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The Temporal Impulse Response Function during Smooth Pursuit

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Abstract

Recent studies indicate that the extent of perceived motion smear is attenuated asymmetrically during smooth pursuit eye movements, based on the relative directions of the target and eye motion. We conducted two experiments to determine if the reduction of perceived smear during pursuit might be associated with an acceleration of the temporal impulse response function (TIRF). In Experiment 1, two-pulse increment sensitivity was determined during fixation and rightward pursuit for sequential flashes of a long horizontal line, presented with stimulus-onset asynchronies between 5.9 and 234 ms. In Experiment 2, temporal contrast sensitivity was measured during fixation and rightward pursuit for a vertical 1 cpd grating with retinal image velocities between 4 and 30 Hz. During pursuit, grating motion was either in the same or the opposite direction as the eye movement. TIRFs were modeled as the impulse responses of a second-order, low-pass linear system, fit to the two-pulse increment sensitivity data by an optimization procedure and to the temporal contrast sensitivity results by iterative Fourier synthesis. The results indicate that the natural temporal frequency of the fitted TIRFs was approximately 10% higher during pursuit than fixation. In experiment 2, the increased natural frequency of the TIRF was restricted to the condition in which the grating moved spatially in the opposite direction of the pursuit eye movement. The results are consistent with the hypothesis that extra-retinal signals reduce the extent of perceived motion smear during pursuit, in part by increasing the speed of visual processing preferentially for one direction of image motion.

Keywords

motion blur; motion smear; two-pulse thresholds; temporal contrast sensitivity; temporal impulse response; smooth pursuit

1. Introduction

Normal observers frequently report that moving objects appear to be smeared, presumably because the sluggish temporal characteristic of the visual system produces responses that persist after the image of the target moves on to new retinal locations. However, the extent of perceived motion smear is less during eye movements than when comparable motion of the retinal image is produced during steady fixation (Bedell & Lott, 1996; Bedell & Yang, 2001;

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Bedell, Chung & Patel, 2004; Bedell & Patel, 2005; Tong, Patel & Bedell, 2005; Tong, Aydin & Bedell, 2007). This reduction of perceived motion smear is asymmetric, occurring only when motion of the target is in the opposite direction with respect to the moving eye (Tong, Patel & Bedell, 2005; Tong, Aydin & Bedell, 2007; Tong, Stevenson & Bedell, 2008). The decrease in the extent of perceived motion smear during eye movements is attributed to the action of extra-retinal signals (Bedell & Lott, 1996; Bedell & Patel, 2005; Tong, Stevenson & Bedell, 2008).

The temporal impulse response function (TIRF) provides a useful way to describe the temporal response of the visual system. In particular, the duration of perceived motion smear should be related to the duration of the initial positive phase of the TIRF (Blommaert & Roufs, 1987). The TIRF has been estimated psychophysically by measuring contrast thresholds for pairs of brief flashes that are separated in time (e.g., Ikeda, 1965; Rashbass, 1970; Burr & Morrone, 1993; Shinomori & Werner, 2003) and by performing a Fourier synthesis of the empirical temporal contrast sensitivity function (TCSF: e.g., Kelly, 1971; Swanson et al., 1987; Roufs, 1972; Georgeson, 1987). The goal of the current experiments was to estimate the TIRF, using each of the above techniques, during fixation and smooth pursuit to determine if the reduction of perceived motion smear during pursuit eye movements is associated with an increase in the speed of the estimated TIRF.

Burr and Morrone (1996) reported that the time course of the TIRF, when measured using pairs of brief luminance pulses, is accelerated during saccadic eye movements compared to steady fixation. Compared to the reduction of contrast sensitivity that accompanies saccades, contrast sensitivity during pursuit is much more similar to that during fixation (Starr et al., 1969; Murphy, 1978; Flipse et al., 1988; Bedell & Lott, 1996; Schütz et al., 2007a, 2007b, 2008). Some of these studies addressed the temporal characteristics of contrast sensitivity during pursuit, which are relevant to the current work. For example, data presented by Flipse et al. (1988) show that contrast sensitivity is better for an 8 cpd stimulus during pursuit than fixation when the grating moves across the retina at high temporal frequencies. More recently, Schütz et al. (2007b) compared temporal contrast sensitivity during pursuit and fixation for 1 cpd Gabor patches presented 4 deg above or below the fovea. They found that peak contrast sensitivity is reduced during pursuit compared to fixation, and that this reduction is significantly greater when the motion of the target is in the opposite direction of pursuit eye movement. However, they reported no significant difference in the overall temporal tuning of the temporal contrast sensitivity function between fixation and pursuit for either direction of relative stimulus motion. We will consider these studies again in the Discussion, after first presenting our own results.

2. Methods

2.1. Observers

Eight observers, including all five of the authors, participated in Experiment 1. Five new observers and one of the authors participated in Experiment 2. All of the observers had normal or corrected-to-normal vision and granted informed voluntary consent before the start of the experiments. The experimental protocols were reviewed beforehand by the University of Houston, Committee for the Protection of Human Subjects.

2.2. Experiment 1. Apparatus and procedure

For each observer, increment sensitivity was measured during fixation and during horizontal smooth pursuit for *pairs* of successively presented flashes of a 15-deg long, 10 min-arc high horizontal line (Bedell et al., 2008). Stimuli were presented in a dark room on a gamma-corrected, Image Systems M21L monchromatic monitor with DP104 phosphor. This phosphor has a peak output at a wavelength of 565 nm and decays to less than 1% of its peak value within 250 μs. Each flashed line was presented for a single frame, corresponding to 5.85 ms at the monitor refresh rate of 171 Hz.

The flashed horizontal lines were presented on a 65 cd/m^2 homogeneous background field. On each trial, the lines were presented sequentially at the same screen location, either 0.9 deg above or below a continuously visible fixation cross. The observer viewed the stimulus display monocularly from a distance of 114 cm, after reflection from a galvanometer-mounted mirror. A constant head position was maintained using a chin rest. The observer initiated each trial by pressing a button on a joystick and, at the end of the trial, used the same 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 5.9 to 234 ms. On each trial, the flashed lines were presented at one of 7 contrast levels, using the method of constant stimuli. The increment sensitivity for each SOA corresponds to 75% correct responses, determined from psychometric functions that were fit to the results of each individual observer. Depending on the observer and the condition, the psychometric functions were fit to between 30 and 60 trials at each contrast level.

