Pergamon

PII: S0042-6989(96)00302-1

Vision Res., Vol. 37, No. 10, pp. 1255–1260, 1997

Printed in Great Britain
0042-6989/97 $17.00 + 0.00

Contrast Affects Flicker and Speed Perception Differently

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Received 7 August 1996; in revised form 8 November 1996

We have previously shown that contrast affects speed perception, with lower-contrast, drifting gratings perceived as moving slower. In a recent study, we examined the implications of this result on models of speed perception that use the *amplitude* of the response of linear spatio-temporal filters to determine speed. In this study, we investigate whether the contrast dependence of speed can be understood within the context of models in which speed estimation is made using the *temporal frequency* of the response of linear spatio-temporal filters. We measured the effect of contrast on flicker perception and found that contrast manipulations produce opposite effects on perceived drift rate and perceived flicker rate, i.e., reducing contrast increases the apparent temporal frequency of counterphase modulated gratings. This finding argues that, if a temporal frequency-based algorithm underlies speed perception, either flicker and speed perception must not be based on the output of the same mechanism or contrast effects on perceived spatial frequency reconcile the disparate effects observed for perceived temporal frequency and speed. © 1997 Elsevier Science Ltd. All rights reserved.

Motion perception Speed discrimination Temporal frequency Counterphase flicker Contrast Area V1 Area MT

INTRODUCTION

There is considerable psychophysical (e.g. Anderson & Burr, 1985; Anderson *et al.*, 1991; Watson & Turano, 1995) and physiological (e.g. Movshon *et al.*, 1978; Hamilton *et al.*, 1989) evidence that the first stage of visual cortex processing decomposes the image into its spatio-temporal frequency components. This fact inspired the development of models of human motion processing that use the output of directionally selective linear spatio-temporal filters as input (Watson & Ahumada, 1983, 1985; Adelson & Bergen, 1985). Because the output of visual cortical neurones (Dean, 1981; Albrecht & Hamilton, 1982; Sclar *et al.*, 1990) and their theoretical idealizations (Watson & Ahumada, 1983; Albrecht & Geisler, 1991) depend on contrast as well as speed, modellers of human motion perception were prompted to develop various schemes to overcome this problem and to generate velocity estimates robust to changes in contrast (Watson & Ahumada, 1985; Adelson & Bergen, 1986). In particular, Adelson & Bergen (1986) proposed a model in which speed is derived by dividing (normalizing) the output of motion–energy units by a term related to the average contrast, thereby producing accurate speed estimates independent of contrast (except possibly at very low contrast). However, such mechanisms are seemingly at odds with our previous finding that human speed estimates do indeed depend on contrast over a wide range of contrasts (Thompson, 1976, 1982; Stone & Thompson, 1992). In an effort to reconcile these results with motion–energy models, Stone & Thompson (1992) suggested that a contrast-normalization scheme might nonetheless explain the observed speed misperception, if the spatio-temporal window over which the normalization occurred were large. In this case, each patch might interfere with the other's normalization and produce the observed contrast dependence of the speed matches. However, recent experiments have ruled out this version of normalization as well (Thompson *et al.*, 1996), leading us to search for other possible explanations for the phenomenon.

A different approach for achieving contrast-robust speed estimates was devised by Watson & Ahumada (1985). Their model computes speed from the temporal frequency of the response of the linear spatio-temporal filters, because such neural signals are largely independent of contrast (e.g. Albrecht & Geisler, 1991, 1994). If speed is computed by using the temporal frequency of the response of spatially tuned channels, then it seems reasonable to expect that any effect of contrast on the perceived speed of a drifting grating should also be

