Available online at www.sciencedirect.com
SCIENCE DIRECT®
Vision Research 45 (2005) 2191–2200
Vision Research
www.elsevier.com/locate/visres

Attenuation of perceived motion smear during the vestibulo-ocular reflex

Harold E. Bedell [a,*], Saumil S. Patel [b]

[a] College of Optometry and Center for Neuro-engineering and Cognitive Science, 505 J. Davis Armistead, Bldg 713/743-2020, University of Houston, Houston TX 77204-2020, United States
[b] Department of Electrical and Computer Engineering and Center for Neuro-engineering and Cognitive Science, University of Houston, Houston, TX 77204-4005, United States

Received 8 March 2004; received in revised form 26 January 2005

Abstract

Previous studies indicated that less motion smear is perceived when a physically stationary target is presented during voluntary eye movements than when similar retinal-image motion occurs during steady fixation. In this study, we assessed whether the perception of motion smear is attenuated also during the involuntary vestibulo-ocular reflex (VOR). Normal observers matched the length of perceived smear in two experimental conditions that were designed to produce similar trajectories of retinal image motion. In the fixation condition, a small bright target was presented for a duration of 50–200 ms in rightward or leftward motion, while the observer remained stationary and maintained fixation. In the VOR condition, the target moved along with the observer, who underwent full-body rotation around a vertical axis in darkness. Horizontal eye movement recordings during VOR trials allowed us to calculate the velocity of retinal image motion on each VOR trial. The principal result was that the extent of perceived motion smear was significantly less during VOR than fixation trials, particularly for target durations of 100 ms or longer. These findings support the conclusion that extra-retinal signals during the involuntary VOR contribute to a reduction of perceived motion smear.

Keywords: Motion; Motion smear; Eye movement; Extra-retinal signals; Vestibulo-ocular reflex

1. Introduction

Because the response of the visual system persists beyond the duration of the physical stimulus (Bowen, Pola, & Matin, 1974; Di Lollo & Bishoff, 1995; Haber & Standing, 1970), the motion of a target's retinal image would be expected to produce the perception of motion smear. Indeed, the perception of substantial motion smear has been reported to occur for isolated visual targets that move physically on either a dark or a homogeneously illuminated background (Bidwell, 1899; Chen, Bedell, & Ögmen, 1995; Lubimov & Logvinenko, 1993; McDougall, 1904). However, the extent of perceived motion smear is reduced for an array of targets that move together (Castet, Lorenceau, & Bonnet, 1993; Chen et al., 1995; Hogben & Di Lollo, 1985), presumably because of inhibitory spatio-temporal interactions between each moving target and the persisting visual signals from its nearby neighbors (Castet, 1994; Di Lollo & Hogben, 1985; Purushothaman, Ögmen, Chen, & Bedell, 1998).

Motion of the retinal image can result also from a physically stationary target when the eyes are in motion. For example, during pursuit tracking, the image of a physically stationary target moves across the retina with a velocity that is equal and opposite to the velocity of eye motion. Qualitatively similar retinal image motion

* Corresponding author. Tel.: +1 713 743 1930; fax: +1 713 743 2053.
E-mail address: hbedell@optometry.uh.edu (H.E. Bedell).

0042-6989/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2005.01.032

of a physically stationary target occurs during post-rotary nystagmus in normal observers and during the involuntary rhythmic eye movements of persons with congenital nystagmus.

Previously, we found that normal observers report a smaller extent of perceived smear when the motion of the retinal image is produced by a stationary target during voluntary eye movements than when comparable retinal image motion results from physical motion of the target during steady fixation. Specifically, the extent of perceived motion smear is reduced significantly if the duration of the target is 100 ms or longer during smooth pursuit and vergence tracking (Bedell, Chung, & Patel, 2004; Bedell & Lott, 1996), and if the duration of the target is 20–30 ms or longer during voluntary saccades (Bedell & Yang, 2001). Some of these experiments were conducted in the absence of any additional visual targets except for the fixation or tracking stimulus, which indicates that the reduction of perceived motion smear during voluntary eye movements cannot be attributed to spatio-temporal interactions between targets. We therefore concluded that the attenuation of perceived motion smear during voluntary pursuit, vergence, and saccades was mediated by extra-retinal eye movement signals.