Pursuit was elicited by a 1 second, constant-velocity rotation of the galvanometer-mounted mirror, which caused the fixation cross and the entire stimulus display to move *en bloc* from left to right at a velocity of 8 deg/s. Mirror motion was produced by the ramp output from a Hewlett-Packard 3314A function generator, which was triggered when the observer initiated a trial. The first target line was flashed after a delay of 490 ms, to allow pursuit tracking to become accurate. The horizontal position of the viewing eye was monitored by infra-red limbal tracking on a sample of each observer's pursuit trials in order to reject trials on which a saccade or blink occurred during the presentation of the target lines. Figure 1A shows a representative eye-movement trace, along with the timing of the two stimulus flashes. Across observers, saccades or blinks occurred on fewer than 10% of the monitored trials. When a trial was rejected, it was repeated on the immediately following trial.

2.3. Analysis of two-pulse data

The TIRF of the visual system was modeled as an impulse response of a linear second-order low-pass system. This model provided substantially better fits to our data than the 4-parameter, damped frequency-modulated sinusoid applied by Burr and Morrone (1996). A possible explanation is that the stimuli used by Burr and Morrone were of substantially lower spatial frequency. As discussed in Bedell et al. (2008), 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. For all of the data obtained in this study, the best fits occurred when $0 \leq D < 1$, which corresponds to an underdamped system and is described by the equation:

$$R(t)=\left(\frac{A^{*}W}{\sqrt{1-D^{2}}}\right)*e^{-D*W*t}*\sin\left(W^{*}\sqrt{1-D^{2}}*t\right)$$

In this equation, 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 $t \leq 0$. A second-order under-damped system of this form exhibits a biphasic impulse response.

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

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

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:

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 following criterion function (Burr & Morrone, 1993):

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

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

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

2.4. Experiment 2. Apparatus and procedure

Contrast sensitivity was measured for a vertically oriented sinusoidal luminance grating during fixation and during rightward pursuit. In an otherwise dark room, the stimulus was viewed monocularly after reflection from a galvanometer-mounted mirror at a distance of 114 cm. Head position was fixed by a chin rest. Stimuli were generated by a VSG2/3 video board and displayed on an Image Systems monochrome 20" monitor with a 171 Hz fresh rate. The spatial frequency of the grating was 1 cpd and, in different blocks of trials, the temporal frequency was chosen randomly from 4, 6, 12, 18, 24 or 30 Hz.[1] The grating was displayed within a virtual circular aperture of 10 deg diameter at the center of screen for a duration of 400 ms, modulated at its onset and offset with a Gaussian temporal window (SD = 93 ms). The mean luminance of the grating and the background were set at 65 cm/ m^2. The direction of stimulus motion on the screen was randomly either to the left or right.

A cross at the center of the screen served as the fixation target in the fixation condition and as the tracking target in the pursuit condition. Horizontal eye position was measured using IR limbal tracking at a sampling rate of 250 Hz, only during pursuit trials. A custom program running on a master PC presented the stimulus on each trial and triggered the ramp output of a Hewlett Packard 3314A function generator to produce left-to-right mirror motion in the pursuit condition, as in Experiment 1. Rotation of the mirror produced motion of the whole screen at a velocity of 8 °/s. A second PC, synchronized with the master PC, monitored and stored the eye position signals. A sample recording of one observer's eye position along with the sequence of stimulus events on one trial is shown in Figure 1B.

[1]We used a 1 cpd grating to minimize the effect of variations in pursuit gain on the retinal temporal frequency of motion. For example, a 1 cpd grating produces a retinal temporal frequency of 16 Hz when the retinal image velocity is 16 deg/s. If the pursuit gain for a target that moves in space at 8 deg/s is 0.9, then the retinal image velocity is reduced by 0.8 deg/s which, for a 1 cpd grating, corresponds to 0.8 Hz. If we had used a 4 cpd grating, then a retinal temporal frequency of 16 Hz occurs when the retinal image velocity is 4 deg/s. In this condition, a 0.8 deg/s tracking error produces a reduction in the retinal temporal frequency of 3.2 Hz.

The observer used a joystick to start a trial. On each trial, the contrast of the grating was randomly selected from 7 pre-determined contrast levels. After each trial, the observer reported whether or not the moving grating was detected. For each temporal frequency, a total of 140 trials (2 directions of grating motion by 7 contrast levels by 10 replications) comprised one block. An estimate of the contrast threshold for each direction of grating motion was determined for each temporal frequency as the grating contrast corresponding to 50% detection, based on the results of one or two blocks of trials.

In both the fixation and pursuit conditions, the onset of the stimulus was approximately 400 ms after the observer initiated each trial. This delay allowed tracking to become accurate in the trials of the pursuit condition. If the pursuit gain is equal to 1.0, then gratings of the same temporal frequency that move spatially ‘with’ and ‘against’ the direction of the pursuit eye movement generate retinal image motion of same speed. On the other hand, if the pursuit gain is lower or higher than 1.0, then the temporal frequency of retinal-image motion is not equal to the temporal frequency on the screen. On each acceptable pursuit trial the velocity of retinal image motion was calculated using the equation

$$TF_{retina} = (\text{Velocity of stimulus grating in space} - \text{Velocity of eye})^{*} SF_{grating},$$

where the eye velocity was the slope of the straight line fit to the eye position signals during the time interval that the grating stimulus was presented. Pursuit trials were rejected following data collection if either of the following occurred: (1) a saccade or blink occurred during the presentation of the stimulus or within 50 ms of its onset or offset, or (2) the calculated temporal frequency of the retinal image motion differed by more than ±15% from the temporal frequency expected on the basis of perfect tracking. For each observer, each temporal-frequency condition during pursuit was repeated at least once to obtain at least 10 acceptable trials for each level of grating contrast.

2.5. Analysis of temporal contrast sensitivity data

The TIRF for a second-order linear system was determined iteratively from the measured temporal contrast sensitivity function using MatLab (Bedell et al, 2008). Like the temporal impulse response, the temporal frequency response of a linear second-order low-pass system depends on the value of the damping ratio, D. Specifically, if the damping ratio is less than 1/Sqrt(2), then the system exhibits a higher response in the region of the corner temporal frequency than at lower or higher temporal frequencies. On the other hand, if the value of D is greater than 1/Sqrt(2), then the temporal frequency response remains relatively flat up to the corner temporal frequency and drops monotonically at higher frequencies. Above the corner temporal frequency, the frequency response of a second-order low-pass system falls at a rate of 12 dB/octave, which provides a good fit to the psychophysical results that were obtained in this experiment.