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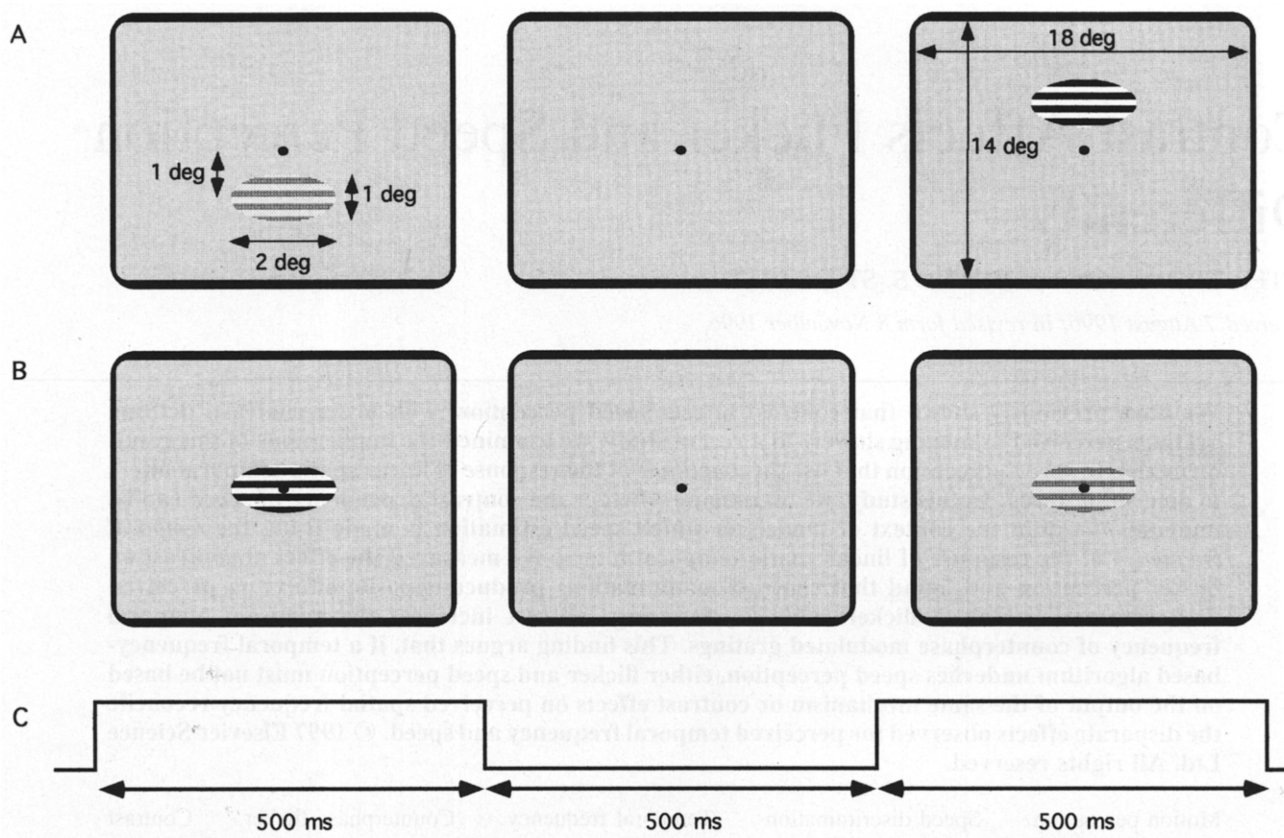


FIGURE 1. Stimulus configuration for (A) Experiment 1 in which perifoveal stimuli were presented and (B) Experiment 2 in which foveal stimuli were presented. The temporal sequence of events in both experiments is shown in (C). In both experiments the windowing of the stimuli was sharp in both space and time.