Despite substantial motion of the retinal image that occurs during their involuntary eye movements, subjects with congenital nystagmus (CN) typically report neither oscillopsia nor motion smear under most normal viewing conditions (Abadi, Whittle, & Worfolk, 1999; Bedell, 2000; Bedell & Bollenbacher, 1996; Tkalcevic & Abel, 2003). Evidence indicates that extra-retinal signals for the involuntary eye movements in persons with CN contribute substantially to perceived stability of the visual world (Abadi et al., 1999; Bedell & Currie, 1993; Goldstein, Gottlob, & Fendick, 1992; Leigh, Dell'Osso, Yaniglos, & Thurston, 1988), although adaptive mechanisms may also play a role (Shallo-Hoffmann, Bronstein, Morland, & Gresty, 1998). Based on our conclusion that the extra-retinal signals for normal, voluntary eye movements attenuate the perception of smear, we suggested that the extra-retinal signals for CN contribute similarly to a reduction of perceived motion smear (Bedell, 2000).

However, controversy exists about whether the extra-retinal signals associated with the *involuntary* eye movements of normal observers exert an influence on perception (Bedell, 2000; Bedell, Klopfenstein, & Yuan, 1989; Chaudhuri, 1990; Freeman, Sumnall, & Snowden, 2003; Hansen & Skavenski, 1977; Heckmann & Post, 1988; Post & Leibowitz, 1985; Whiteside, Graybiel, & Niven, 1965). For example, Chaudhuri (1990) accounted for the suppressive effect of a visual fixation target on induced afternystagmus by postulating that an oppositely directed pursuit command resulted in the cancellation of the nystagmus. To explain the illusory motion of the fixation target that occurs in this condition, he proposed that only the extra-retinal signal for the pursuit command, and not the involuntary afternystagmus, produces an influence on perception. In contrast, Bedell et al. (1989) showed that observers point accurately in the direction of a visual target that is flashed during optokinetic afternystagmus, which indicates that an extra-retinal signal for eye position during the involuntary afternystagmus influences perceived target direction. A possible explanation for this discrepancy is offered, below, in Section 4.

Even if the extra-retinal signals for involuntary eye movements contribute to normal perception, it is not clear how these signals might influence the perceived extent of motion smear. During *voluntary* eye movements, extra-retinal signals are thought to be compared to the change in the retinal location of the target's image which, for a physically stationary target, yields an approximately stable perception of the target's location in space (von Holst & Mittelstaedt, 1950/1971; Bridgeman, 1995). One possibility is that the extent of perceived motion smear is reduced during an eye movement if, after retinal and extra-retinal information are compared, the target is perceived to be stationary in space. It should be noted that this explanation would account for the reported reduction of perceived motion smear during voluntary pursuit and saccadic eye movements[1] and during involuntary eye movement in CN. However, if the perception of a world-stationary target is required for motion smear to be reduced, then the extent of perceived motion smear may *not* be attenuated when retinal image motion is produced by a normal involuntary eye movement, the goal of which is to maintain an approximately stable direction of gaze. This prediction follows from the recognition that a target would have to move physically to result in substantial motion of the retinal image during normal reflexive eye movements such as the VOR, assuming that the VOR gain is close to 1.

The goal of this study was to compare the extent of motion smear that normal observers perceive when motion of the retinal image occurs in the following two conditions: (1) when the eyes remain stationary, and (2) during the involuntary vestibulo-ocular reflex (VOR). Consequently, we compared the extent of perceived mo-

[1] Contrary to the findings reported by Bedell et al. (2004), this explanation predicts *no* reduction of perceived motion smear for a physically stationary target that is presented to one eye during symmetric vergence tracking. According to the Wells–Hering laws of visual direction (c.f., Ono & Mapp, 1995), the perceived egocentric direction of a tracked binocular or monocular target should remain unchanged during symmetric convergence, whereas the perceived direction of a stationary monocular target should shift toward the viewing eye. However, the velocity of the vergence stimulus in the experiment by Bedell et al. was only 2 deg/s/eye which, even for the maximum target duration of 400 ms, may not have produced a sufficient change in the retinal image position of the physically stationary target to yield an unambiguous change in perceived egocentric direction.

tion smear that results from the physical motion of a target when the eye is stationary vs. moving.

2. Methods

2.1. Subjects

Five observers with normal vision and oculomotor control participated in these experiments. Two of the observers were the authors. Although the other three observers also had experience in psychophysical experiments, observers KC and VN were naive as to the purpose of the experiments. Before participation, all of the observers granted voluntary informed consent, in accordance with federal and University guidelines.