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 2.3, above) 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.

3. Results

3.1. Experiment 1

Average 2-pulse increment sensitivity for the 8 normal observers decreases to a minimum at a SOA of approximately 50 ms during both fixation and pursuit and increases slightly at longer SOAs (Figure 2). The TIRFs fitted to the average data during fixation and pursuit are shown in Figure 3. Both of the estimated TIRFs have a biphasic shape with a peak near 20 ms and a trough in the vicinity of 75 ms. However, the peak and trough occur slightly earlier for the TIRF fit to the sensitivity data obtained during pursuit. Consequently, the TIRF fit to the data for pursuit has a higher mean natural temporal frequency (11.1 Hz) than that fit to the data for fixation (9.8 Hz). This difference in temporal frequency is statistically significant (paired $t_{[df = 7]} = 3.79$, $p = 0.007$). The TIRF for pursuit also exhibits significantly more damping than the TIRF for fixation (mean damping ratios = 0.61 *vs*. 0.44; paired $t_{[df = 7]} = 2.66$, $p = 0.032$), but no significant difference in amplitude (paired $t_{[df = 7]} = 0.12$, $p = 0.91$). All of the parameters for the TIRFs that were fitted to each observer's data are provided in Table 1. Standard errors of estimate are shown also for the individual parameter fits, determined using a resampling technique.

3.2. Experiment 2

The pursuit gains for the 6 observers in Experiment 2 are shown for the different experimental conditions in Table 2. These values indicate that the average temporal frequency of grating motion during pursuit was within ±4% of the intended value. Statistical analysis indicates that pursuit gain was similar when the stimulus grating moved in the same and the opposite direction of the eye movement ($t_{[df=5]} = 2.12$, $p=0.086$). The presentation of gratings with different directions of motion during pursuit therefore had no systematic effect on the temporal frequency of the retinal image motion in this study.

Each trial in Experiment 2 was categorized according to whether the stimulus moved leftward or rightward in the fixation condition or, equivalently, 'with' or 'against' the direction of the eye movement in the pursuit condition. The estimated parameters of the TIRFs (A, W, D) showed no significant differences (A: $t_{[df=5]} = 2.01$, $p = 0.10$;W: $t_{[df=5]} = 0.19$, $p = 0.86$; D: $t_{[df=5]} = 2.23$, $p = 0.076$) during leftward vs. rightward motion of the grating stimulus in the fixation conditions. Therefore, the results from the two directions of grating motion during fixation were averaged to produce a single function. The average contrast sensitivity across observers and the fitted temporal contrast sensitivity function during fixation are shown in Figure 4, as well as the average results for the 'with' and 'against' conditions of grating motion during pursuit. The temporal contrast sensitivity functions in all three conditions are approximately low pass, which agrees with the functions reported previously for a 1 cpd stimulus by Kelly (1979) and Hess & Snowden (1992). In Figure 4, temporal contrast sensitivity for grating motion 'against' the direction of pursuit differs from the other two conditions primarily at the two lowest temporal frequencies. The measurement of contrast sensitivities at even lower temporal frequencies was impractical because of the 400 ms duration of the grating stimulus. Nevertheless, the reduction of contrast sensitivity at low temporal frequencies accounts for the higher natural frequency of the TIRF estimated for the 'against' condition during pursuit.

The average contrast sensitivities shown in Figure 4 are considerably higher than those in Figure 2 because of the opportunity for increased temporal and spatial summation. Because different observers had slightly different pursuit gains for each temporal frequency of the stimulus, the average temporal contrast sensitivity functions for the two pursuit conditions were constructed by averaging both the contrast sensitivity and the calculated retinal temporal frequency across observers. The estimated parameters of the TIRFs that best fit the contrast sensitivity function measured for each observer, along with standard errors of estimate, are listed in Table 3. Figure 5 shows the TIRFs fit to the averaged temporal contrast sensitivity data for each experimental condition. Very similar functions were obtained when the TIRFs were fit to all of the individual contrast sensitivity data of the six observers at the same time.

Repeated-measures ANOVA indicates that the natural frequency of the TIRF differs significantly among the 'against pursuit', 'with pursuit,' and 'fixation' conditions ($F_{[2,10]}$=4.87, p = 0.036). Comparisons among the three conditions reveal that the natural frequency of the TIRF in the 'against pursuit' condition is significantly higher than in the 'with pursuit' ($F_{[1,10]}$=8.67, p=0.016) and the 'fixation' conditions ($F_{[1,10]}$=5.62, p=0.041). On the other hand, the natural temporal frequency of the TIRF fit to the results of the 'with pursuit' and 'fixation' conditions is similar ($F_{[1, 10]}$=0.33, p=0.57).Neither the damping constant ($F_{[2,10]}$=0.18, p=0.79) nor the amplitude ($F_{[2,10]}$=1.09, p=0.37) of the fitted TIRFs are significantly different among the three experimental conditions.

4. Discussion

The present study demonstrates that the normal TIRF accelerates significantly during smooth pursuit compared to steady fixation, both when estimated from two-pulse increment sensitivity data and when determined by Fourier synthesis of the empirically determined temporal contrast sensitivity function.

Several previous studies addressed the effects of pursuit eye movements on temporal contrast sensitivity. Murphy (1978) compared contrast sensitivity for a 5.1 cpd grating when the eyes moved across the stationary stimulus and when the eyes were stationary and the grating moved. He found no significant differences in contrast sensitivity between these two conditions when the retinal image velocities were similar. However, the highest mean retinal image velocity achieved during pursuit was only about 1 deg/s. Flipse et al. (1988) extended Murphy's study by comparing contrast sensitivity during fixation and pursuit at different speeds for spatial frequencies between 0.2 and 12 cpd. The results reported for representative spatial frequencies of 0.5 and 8 cpd confirm that smooth pursuit has *relatively* little impact on contrast sensitivity when the velocity of the retinal image motion is similar to that during fixation. However, close inspection of the data indicates that peak contrast sensitivity for 0.2 cpd gratings is reduced slightly in the pursuit condition and that the contrast sensitivity for 8 cpd gratings is higher during pursuit than fixation for retinal image speeds greater than approximately 2 deg/s (16 Hz). This increase in contrast sensitivity during pursuit at high temporal frequencies of motion is consistent with an increase in the natural frequency of the TIRF during pursuit, at least for high spatial frequency targets.