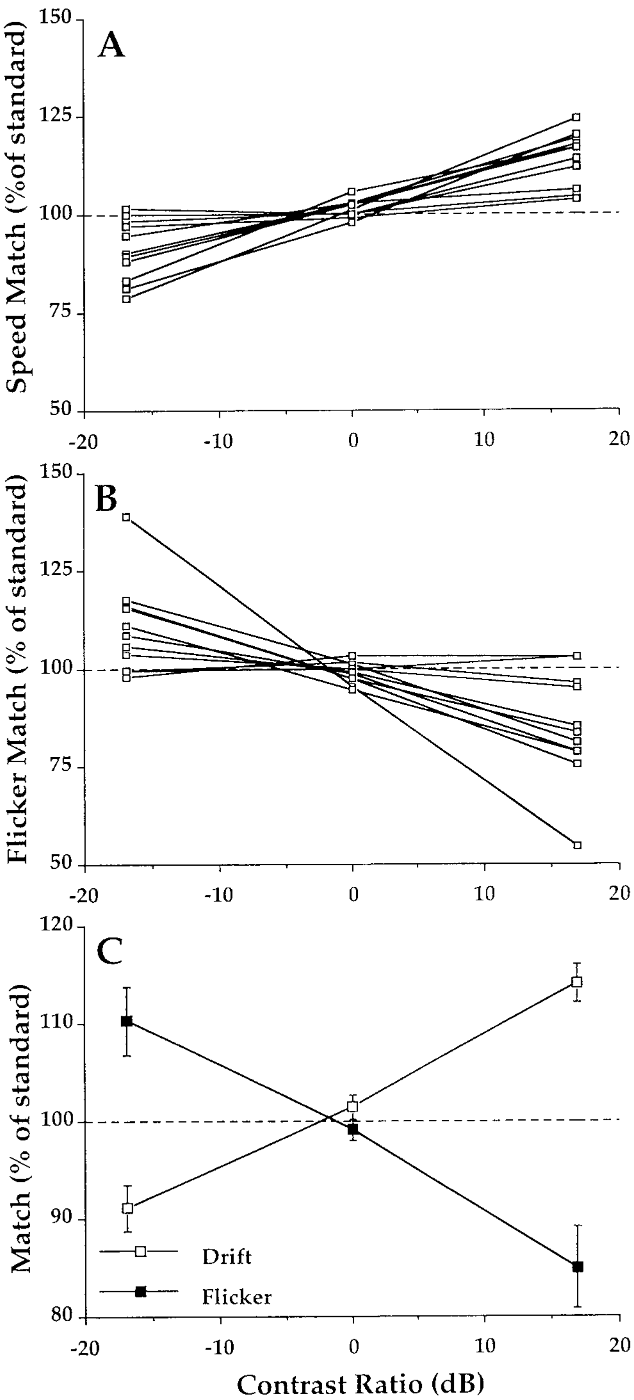
manifest in the perceived temporal frequency of a counterphase flickering stationary grating. In this study, we examine the effect of contrast on speed and temporal frequency under identical experimental conditions. We find that both are indeed affected by contrast but that the effects are opposite in direction. A preliminary report of our findings was made at the annual meeting of the Association for Research in Vision and Ophthalmology (Thompson & Stone, 1996).

*Because our presentation intervals lasted 500 msec it is possible that our drifting stimuli elicited smooth eye-movement responses despite the presence of a fixation point. However, given that our previous study documenting the effect of contrast on perceived speed (Stone & Thompson, 1992) was performed using a simultaneous spatial forced-choice task, the main effect of contrast on perceived speed cannot merely be the result of an eye-movement artifact, because any eye movement would have affected the motion of the two patches identically. Nonetheless, because the present study uses a sequential task, and as the magnitude and latency of ocular following may depend on contrast (Miles *et al.*, 1986), it is possible that a differential eye-movement response in the foveal vs perifoveal conditions could be responsible for the small differences observed (see Results). Flickering gratings are unlikely to elicit smooth eye movements, therefore the above caveat does not apply to our flicker results, the main finding of this paper.

GENERAL METHODS

We performed two experiments. Experiment 1 investigated the dependence of speed and flicker judgements upon contrast for perifoveally presented stimuli, while Experiment 2 investigated these effects for foveal stimuli. In both experiments, a trial consisted of two stimulus intervals. In each interval, a horizontal, 2 cycles/deg sinusoidal grating patch (2 deg wide by 1 deg high) was presented for 500 msec separated by a blank period of 500 msec in which only the mean luminance (70 cd/m^2) was present.* In Experiment 1, one patch was centred 1 deg above and one centred 1 deg below the fixation point (in random order), while in Experiment 2 both patches were centred on the fixation point (see Fig. 1). Within each experiment, two separate conditions were run to investigate two types of discrimination. In the drift condition, observers were shown grating patches drifting upwards within each interval and were asked to report which of the two intervals contained the patch which moved faster. In the flicker condition, observers were shown counterphase flickering grating patches within each interval and were asked to report which of the intervals contained the patch that flickered more rapidly. In both tasks, one of the pair of gratings, the "standard", was always modulated at 4 Hz, the modulation of the other, the "test", was determined by a staircase procedure (Findlay, 1978). Each staircase terminated after a total of 12 reversals (about 30 trials). We define the match as the ratio of the test modulation frequency to that of the standard (expressed as a percentage) at the point of subjective equality (determined by taking the mean of the last eight reversals). In all conditions reported here, four test–standard pairs of grating contrasts were investigated within interleaved independent staircases. Two baseline conditions consisted of standard and test gratings of equal contrast, at 10 or 70% contrast. Two mixed-contrast conditions were run: one with standard 10% and test 70% contrast, the other with standard 70% and test 10% contrast. Veridical perception would yield a mean match of 100%. In Experiment 1 (Fig. 2), ten naïve observers and one of the authors (PT) participated. In Experiment 2 (Fig. 3), nine naïve observers and one of the authors (PT) participated. Six of the naïve observers (in addition to PT) participated in both experiments. All conditions were run three times by each observer.