2.2. VOR condition

Horizontal vestibular-driven eye movements were induced by whole-body rotation in the dark, using a non-motorized Tracoustics torsion-swing chair. This chair produces rotation about a vertical axis with a temporal frequency of approximately 0.12 Hz and a peak-to-peak amplitude of approximately 60°. The visual target was produced by a green laser diode, reflected from a galvanometer-mounted mirror onto a large (180° × 90°) cylindrical screen. The screen, the mirror-galvanometer, and laser diode were attached firmly to the torsion chair, and therefore moved en bloc along with the observer during rotation (Fig. 1). Consequently, a projected target that was fixed with respect to the moving screen produced retinal image smear with a velocity equal and opposite to the velocity of the observer's eye movement. Targets were presented at a distance of 60 cm and were viewed monocularly to avoid the possibility of diplopia. From trial to trial, the duration of the laser target varied randomly among the following values: 50, 100, 150, and 200 ms. The target luminance was approximately 2.5 log units above its detection threshold, when presented for a duration of 50 ms after 10 min of dark adaptation.

The observer's head position was restrained using a molded neck brace, attached to the back of the chair. The horizontal positions of both the viewing and occluded eyes were monitored using an ASL model 210 Eye Trac, that compared the amounts of diffuse infrared reflection from the nasal and temporal limbi. Analog signals from the eyetracker were sampled at 1 kHz by a Scientific Solutions labmaster board in a PC computer and stored for off-line analysis. Horizontal eye position was calibrated before and after each set of 20 trials by having the stationary observer fixate successively on five small LEDs, spaced horizontally between ±10° of the straight-ahead position. Each presentation of the screen-stationary (i.e., physically moving) laser target was triggered to occur randomly between 50 and 150 ms after the onset of a VOR quick phase, detected by applying a velocity criterion to the sampled eye-position signals on-line (Bedell & Currie, 1993). From trial to trial, triggering occurred alternately during rightward and leftward chair rotation. The sequence of events on a representative VOR trial is shown in Fig. 2. Five sets of 20 trials were run on each observer, yielding a total of 25 trials for each duration of the target. The observers were instructed to look straight ahead in the dark during chair rotation and to note the horizontal extent of perceived target smear.

Approximately 3 s after each presentation of the laser target, the torsion chair was brought to a stop and a bright horizontal line of adjustable length was back-pro-

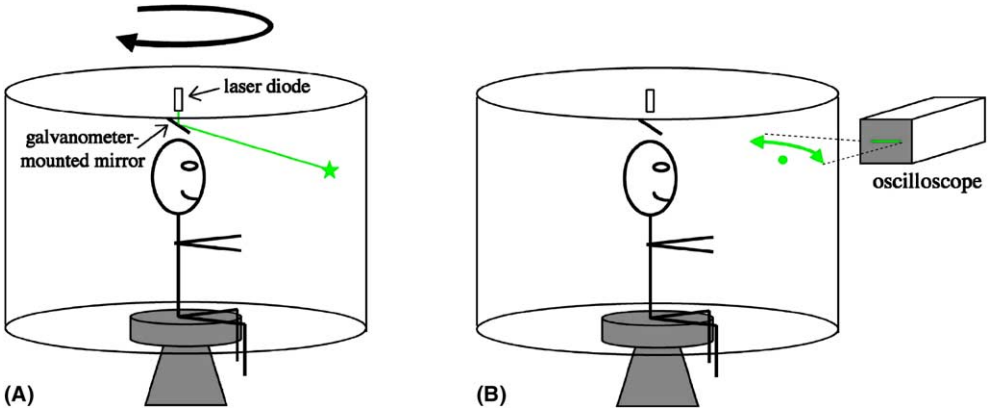

Fig. 1. An illustration of the experimental setup. Observers sat in a spring-loaded torsion chair with an attached cylindrical translucent white screen. Also attached to the chair and screen were a galvanometer driven mirror, a green laser diode, and five green LEDs (one of these LEDs is shown in panel B). Panel A depicts the presentation of the laser spot during rotation of the observer on a VOR trial. Panel B shows the observer fixating on an illuminated LED and matching the extent of perceived motion smear. Matches were made by adjusting the length of a bright line, projected by an optical system (not shown) from an *x–y* oscilloscope onto the back surface of the translucent screen.

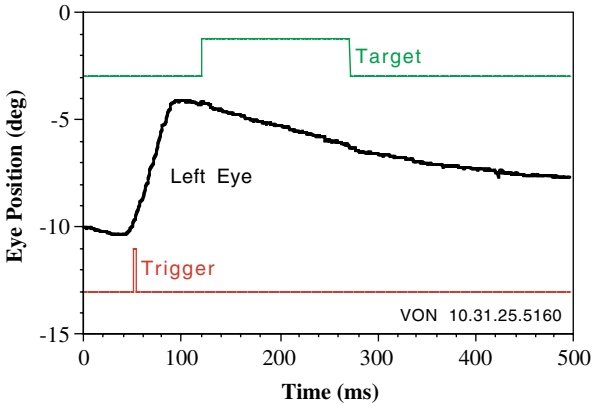

Fig. 2. A representative trial from the VOR condition. A saccade was detected by the computer after receiving a ready signal from the observer. Following a random delay, the target was presented for 50, 100, 150 (as in this trial), or 200 ms during the slow-phase of a VOR movement.