Recently, Schütz et al. (2007a, 2007b) investigated changes in contrast sensitivity associated with the initiation and the steady-state phases of smooth pursuit. In one study, the stimulus was a long horizontal line that was flashed for 10 ms at various times between 200 ms before and 400 ms after the onset of pursuit. In contrast to the marked depression of sensitivity that occurs near the time of a saccade, the authors found little or no change in the percentage of correct-detection responses during the initiation of smooth pursuit. Subsequently, Schütz et al., (2007b) measured contrast sensitivity during the steady state phase of smooth pursuit. As in our Experiment 2, they presented a 1 cpd grating that moved either in the same or the opposite direction of the pursuit eye movement. Their data show that peak contrast sensitivity is on the order of 15% lower during pursuit than fixation for both directions of grating motion. However, the reduction of contrast sensitivity was greater when the grating moved in the opposite (i.e., 'against') compared to the same direction ('with') as the pursuit eye movement. Schütz et al. (2007b) presented the test gratings 4 deg from the pursuit target and interpreted their results

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in terms of a limited ability to shift attention away from the tracked stimulus during smooth pursuit.

Schütz et al. (2008) confirmed that contrast sensitivity is reduced slightly during pursuit for a spatially low-pass filtered line (fundamental SF ≈ 1 cpd), flashed either 2 deg above or below the pursuit stimulus. This study also reported that contrast sensitivity is approximately 5% *higher* during pursuit than fixation for a 14 cpd grating and for a flashed line that is defined only by chromatic contrast. Taken together with the results of Flipse et al. (1988), the data of Schütz et al. (2007b, 2008) suggest that contrast sensitivity is reduced during pursuit for low spatial frequency targets, but improves for higher spatial frequency targets, especially when the temporal frequency of the retinal image motion is high. The data from these studies also suggest that the decrease in contrast sensitivity for low spatial frequencies and the increase in contrast sensitivity for higher spatial frequencies occurs preferentially when the visual target moves ‘against’ the direction of pursuit. Both of these changes in contrast sensitivity would tend to reduce the perception of motion smear during pursuit.

The data from our Experiment 2 show that peak temporal contrast sensitivity for a drifting 1 cpd grating decreases during smooth pursuit compared to fixation (Figure 4; see also Table 3), although this decrease does not reach statistical significance. However, both in our experiment and in the experiments reported by Flipse et al. (1988) the pursuit target was superimposed on the test grating, making it unlikely that reduced contrast sensitivity during pursuit can be attributed primarily to an inappropriate spatial distribution of attention. Using the procedure described in section 2.5, above, we fit TIRFs to the mean temporal contrast sensitivity data for the three motion conditions that are plotted in Figure 10 of Schütz et al. (2007b). The fitted natural frequency is highest for their ‘motion opposite’ condition, lowest for their ‘motion same’ condition, and intermediate for the fixation condition. Although the differences in the fitted natural frequencies are small (range = 13.7 to 14.8 Hz) and probably not statistically significant, these outcomes agree qualitatively with the results of our experiment 2.

Although the differences between the TIRFs during pursuit and fixation in our two experiments are statistically significant, they may not be sufficient to account for the reduction of perceived motion smear during pursuit. However, our study estimated TIRFs using threshold stimuli, whereas the perception of motion smear is assessed using supra-threshold moving targets. The TIRF is reported to speed up for higher contrast stimuli (Georgeson, 1987; Stromeyer & Martini, 2003) and it is feasible that differences between the TIRF during pursuit and fixation (and for stimuli that move ‘with’ vs. ‘against’ the direction of pursuit) could be larger if measurements were performed using supra-threshold targets.

Additional evidence that the reduction of perceived motion smear is related to an increase in the speed of the TIRF is provided by recent studies on patients with infantile nystagmus (IN). Like the results shown here during pursuit eye movement, the natural temporal frequency of the TIRF is significantly higher in patients with involuntary IN than in normal observers during steady fixation (Bedell et al., 2008). Similar to the observations made by normal subjects during pursuit, patients with IN also report that the extent of perceived motion smear is reduced for targets that move ‘against’ compared to ‘with’ the direction of the nystagmus slow phase (Bedell & Tong, 2009). However, both the reduction of perceived motion smear and the acceleration of the TIRF during eye movement are more pronounced in patients with IN than in normal observers during pursuit. We interpret these results to indicate that the extra-retinal signals associated with IN exert a qualitatively similar but quantitatively stronger influence on the time course of the TIRF and perceived motion smear than the extra-retinal signals that accompany normal slow eye movements.

Georgeson (1987) and Stromeyer & Martini (2003) attributed the increase in the speed of the TIRF that they observed when the stimulus contrast increased to a change in the response gain with in the neural pathway that processes the stimulus. Neurophysiological studies indicate that the response gain of non-linear magno-cellular neurons decreases with an increase in stimulus contrast, primarily for low temporal frequency stimuli (e.g., Shapley & Victor, 1978; Benardete, Kaplan & Knight, 1992; Carandini, Heeger & Movshon 1997). Little or no gain change is reported for pre-cortical parvo-cellular neurons (e.g., Benardete et al., 1992). Burr and Morrone (1996; also Zhang, Cantor & Schor 2008) suggested that reduced sensitivity to luminance modulation and the reported speeding up of the TIRF during saccades also could be accounted for by a *decrease* in the response gain of magno-cellular neurons, contingent on a signal that accompanies the saccadic eye movement.

Schütz et al. (2008) attributed improved contrast sensitivity for high-spatial frequency and chromatic stimuli during pursuit to an *increase* in the gain of the parvo- and konio-celluar pathways, which they suggested might occur in either the medial superior temporal cortex or in the frontal pursuit area. As noted above, these authors attributed the small loss of contrast sensitivity for low spatial frequency stimuli during pursuit (Schütz et al., 2007b) to reduced attention, rather than to a decrease in the gain of the magno-cellular pathway.

The results of our second experiment indicate that sensitivity is reduced at relatively low temporal frequencies during pursuit, which would be consistent with a decrease in gain in the magno-cellular pathway. However, to account also for the results of Schütz et al. (2008), a decrease in magno-cellular pathway gain would have to be accompanied by a concurrent increase in the gain of the parvo- (and konio-) cellular pathways.