Stimuli were generated on a Barco Calibrator 7651 screen using a Cambridge Research Systems VSG 2.1 graphics display card (100 Hz refresh rate) housed in a Compaq Deskpro 386/20 computer. Observers sat 114 cm from the screen at which distance the screen subtended 18 deg by 14 deg of visual angle. The gamma nonlinearity of the monitor was corrected using a look-up table.



RESULTS

Experiment 1: Perifoveal presentation

The speed matches for the drifting gratings presented perifoveally are shown in Fig. 2(A) for all 11 observers. In line with previous findings (Thompson, 1982; Stone & Thompson, 1992; Hawken *et al.*, 1994; Ledgeway & Smith, 1995; Gegenfurtner & Hawken, 1996; Thompson *et al.*, 1996), we found that at low contrast perceived rate of motion is decreased and at high contrast perceived rate of motion is increased. The mean size of the effect (i.e., slope of speed match vs log contrast ratio from linear regression with 4 points) is 0.68%/dB with y-intercept 102.0% (mean r^2: 0.81). Although there is clearly considerable inter-subject variability in the size of the effect (the largest effect is 1.35%/dB while the smallest is 0.18%/dB), all observers perceived lower contrast gratings as drifting slower (i.e., had positive slopes).

The flicker matches for the counterphase gratings are shown in Fig. 2(B) for the same 11 observers. The effects of contrast are now reversed: increasing contrast decreases perceived flicker rate. The mean size of the effect is −0.75%/dB with y-intercept 98.4% (mean r^2: 0.79). Again, although there is a considerable range of inter-subject variability in the data (from −2.49 to

FIGURE 2. Speed and flicker matching in the perifovea. For clarity, the data for contrast ratio zero are represented by the average of the two equal contrast conditions. All P values were obtained from unpaired two-tailed t-tests. (A) The mean speed matches across three runs of all 11 observers in response to drifting gratings at three different contrast ratios. All observers showed an increase in perceived speed at higher contrast. For five observers, the difference between the matches in the 70:10 and 10:70 conditions was significant across the small number of runs ($P < 0.05$) with two more observers borderline significant ($P < 0.08$). The average difference was very significant across observers ($P < 0.001$) as well as the average slope ($P < 0.001$). (B) The mean flicker matches across three runs of the same 11 observers in response to flickering gratings at three different contrast ratios. Nine showed a decrease in perceived temporal frequency at higher contrast. Again, for five observers, the difference between the matches in the 70:10 and 10:70 conditions was significant across the small number of runs ($P < 0.05$) with two more observers borderline significant ($P < 0.09$). The average difference was very significant across observers ($P < 0.001$) as well as the average slope ($P < 0.008$). (C) Mean speed and flicker matches, with the error bars being standard error across observers.