jected onto the screen approximately 2.5 deg above a stationary fixation target (LED). Using a joystick, the observer adjusted the length of this line to match the full extent of the perceived motion smear during the preceding presentation of the laser target. A control experiment performed on 1 observer indicated that the extent of matched smear is unaffected by up to a 30-s delay between the presentation of the moving target and the matching line. After data collection, the eye position record for each trial was examined off-line. Trials were discarded if a blink or a saccade occurred, or if the eye velocity was less than 5 °/s during the presentation of the target. Based on these criteria, approximately 25% of the VOR trials were rejected in the five observers (range = 16–36%). On the trials that were retained, eye velocity was determined as the slope (in °/s) of the best fitting straight line through the eye position data during the interval that the laser target was presented (i.e., 50–200 ms).

2.3. Fixation condition

Comparison measures for the length of perceived motion smear were obtained subsequently during fixation by the stationary observer, when the laser target moved physically with respect to the (stationary) cylindrical screen. The trials in the fixation condition were conducted after the VOR trials were completed, to allow us to approximately match the average retinal image velocity for each observer in the two sets of trials. The horizontally moving laser target was presented monocularly in darkness at a distance of 60 cm, 2 deg above a continuously visible fixation LED in the straight-ahead direction. From trial to trial, the direction of motion of the laser target was randomly to the left or the right, its duration varied randomly among 50, 100, 150 and 200 ms, and its velocity varied randomly within a range

Table 1
Distribution of retinal image velocities in the VOR and fixation conditions

Observer	Median retinal image velocity on VOR trials[a] (deg/s)	*N*	Median retinal image velocity on fixation trials[a] (deg/s)	*N*
KC	24.4 (17.9–32.7)	84	9.2 (7.2–11.6)	198
HB	12.0 (9.0–16.5)	74	14.6 (9.6–20.1)	200
SP	15.9 (11.6–23.0)	65	16.1 (11.9–20.3)	400
VN	22.4 (15.5–29.5)	76	20.0 (15.1–25.2)	200
SC	29.3 (20.0–36.8)	70	23.4 (14.3–34.4)	400

[a] Values in parentheses indicate 25th and 75th percentiles.

of values that was intended to approximate the retinal image velocities produced for each observer in the VOR condition (see Table 1). In addition, the mean position of the moving laser target on each trial varied randomly among five visual-field locations, spaced evenly between 10° right and left of straight ahead. This range of horizontal visual-field locations roughly spanned the range of off-foveal target locations that were sampled during the VOR trials. As in the VOR condition, the observer adjusted the length of a bright stationary line after each target presentation to match the length of perceived motion smear on that trial. For three of the observers, 10 trials were accumulated across two sessions, for each combination of target duration and visual-field location. A total of 20 trials were obtained for each fixation condition for observers SP and SC.

Eye position was not measured during the fixation condition, as our previous experiments (Bedell et al., 2004; Bedell & Lott, 1996) verified that fixation remains accurate and precise on virtually all of these trials. As in these previous studies, the observers in this study were warned against blinking and initiated each fixation trial only when they were carefully fixating the LED.

2.4. Statistical analyses

The results from the VOR and fixation conditions were compared using a two-factor, full-interaction, repeated-measures analysis of variance (ANOVA), performed with SuperANOVA software (Abacus Concepts, Berkeley, CA). The two factors were eye-movement condition (2 levels: fixation and VOR) and target duration (4 levels: 50, 100, 150 and 200 ms). Because each observer completed different number of useable trials in the various conditions, we analyzed the median extents of perceived smear for each combination of experimental condition (VOR vs. fixation) and target duration. For the fixation condition, median values were computed across all of the visual field locations at each duration. Subject-interaction terms provided the error estimates for the *F* ratios for each effect; viz., eye-movement × subject for the main effect of eye-movement, duration × subject for the main effect of duration, and