The change in temporal contrast sensitivity, and in the speed of the TIRF, that occurred in our second experiment pertains only to stimuli that move in the opposite direction of pursuit. To achieve this outcome, any changes in gain that occur during eye movement should be restricted to specific subsets of cortical neurons. Carandini et al. (1997) attributed contrast-related gain changes within magno-cellular neurons primarily to a division of each neuron’s response by the sum of the responses of a large number of cortical neurons, called the normalization pool. Carandini et al. (1997) entertained the possibility that neurons tuned to specific orientations and spatial frequencies might be afforded different weights in the normalization pool, but found that the evidence to support this possibility was not compelling. If neural response gain is modulated by extra-retinal eye movement signals during pursuit, then the weighting of the signals that contribute to the normalization pool might depend on the preferred direction of motion of the contributing cells with respect to the direction of pursuit. To achieve this type of specificity, we agree with Schütz et al. (2008) that the modulation of neural gain would most likely occur in cortical areas that exhibit sensitivity to visual stimuli and also receive information about eye movements.

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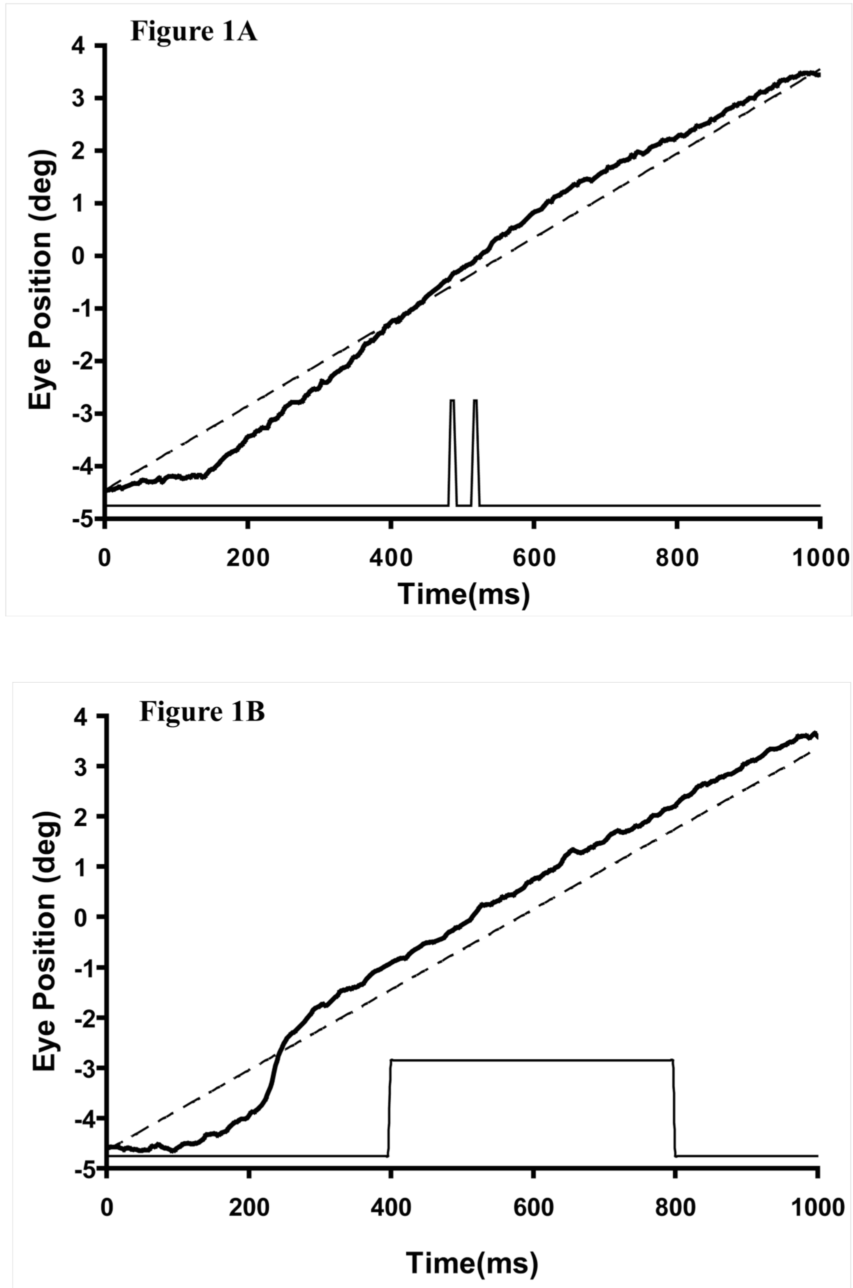

Figure 1.

Sample eye position (solid line) and stimulus (pursuit target, dashed line) traces are shown for rightward pursuit by observer Ob3 in Experiment 1 (panel 1A) and observer Ob11 in Experiment 2 (panel 1B). The traces at the bottom of each panel indicate the timing of stimulus presentation(s): two 5.9 ms pulses of a bright horizontal line, separated by a stimulus onset asynchrony (here, 35 ms) in panel 1A, and a 400-ms presentation of a drifting vertical grating in panel 1B. The Gaussian temporal windowing that occurred at grating onset and offset in Experiment 2 is not represented in panel 1B.

