O.	2.17	10.54	0.78
S.S.	2.40	8.18	0.82
Normal averages ± SE	1.99 ± 0.20	8.66 ± 0.63	0.63 ± 0.11
Subjects with IN			
F.R.	0.52	14.94	0.79
T.F.	1.30	11.60	0.76
J.C.	1.92	12.54	1.00
IN Average ± SE	1.24 ± 0.41	13.02 ± 0.99	0.85 ± 0.07

and Morrone did not specify the origin of the hypothesized gain control signal during saccades, they interpreted the results of a subsequent experiment to indicate that gain control occurs before the extraction of motion signals in the primary visual cortex (Burr, Morgan, & Morrone, 1999). However, as noted above, the subjects with IN did not show a significant reduction of contrast sensitivity for the stimuli in our experiments.

We propose that extra-retinal signals, which accompany the eye movements in IN, are responsible for the speeding of the TIRF that we observed. Elsewhere, we proposed that extra-retinal signals mediate a similar, but less pronounced, speeding up of the TIRF during normal smooth pursuit (Bedell et al., 2003; Tong et al., 2006b), with little or no loss of visual sensitivity (Bedell & Lott, 1996; Schütz, Braun, & Gegenfurtner, 2007a, Schütz, Delipetkos, Braun, Kerzel, & Gegenfurtner, 2007b; Starr, Angel, & Yeates, 1969). Evidence exists from a number of studies that extra-retinal signals accompany the involuntary eye movements in IN and contribute to perceptual stability (Abadi, Whittle, & Worfolk, 1999; Bedell & Currie, 1993; Goldstein, Gottlob, & Fendick, 1992; Leigh, Dell'Osso, Yaniglos, & Thurston, 1988). Other studies indicate that extra-retinal information, from efference copy signals as well as from eye-muscle proprioception, act to modulate neural responses at multiple processing sites in the visual system, from the superior colliculus to cortical areas V1 through MST (e.g., Ashton, Boddy, & Donaldson, 1984; Duffy & Burchfiel, 1975; Krauzlis, 2001; Newsome, Wurtz, & Komatsu, 1988; Thier & Erickson, 1992; Toyama, Komatsu, & Shibuki, 1984). In some visual areas, the combination of retinal and extra-retinal signals is thought to produce an accurate reconstruction of the location and velocity of visual targets in space (e.g., Duhamel, Colby, & Goldberg, 1992; Galletti, Battaglini, & Fattori, 1990; Newsome et al., 1988; Thier & Erickson, 1992; Sommer & Wurtz, 2004). The influence of extra-retinal eye-movement signals on the *dynamic* properties of individual neuronal responses is less clear. Toyama et al. (1984) reported that a substantial proportion of cat striate cortical neurons exhibit more prolonged responses when motion of the retinal image is produced during a saccade than when comparable motion of the image occurs while the eye is still. On the other hand, Reppas et al. (2002) found that the impulse response of primate magno-cellular LGN neurons is accelerated when the animal makes a saccade.

4.2. Characteristics of the TIRF during IN

Although statistically non-significant, the TIRFs fit to TCSF data show a tendency for more damping, compared to the TIRFs that were determined from 2-pulse data. A likely reason for a change in damping is the difference between the stimuli that were used in the two experiments, i.e., a single flashed line vs. an extended flickering square-wave grating. In particular, a single line contains considerable contrast energy in a broader range of spatial frequencies than the grating stimulus. If low spatial frequencies contribute significantly to the detection of the line then, based on the changes in the TIRF that occur with the spatial frequency of the stimulus (Georgeson, 1987; Watson & Nachmias, 1977), the TIRF determined from 2-pulse data would be expected to exhibit a higher natural TF and a smaller amount of damping (i.e., a larger inhibitory phase). The observed differences between the TIRFs determined from 2-pulse vs. TCSF data are in agreement with these expectations.

As noted in Section 1, similar TCSFs were determined by Waugh and Bedell (1992) for normal observers and subjects with IN. However, the stimulus was a large homogeneous flickering field, which

would be expected to generate a rapid TIRF with relatively little damping (Kelly, 1971). Wilson, Mets, Nagy, and Kressel (1988) measured similar temporal contrast sensitivities (range of TFs tested ≈10– 40 Hz) in normal observers and in two subjects with nystagmus and albinism. The temporally-modulated stimulus in their study was a horizontal 0.5 cpd sine-wave grating, presented within an 8° field. When taken in conjunction with the results of this study, these data suggest that the extra-retinal signals for nystagmus produce acceleration of the TIRF only for visual stimuli that contain contrast energy at moderate to high spatial frequencies.