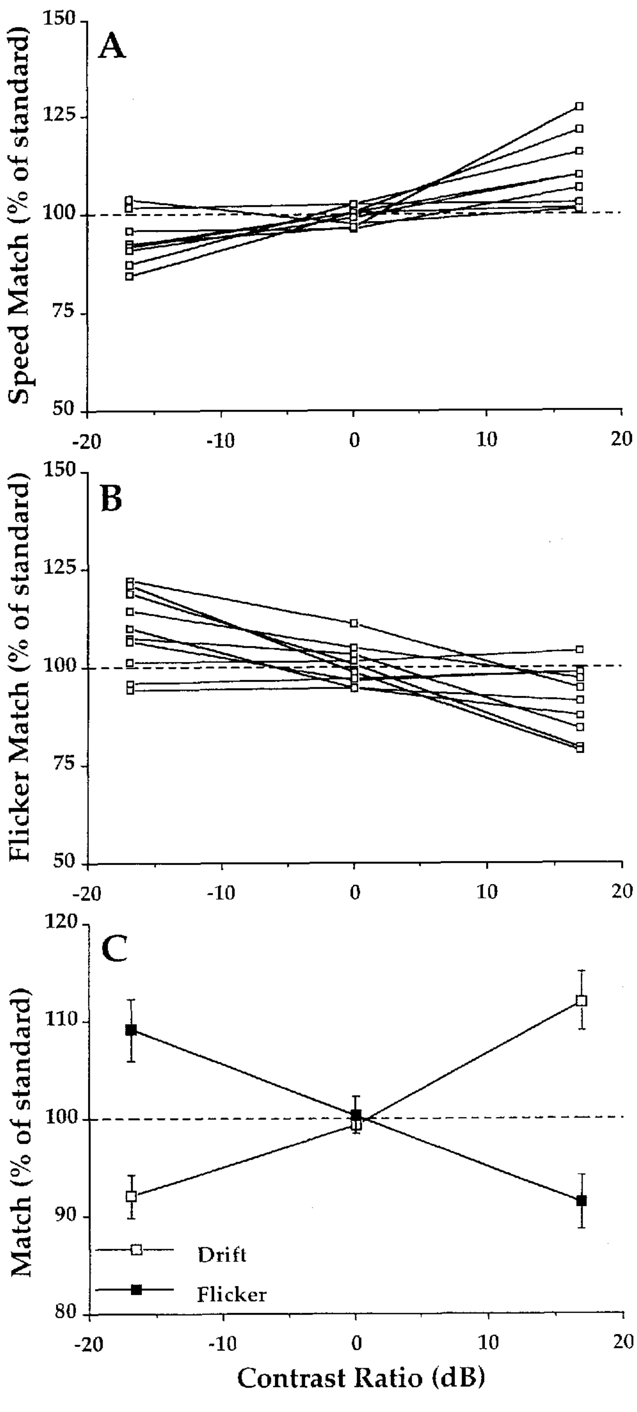


FIGURE 3. Speed and flicker matching in the fovea. For clarity, the data for contrast ratio zero are represented by the average of the two equal contrast conditions. All P values were obtained from unpaired two-tailed t-tests. (A) The mean speed matches across three runs of all 10 observers in response to drifting gratings at three different contrast ratios. Nine showed an increase in perceived speed at higher contrast. For six observers, the difference between the matches in the 70:10 and 10:70 conditions was significant across the small number of runs ($P < 0.05$). The average difference between the matches in the 70:10 and 10:70 conditions was very significant across subjects ($P < 0.001$) as well as the average slope ($P < 0.003$). (B) The mean flicker matches across three runs of the same 10 observers in response to flickering gratings at three different contrast ratios. Nine showed a decrease in perceived speed at higher contrast. For three observers, the difference between the matches in the 70:10 and 10:70 conditions was significant across the small number of runs ($P < 0.05$). The average difference between the matches in the 70:10 and 10:70 conditions was very significant across subjects ($P < 0.001$) as well as the average slope ($P < 0.006$). (C) Mean speed and flicker matches, with the error bars being standard error across observers.

0.15%/dB), nine observers perceived lower contrast gratings as faster (i.e., had negative slopes).

Experiment 2: Foveal presentation

The speed matches for the foveally presented stimuli are shown in Fig. 3(A) for 10 observers. Nine observers perceived the lower contrast gratings as slower. The mean size of the effect was 0.59%/dB (range: −0.08 to 1.26%/dB) with a y-intercept of 100.8% (mean r^2: 0.73). The effect is qualitatively the same as in the perifovea, although the magnitude of the effect appears smaller in the fovea.

The flicker matches for the foveally presented counterphase gratings are shown in Fig. 3(B) for the same 10 observers. Eight observers perceived the lower contrast gratings as flickering faster. The mean size of the effect was −0.52%/dB (range: −1.25 to 0.09%/dB) with y-intercept 100.4% (mean r^2: 0.79). These results are qualitatively the same as those seen in the perifovea, again the magnitude of the effect appears smaller in the fovea.

Given that the effects of contrast on flicker and speed perception are in opposite directions and of approximately the same size, it is tempting to think that the two effects might be mirror images of one another. However, we found no significant correlation between observers' slopes for speed and flicker matches ($r^2 = 0.006$).