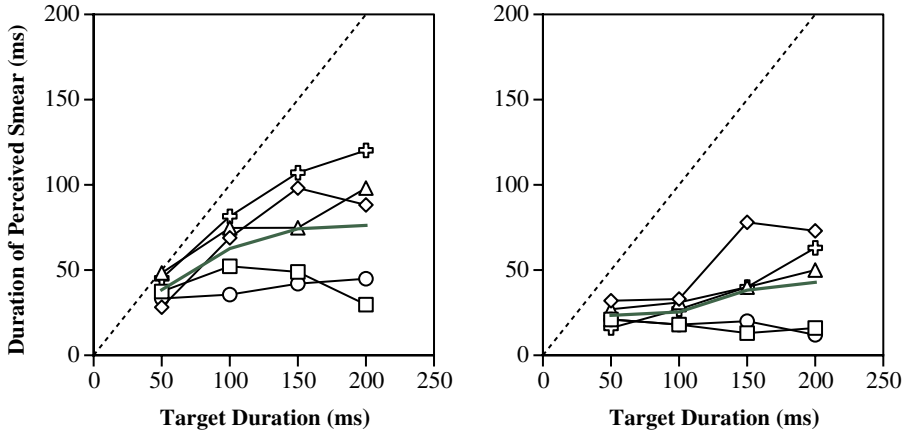

Fig. 3. The extent of perceived motion smear (in ms) as a function of target duration in the fixation (left panel) and VOR (right panel) conditions. The symbols joined by thin lines indicate the *median* data of the individual observers (KC circles, HB diamonds, SP squares, VN triangles, and SC crosses). The median values for each condition were computed from the data at all visual-field locations of the target. The thick line represents the average of the medians of the five observers.

eye-movement × duration × subject for the interaction between eye-movement and duration. All probability values were corrected for sphericity using the Huynh–Feldt or the Geisser–Greenhouse correction.

For the data obtained in the fixation condition, the effect of visual field location was examined using a second two-factor, full-interaction, repeated-measures ANOVA. The two factors were visual field location (five levels: −10, −5, 0, 5 and 10 deg) and target duration (four levels: 50, 100, 150 and 200 ms). Other aspects of this analysis were as described in the previous paragraph.

3. Results

Across observers, the median retinal image velocity ranged from 12 to 29°/s on acceptable VOR trials and from 9 to 23°/s on fixation trials (Table 1). Some of the variability in the retinal image velocity within and between the observers on the VOR trials resulted from differences in the temporal frequency of chair rotation (somewhat higher for lighter subjects) and from trial-to-trial differences in the phase of the sinusoidal rotation when the visual stimulus was triggered. In addition, the VOR gain may have varied among observers as well as within each observer from trial to trial. However, because we did not record a signal of the chair velocity, we were not able to calculate the range of our observers' VOR gains. To compare the extent of perceived motion smear for the different velocities of retinal image motion, we converted the matched extent of perceived smear on each trial from units of visual angle to units of duration (Bedell & Lott, 1996; Chen et al., 1995; Hogben & Di Lollo, 1985):

$$\text{Smear (ms)} = \text{Smear (deg)}/\text{Image velocity (deg/ms)}.$$

The individual and average data for the extent of perceived motion smear are compared for the VOR and fixation trials in Fig. 3. Despite the substantial individual differences that are apparent in the figure, each observer reported a smaller extent of perceived motion smear in the VOR than in the fixation condition. A repeated-measures ANOVA confirmed that the extent of perceived motion smear is significantly less in the VOR than the fixation condition ($F_{[df=1,4]} = 22.92$; $p = 0.009$).[2] Post hoc comparisons indicated that the extent of perceived smear in the VOR condition is significantly smaller for each target duration (*smallest* $F_{[df=1,12]}$, for a duration of 50 ms = 13.1; $p = 0.006$; for all other durations, $p \leqslant 7 \times 10^{-6}$). The individual and average differences between the extent of perceived smear in the VOR and fixation conditions are shown in Fig. 4. For target durations of 100 ms and longer, the average difference between the extent of perceived smear in the VOR and fixation conditions corresponds to an approximately constant value of 35 ms.

Because of a programming error, the median velocity of retinal image motion was faster during VOR than fixation trials for one of the five observers (Table 1). Therefore, for observer KC we compared the mean extent of perceived smear in the fixation condition to that on the subset of his VOR trials with similar image velocities (i.e., for eye velocities <14°/s). Pooled across durations of the target, the mean extent of perceived smear was significantly less on VOR trials (29.0 ± 5.4 ms) than on fixation trials (43.5 ± 6.8 ms; $t_{[df=210]} = 2.02$; $p = 0.044$). Further, when the data for all of the VOR and fixation trials were considered for this observer, the extent of

[2] In addition to the main effect of experimental condition, the interaction between condition and duration also was significant ($F_{[df=3,12]} = 6.23$; $p = 0.014$). The main effect of duration did not reach statistical significance ($F_{[df=3,12]} = 4.14$; $p = 0.074$).