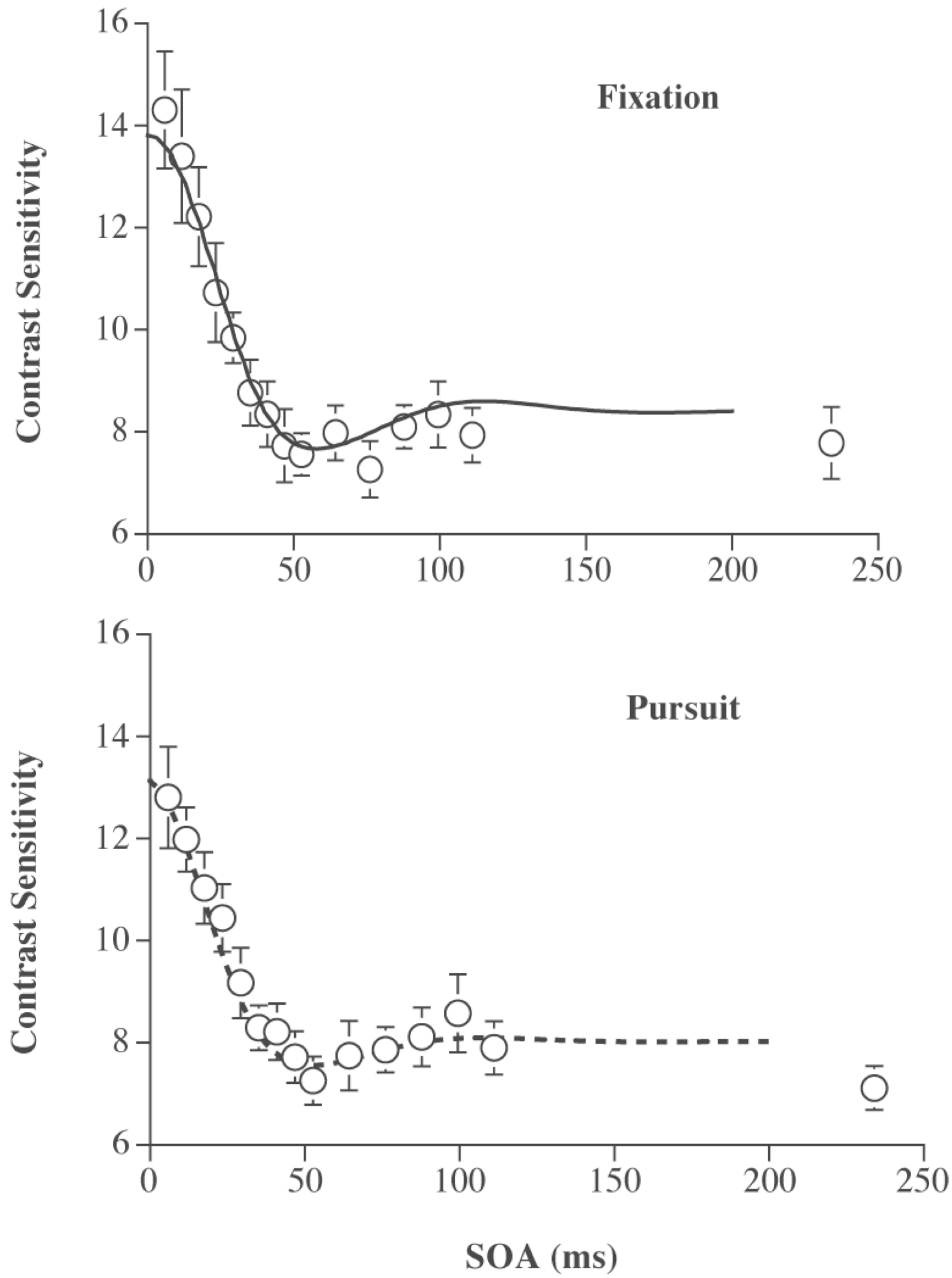

Figure 2.
Average 2-pulse increment sensitivity data are shown for 8 normal observers during fixation (top panel) and smooth pursuit (bottom panel), as a function of the SOA. Error bars are ±1 standard error of the mean, across the 8 observers. The solid and dashed lines are fit to the 2-pulse increment sensitivity, based on the temporal impulse response functions shown below in Figure 3.

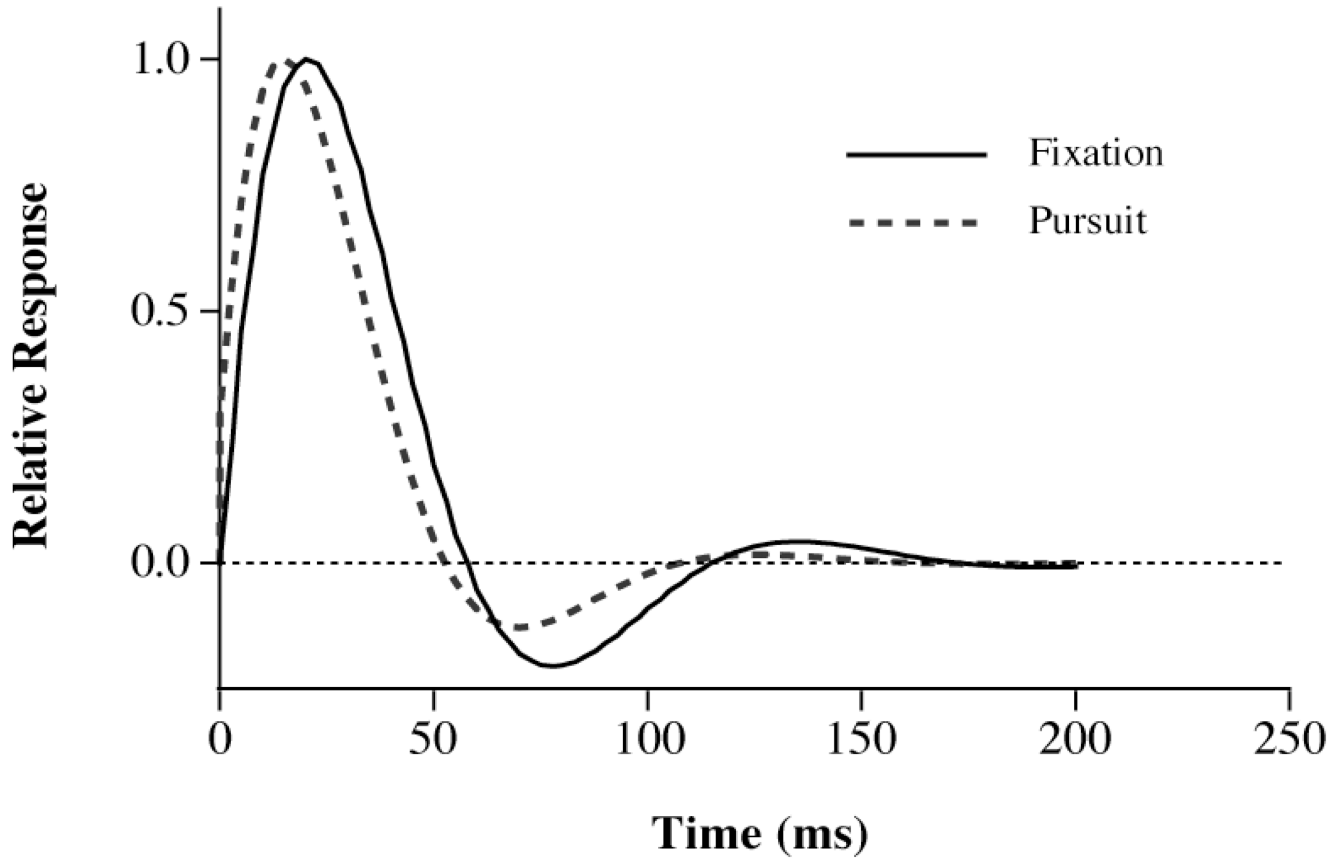

Figure 3.
Temporal impulse response functions (TIRFs) are estimated from the average two-pulse increment sensitivity data during steady fixation (solid line) and smooth pursuit (dashed line) in Figure 2. The parameters of the TIRFs fit to the data of the individual observers are listed in Table 1.