DISCUSSION

McKee *et al.* (1986) found evidence that humans can perceive speed with high precision, even in the presence of random fluctuations in stimulus contrast. This finding led theoretical neuroscientists to generate computational models of human motion processing that attempt to generate speed estimates uncontaminated by stimulus contrast. Given that motion–energy filters are inherently sensitive to stimulus contrast, Adelson, Bergen, and others achieved robustness to variation in contrast by using a contrast-normalization procedure (Adelson & Bergen, 1986; Heeger, 1987; Wilson *et al.*, 1992). Yet, the fact that speed perception is contrast dependent over a wide range of contrasts (Stone & Thompson, 1992) demonstrates that, if such a normalization procedure is used, it is only partially effective. The effectiveness of normalization might be reduced if the spatio-temporal window over which the normalization contrast is calculated were large enough to cause the two patches to interfere with each other's normalization. However, contrast-induced speed misperceptions are resistant to manipulations of surrounding contrast and are observed even for matches across presentations made up to 5 sec apart in time (Thompson *et al.*, 1996). These data rule out the hypothesis that normalization is a rather global process and that our specific spatio-temporal arrangement caused each patch to interfere with the other's otherwise proper normalization. For a more local version of normalization to explain our results, it would have to be fundamentally incomplete. The output of motion filters is generally idealized as a power function of contrast with exponent n. Full normalization posits that this raw output is divided by a measure of average contrast taken to the same exponent (see, e.g. Albrecht & Geisler, 1991). If the exponent of the normalizing denominator is less than n, the normalization would only be partially effective. Therefore, partial normalization might indeed explain our previous results. However, to explain our present results, different normalization would be required for motion and flicker mechanisms. In conclusion, fully contrast-normalized motion–energy models are inconsistent with the observed contrast effect on perceived speed and flicker, although partial normalization schemes, local in space and time, are possible and deserve further examination.

Watson & Ahumada (1985) suggested an alternative method of computing speed, independent of contrast. Their model derives speed from the ostensibly contrast-invariant temporal frequency responses of directionally selective spatio-temporally tuned input units. The original version of the model does not take into account the fact that human speed estimates are contrast dependent. However, if temporal frequency estimates within human cortex are themselves contrast dependent, then perhaps a modified version of their model could explain our previous results. To investigate this possibility, we examined the effect of contrast on temporal frequency estimation by measuring flicker perception. If the temporal frequency signal used to compute stimulus speed in their model were in fact contrast dependent, then the model might be able to explain our previous results. We reasoned that any effect of contrast on speed should also be manifest in judgements of temporal frequency. However, rather than finding that the effects on speed and flicker perception were the same, we found them to have opposite sign.

Three possible conclusions can be made from these results. First, it could be the case that the Watson–Ahumada model does not accurately describe the means whereby humans determine speed. Second, it could be that the flicker rate that we measured in our experiments is not tapping the same underlying temporal frequency mechanism used for speed estimation in the Watson–Ahumada model and that something like their algorithm supports human speed perception. Little in the literature would contradict such a claim; McKee and colleagues (1986) clearly believe that speed discriminations are not derived from flicker-rate discriminations, a view supported by Pasternak (1987). Thirdly, it could be the case that the Watson–Ahumada model is correct and that the discrepancy between our perceived flicker and perceived speed judgements as a function of contrast can be reconciled by the fact that perceived spatial frequency is also influenced by contrast. In support of this possibility, Georgeson (1980) has demonstrated that reducing contrast increases perceived spatial frequency. Furthermore, the amplitude of this effect may be large enough to override the effect on temporal frequency. This effect therefore has the potential to reconcile the observed increase in perceived temporal frequency and decrease in perceived speed with reduced contrast, thereby rescuing temporal-frequency based speed models. Future measurements of perceived spatial frequency, temporal frequency, and speed as a function of contrast under identical conditions will be needed to determine if the three data sets are quantitatively linked as predicted by this explanation.

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Acknowledgements—We thank our subjects for their participation, Rob Stone for programming, Preeti Verghese and Brent Beutter for comments on an earlier draft. LS was supported by NASA RTOP 199-16-12-37. Some of this work was presented at the Association for Research in Vision and Ophthalmology conference in Fort Lauderdale, April 1996.