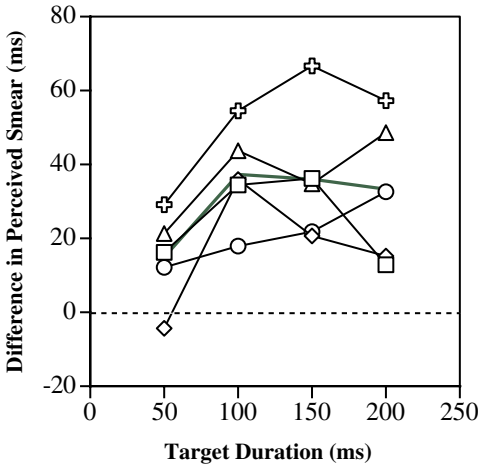

Fig. 4. The difference (in ms) between the extent of perceived motion smear in the fixation and VOR conditions as a function of target duration. Each of the data points joined by thin lines represents the difference between the median values that are plotted for each observer in Fig. 3. The thick line is the mean across the observers.

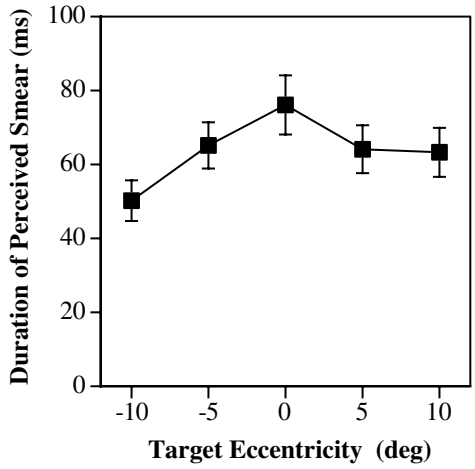

Fig. 5. The extent of perceived motion smear as a function of target eccentricity in the fixation condition. Each plotted point represents the average (±1 SE) of the median values for the five observers, determined for the four durations of the target.

perceived motion smear was not related to the velocity of retinal image motion (for VOR trials, $r = -0.06$; $p = 0.59$; for fixation trials, $r = -0.08$; $p = 0.28$). These analyses indicate that the differences in perceived smear that are shown for observer KC in Figs. 3 and 4 cannot be attributed to an inequality between the average retinal image velocities in the VOR and fixation conditions.

Another potential concern is that the data shown for each observer in Figs. 3 and 4 are aggregated across all of the visual-field locations at which the moving target was presented. If the extent of perceived motion smear were to vary according to the visual-field location of the target, then a dissimilar distribution of target locations in the fixation and VOR conditions could have been responsible for the smaller extent of perceived motion smear on VOR trials. Indeed, a repeated-measures ANOVA of all of the observers' data in the *fixation* condition revealed a significant effect of visual-field location on the perceived extent of smear ($F_{[df=4,16]} = 9.50$; $p = 0.004$).[3] Across observers, the extent of perceived motion smear was significantly greater for targets in the central field, and decreased for targets at 10 deg in the left and right visual field (Fig. 5). A similar analysis of the data in the VOR condition was not possible because the distribution of target locations varied non-systematically within and among the observers, depending on the eye positions at which the target was triggered from trial to trial. Consequently, in order to minimize the possible influence of visual-field location on the results, we recomputed the extent of perceived motion smear for just those VOR trials on which the target's path of motion was centered between ±5 deg of the straight-ahead direction ($N = 221$ of the acceptable 369 VOR trials, when pooled across observers and durations). Fig. 6 compares these average data to the average results from the fixation condition for target eccentricities of 0, −5 and 5 deg. Clearly, the extent of perceived motion smear is less in the VOR than in the fixation con-

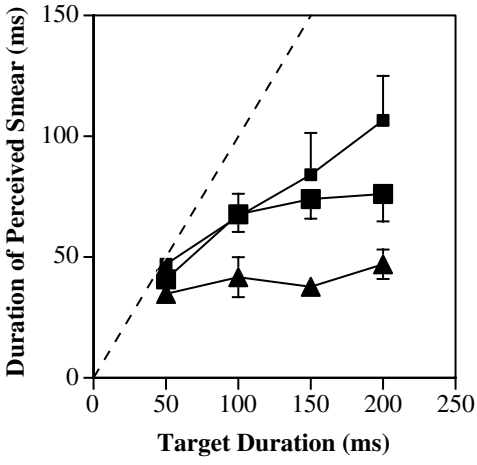

Fig. 6. The extent of perceived motion smear in the fixation and VOR conditions as a function of target duration, for targets restricted to the central visual field. The data for the VOR condition (triangles) are the averages of the median values for the five observers (±1 SE), for all trials in which the target's retinal image motion was centered between ±5 deg of the fovea. Two sets of data are shown for comparison in the fixation condition, i.e., trials on which the retinal image motion of the target was centered above the fovea (smaller squares) and trials on which the retinal image motion of the target was centered at ±5 deg (larger squares). To avoid clutter, the error bars (SE) for the data in the fixation condition are plotted in only one direction.