For a broadband stimulus, such as the flashed line that was used in Experiment 1, it is possible that the TIRF is accelerated in the subjects with IN because they detected the stimulus using spatial channels tuned to lower spatial frequencies than the channels used for detection by normal observers. This possibility is based on the inverse relationship between stimulus spatial frequency and the speed of the TIRF that is reported in normal observers (Georgeson, 1987; Watson & Nachmias, 1977). However, the TIRFs determined from temporal contrast sensitivity for a 3-cpd flickering grating also are faster in subjects with IN than in normal observers. Because the spatially and temporally extended grating stimuli that we used are relatively narrow band, the spatial channel that mediates detection should be very similar in subjects with IN and normal observers. Consequently, we conclude that the differences in the speed of the TIRFs that we report here represent differences in the temporal processing of stimuli by subjects with IN and normal observers.

4.3. Perceived motion smear in subjects with IN

It is not clear to what extent the speeding up of the TIRF may account for the reduction of perceived motion smear in subjects with IN. As pointed out by Blommaert and Roufs (1987), the positive phase of the TIRF provides a plausible estimate for the duration of temporal integration and, hence, the extent of perceived motion smear.[4] Although the duration of the positive phase of the TIRF is reduced in the subjects with IN compared to normal observers, the magnitude of this reduction, when expressed in milliseconds, is not very large. Despite this relatively small difference in the duration of the positive phase of the TIRF, many subjects with IN report virtually no motion smear during nystagmus (Bedell & Bollenbacher, 1996).

One important consideration is that the influence of extra-retinal eye movement signals on the TIRF may be specific to certain types of stimuli. For example, Tong, Aydin, and Bedell (2007, 2005) reported that normal observers perceive a reduced extent of perceived motion smear for a bright spot that is flashed during smooth pursuit, compared to when similar motion of the retinal image occurs during fixation. However, the reduction of perceived smear occurs primarily when the relative motion of the spot with respect to the eye is in the opposite direction of the eye movement. For example, during rightward pursuit at 8°/s perceived smear is significantly less for a target that moves physically to the right at 4°/s compared to one that moves at 12°/s, although both targets generate the same speed of retinal image motion. A similar asymmetrical reduction of perceived motion smear exists also in subjects with IN, for stimuli that move relative to the eye in the opposite compared to the same direction as the nystagmus slow phase (Bedell, Tong, Patel, & White, 2008). All of the stimuli used in the current study were extended in the horizontal direction, in order to minimize motion of the retinal image during horizontal eye movements. Consequently, the difference between the TIRFs that we measured in subjects with IN and in normal observers during fixation may underestimate the change that occurs for non-horizontal stimuli that move opposite the direction of eye movement.

A second important consideration is that our estimates of the TIRF in normal observers and subjects with IN are based on their responses to threshold stimuli. On the other hand, normal observers report that motion blur is most noticeable for *supra*-threshold targets (e.g., Bedell & Bollenbacher, 1996). The normal TIRF has been reported to speed up with an increase in the contrast of the stimulus (Georgeson, 1987; Stromeyer & Martini, 2003). It is therefore possible that a greater difference exists between the TIRFs of normal observers and subjects with IN for supra-threshold stimuli, which could account quantitatively for the substantial reported differences in perceived motion blur. Additional measurements of the TIRF using supra-threshold stimuli would be necessary to evaluate this possibility.

Finally, mechanisms in addition to a speeding up of the TIRF during eye movement could contribute to the reduced extent of motion smear that is reported by subjects with IN. One possible mechanism is adaptation to the more-or-less incessant retinal image motion, which already has been proposed to contribute to the poorer than normal motion sensitivity that is found in subjects with IN (Bedell, 1992; Bedell, 2000; Shallo-Hoffmann, Bronstein, Morland, & Gresty, 1998). Adaptation also might reduce the extent of perceived motion smear in subjects with IN, although it is not immediately apparent why this reduction should occur specifically for one direction of target motion (Bedell et al., 2008).

[4] The effect of the second, negative lobe of the TIRF on the perceived extent of motion smear is less apparent, particularly for the condition in which a bright stimulus is presented in an otherwise dark field.

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