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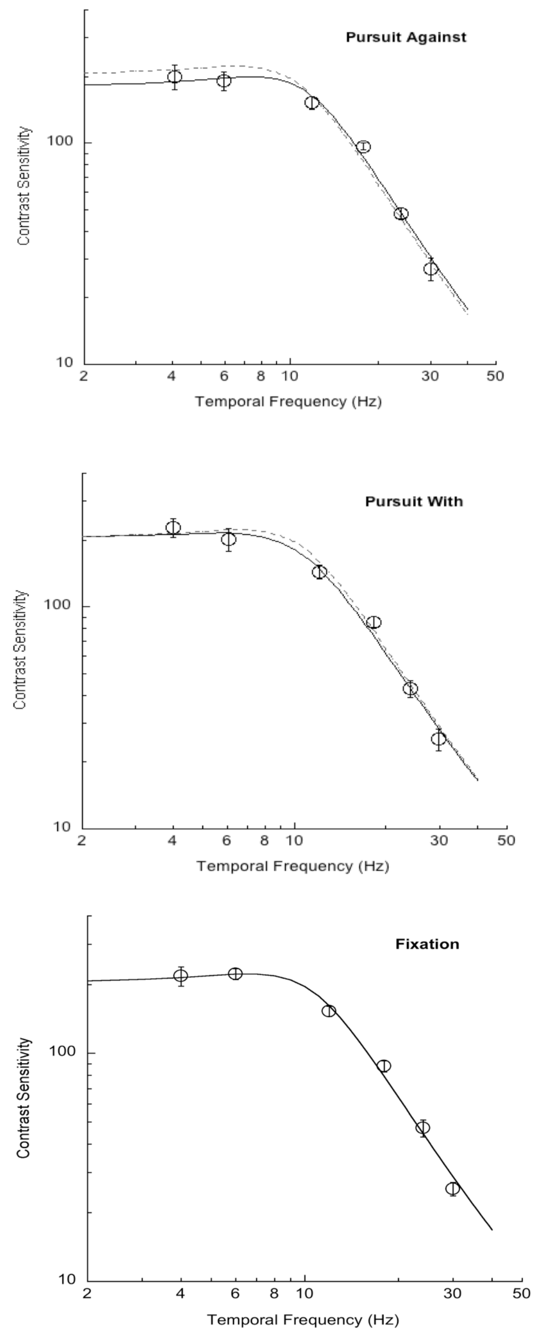

Figure 4.

Average temporal contrast sensitivity functions are plotted for 6 normal observers for a 1 cpd drifting grating target, viewed during steady fixation (bottom panel) and during motion of the grating 'with' (middle panel) and 'against' the direction of smooth pursuit (top panel). Error bars are ±1 standard error of the mean, across the 6 observers. The solid line in each panel is the Fourier transform of the best-fitting temporal impulse response function, shown in Figure 5, below. For comparison, the Fourier transform of the TIRF fit to the results of the fixation condition is repeated as the dashed curve in each of the two top panels.