[3] This ANOVA also revealed a significant main effect of target duration ($F_{[df=3,12]} = 7.56$; $p = 0.031$), and a significant interaction between duration and eccentricity ($F_{[df=12,48]} = 2.66$; $p = 0.031$).

dition for targets that are presented at similar visual-field locations.

4. Discussion

4.1. Attenuation of perceived motion smear during the VOR

The principal finding of this study is that a smaller extent of motion smear is perceived when motion of the retinal image is produced by a *subject*-stationary (but physically moving) stimulus that is presented during the slow phase of the VOR, than when similar motion of the retinal image results from the physical motion of a target during steady fixation. Although the motion of the retinal image was similar during the VOR and fixation trials in our experiment, the retinal stimulation was not completely identical in the two types of trials. Consequently, before we consider the implications of our results we will first evaluate the likely impact of the differences in the retinal stimulation between the fixation and VOR conditions.

One clear difference between the two conditions is that a fixation stimulus was visible throughout each fixation trial, but not in the VOR trials. As noted in Section 1, the presence of additional nearby targets has been shown to *reduce* the extent of perceived motion smear during fixation (Castet et al., 1993; Chen et al., 1995; Hogben & Di Lollo, 1985). Specifically, Chen et al. (1995) found that the extent of perceived motion smear for a horizontally moving target was reduced in the presence of additional targets if the *vertical* separation between the targets was less than approximately 0.4 deg. For larger vertical separations between the targets, the extent of perceived motion smear did not differ from that when the target was an isolated moving spot. Because the stationary fixation stimulus in our experiment was separated vertically from the horizontally moving target by approximately 2 deg, this fixation stimulus is unlikely to have either decreased or increased the extent of perceived motion smear.

The fixation target also can influence the observers' attention. However, Bedell et al. (2004) manipulated the level of attention that observers needed to direct to the fixation target and found no systematic influence on the extent of smear that was perceived in a nearby moving target.

The retinal image velocity of the target varied substantially from trial to trial in both the VOR and fixation conditions. However, for four of the five observers, we approximately matched the distribution of retinal image velocities in the two conditions (Table 1). Further, our statistical analysis used only the median response of each observer for each combination of experimental condition and target duration, which minimizes the influence of any sampling differences between the various conditions. Finally, an analysis of all of the data for each observer indicated no systematic relationship between the extent of perceived smear and the velocity of retinal image motion, for either the VOR (average correlation = -0.15 ± 0.13 [SE]) or the fixation condition (average correlation = 0.18 ± 0.10).

Although the target was always presented physically straight ahead in the VOR condition of the current experiment, variations in the observers' horizontal eye position from trial to trial produced a range of retinal image locations (5th–95th percentile across observers and target durations = −11.4 to 14.5 deg). In order to approximately match this range of image locations in the fixation condition, we presented targets at visual-field eccentricities between 10 deg of straight ahead. The results from the fixation condition indicate that the extent of perceived smear decreases with the eccentricity of the target in the visual field (Fig. 5). Because perceived smear should depend on the temporal response speed of the visual system, an increase in the transience of peripheral compared to foveal visual responses (McKee & Taylor, 1984; Tyler, 1985) could account, at least in part, for this influence of target eccentricity. However, the line used to match perceived smear was always presented at the same near-foveal location. Consequently, the underestimation of perceived size that occurs for stimuli presented at peripheral retinal locations (Bedell & Johnson, 1984; Schneider, Ehrlich, Stein, Flaum, & Mangel, 1978) could contribute also to the measured reduction in the extent of perceived smear. Regardless of the reason for the effect of retinal eccentricity, the extent of perceived smear remains smaller in the VOR condition when the comparison with the fixation condition is restricted to targets with mean positions within ±5 deg of the straight-ahead location in the visual field (Fig. 6).

4.2. Comparison with previous results

Quantitatively, the average extents of perceived motion smear that our observers reported in the VOR and fixation conditions are smaller than the values in our previous studies of pursuit and vergence eye movements (Bedell et al., 2004; Bedell & Lott, 1996), particularly for target durations longer than 50 ms. We attribute this quantitative discrepancy from the results of our previous experiments primarily to individual variability, which was particularly striking among the observers in the present study (see Fig. 3). In spite of the considerable individual differences among their results, all five of the observers in this study reported less motion smear in the VOR condition than in the fixation condition. On the other hand, the normal observers in this study reported a *greater* extent of perceived motion smear during VOR slow phases than was reported by

subjects with congenital nystagmus (CN) during their involuntary eye movements (Bedell & Bollenbacher, 1996). Presumably, one or more mechanisms in addition to the one that controls the perception of smear during normal eye movements contribute to the reduction of perceived motion smear in subjects with CN.