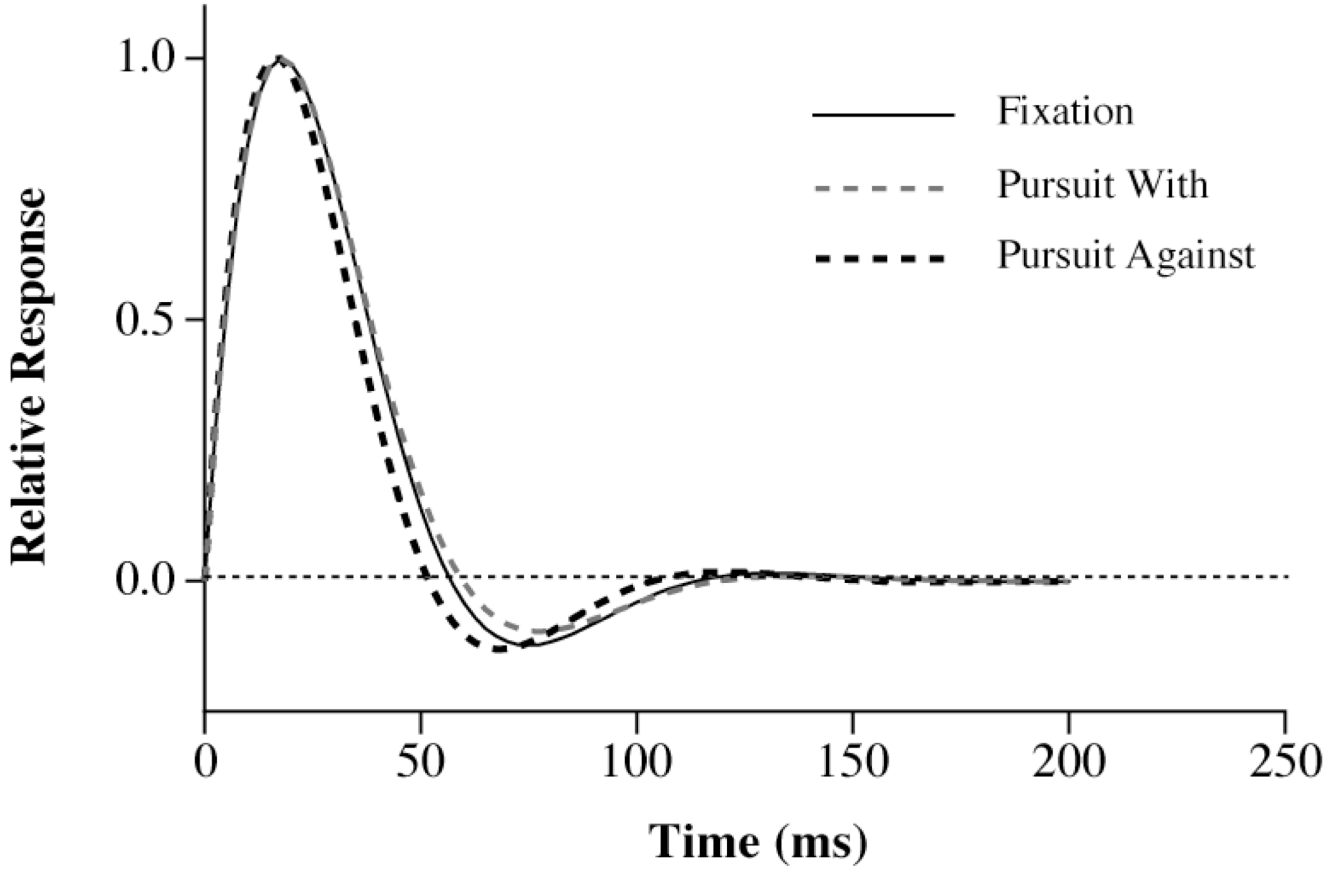

Figure 5.
Temporal impulse response functions (TIRFs) are estimated from the average temporal contrast sensitivity data shown in Figure 4, during fixation (solid line) and during grating motion 'with' (lighter dashed line) and 'against' (darker dashed line) the direction of pursuit. The parameters of the TIRFs fit to the data of the individual observers are listed in Table 3.

Table 1

Parameters of Fitted Temporal Impulse Response Functions ± 1SE* (2-Pulse Data)

		Amplitude	Natural TF	Damping
	Fixation:			
Ob1		0.071 ± 0.004	8.3 ± 0.39	0.51 ± 0.09
Ob2		0.066 ± 0.005	10.1 ± 1.10	0.57 ± 0.13
Ob3		0.089 ± 0.007	7.9 ± 0.64	0.28 ± 0.08
Ob4		0.063 ± 0.006	11.6 ± 1.65	0.56 ± 0.12
Ob5		0.061 ± 0.005	11.2 ± 0.84	0.31 ± 0.05
Ob6		0.069 ± 0.004	10.1 ± 0.91	0.39 ± 0.05
Ob7		0.063 ± 0.005	10.4 ± 1.02	0.59 ± 0.10
Ob8		0.051 ± 0.005	8.8 ± 0.74	0.32 ± 0.11
Mean:		**0.064** ± 0.002	**9.80** ± 0.47	**0.44** ±0.05
	Pursuit			
Ob1		0.057 ± 0.005	10.2 ± 1.06	0.66 ± 0.13
Ob2		0.071 ± 0.007	9.6 ± 0.83	0.46 ± 0.12
Ob3		0.070 ± 0.006	10.6 ± 0.80	0.42 ± 0.08
Ob4		0.062 ± 0.007	12.5 ± 3.86	0.83 ± 0.32
Ob5		0.080 ± 0.008	12.8 ± 1.49	0.64 ± 0.14
Ob6		0.077 ± 0.008	11.5 ± 1.25	0.72 ± 0.16
Ob7		0.056 ± 0.006	11.9 ± 1.65	0.52 ± 0.14
Ob8		0.066 ± 0.006	9.3 ± 1.01	0.61 ± 0.12
Mean		**0.067** ± 0.003	**11.08** ± 0.46	**0.61** ± 0.05

*Standard errors of the parameters fit to the individual observers' data represent the distribution of 1000 estimates for each parameter, obtained by statistical resampling. Standard errors of the mean parameter estimates are calculated from the variability between the fitted values for the different observers.

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Table 2

Pursuit Gains (±1 SE) during 'With' and "Against" Motion of the Grating Stimulus in Experiment 2

	Gain 'with'	**Gain 'against'**
Ob2	1.04 ± 0.029	1.02 ± 0.028
Ob9	0.97 ± 0.025	0.97 ± 0.024
Ob10	1.00 ± 0.025	1.00 ± 0.024
Ob11	1.02 ± 0.008	1.02 ± 0.014
Ob12	1.00 ± 0.021	0.98 ± 0.021
Ob13	0.975 ± 0.010	0.96 ± 0.012
Mean	**1.00 ± 0.011**	**0.99 ± 0.010**

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Table 3

Parameters of Fitted Temporal Impulse Response Functions ± 1SE* (TCSF Data)

	Amplitude	Natural TF	Damping
Fixation:			
Ob2	1.06 ± 0.04	9.2 ± 0.19	0.40 ± 0.03
Ob9	1.77 ± 0.11	9.2 ± 0.25	0.98 ± 0.06
Ob10	0.98 ± 0.03	10.0 ± 0.21	0.55 ± 0.03
Ob11	0.96 ± 0.02	11.4 ± 0.12	0.51 ± 0.01
Ob12	0.90 ± 0.03	11.8 ± 0.18	0.53 ± 0.02
Ob13	0.79 ± 0.02	11.6 ± 0.17	0.44 ± 0.02
Mean	**1.08** ± 0.14	**10.5** ± 0.50	**0.57** ± 0.09
Pursuit 'against':			
Ob2	0.82 ± 0.03	11.5 ± 0.24	0.43 ± 0.03
Ob9	1.47 ± 0.18	9.1 ± 0.43	0.77 ± 0.08
Ob10	0.58 ± 0.02	12.0 ± 0.20	0.39 ± 0.02
Ob11	1.11 ± 0.03	11.3 ± 0.15	0.58 ± 0.02
Ob12	0.84 ± 0.04	12.6 ± 0.33	0.64 ± 0.04
Ob13	0.90 ± 0.03	11.7 ± 0.19	0.46 ± 0.02
Mean	**0.95** ± 0.12	**11.4** ± 0.49	**0.54** ± 0.06
Pursuit 'with':			
Ob2	1.16 ± 0.05	9.3 ± 0.17	0.55 ± 0.04
Ob9	1.39 ± 0.16	9.4 ± 0.40	0.73 ± 0.08
Ob10	0.67 ± 0.03	10.6 ± 0.20	0.48 ± 0.02
Ob11	1.14 ± 0.03	10.9 ± 0.13	0.58 ± 0.02
Ob12	0.90 ± 0.03	11.0 ± 0.23	0.61 ± 0.04
Ob13	0.99 ± 0.05	10.7 ± 0.24	0.48 ± 0.03
Mean	**1.04** ± 0.10	**10.3** ± 0.32	**0.57** ± 0.04

*Standard errors of the parameters fit to the individual observers' data represent the distribution of1000 estimates for each parameter, obtained by statistical resampling. Standard errors of the mean parameter estimates are calculated from the variability between the fitted values for the different observers.