4.3. Mechanism of smear attenuation during eye movements

We concluded above that the reduced extent of perceived motion smear during VOR slow phases cannot be accounted for readily on the basis of a difference in retinal stimulation in the VOR and fixation conditions. Consequently, in agreement with our previous proposal for the attenuation of perceived motion smear during voluntary eye movements, we attribute the reduced extent of perceived motion smear during the involuntary VOR slow phases to the influence of extra-retinal signals. However, because sensed head movement is the necessary stimulus for the VOR, it is difficult to distinguish whether the reduction of perceived smear that we observed in this study is based on the vestibular signal for head movement or the extra-retinal signal that accompanies the resulting eye movement.

Previous results from our lab indicate that normal observers appropriately combine information about a target's retinal image location with extra-retinal eye-position signals to specify the target's direction during involuntary optokinetic afternystagmus (Bedell et al., 1989) and rebound nystagmus (Bedell, 2000; Lott & Bedell, 1995). Earlier, Hansen and Skavenski (1977) reported that normal observers could accurately strike the location of a visual stimulus that was flashed briefly during full body rotation in the dark. Because rotation in the dark elicits VOR eye movements, the accurate directionalization of these flashed targets implies that the observers had access to veridical extra-retinal eye and/or head position signals at the time each visual target was presented. In contrast, some other previous studies concluded that extra-retinal signals do not inform perception about *involuntary* eye movements (e.g., Chaudhuri, 1990; Heckmann & Post, 1988; Whiteside et al., 1965). However, this conclusion was based primarily on the perception of illusory motion when both involuntary and voluntary (i.e. pursuit) eye-movement systems are activated simultaneously. Consequently, rather than indicating that extra-retinal signals for involuntary eye movements exert no perceptual influence, these motion illusions might reflect instead an inappropriate interaction between concurrently available signals for involuntary and voluntary eye movements.

As noted above in Section 1, one reason that a physically stationary target is perceived to remain stationary during voluntary eye movements is that the retinal image motion of the target is compared to extra-retinal signals for the ongoing eye movement (von Holst & Mittelstaedt, 1950/1971; Bridgeman, 1995). The influence of extra-retinal eye movement signals on the attenuation of perceived motion smear might be a consequence of this comparison process, if smear is reduced perceptually for targets that appear to remain stationary in space. Alternately, extra-retinal eye and/or head movement signals might act to attenuate the extent of perceived motion smear independently of this comparison process, whether or not the target is perceived to remain stationary in space. The outcome of our experiment favors the second alternative, as the extent of perceived motion smear is reduced during the VOR, when the motion of the retinal image resulted from physical motion of the target in space, in tandem with the rotating observer. We conclude that the attenuation of perceived motion smear by extra-retinal eye or head movement signals does not require the perception of a stationary target, and could occur at a relatively low level of visual processing. Consequently, one possible mechanism for the attenuation of perceived smear could be the documented influence of eye and head movement signals on the responses of subcortical and visual cortical neurons (e.g., Duffy & Burchfiel, 1975; Fukushima et al., 2004; Jeannerod & Putkonen, 1970; Kawano, Sasaki, & Yamashita, 1984; Thier & Erickson, 1992; Toyama, Komatsu, & Shibuki, 1984; Vanni-Mercer & Magnin, 1982).

Recently, we found that the extent of perceived motion smear is reduced also during VOR *suppression*, when observers maintain accurate fixation on a small stimulus that rotates with them in the dark (Tong, Patel, & Bedell, 2005). One possible explanation for this result is that an extra-retinal signal for pursuit, in the opposite direction of the reflexive VOR eye movement that otherwise would be elicited during rotation (Barnes, Benson, & Prior, 1978; Misslisch, Tweed, Fetter, Dichgans, & Vilis, 1996), is responsible for the reduction of perceived motion smear. Although this explanation is consistent with our finding that the extent of perceived motion smear is reduced during smooth pursuit (Bedell et al., 2004; Bedell & Lott, 1996), it is *not* consistent with the results of the present experiment, which show a decrease in perceived smear during the VOR in darkness, when no pursuit signals are present. In addition to the extra-retinal signal for pursuit, extra-retinal signals associated with head movement and/or with the involuntary VOR also must contribute to the reduction of perceived motion smear.

Acknowledgments

This study was supported by research grant R01-EY05068 and Core Center grant P30-EY07551 from the National Institutes of Health, and Advanced Re-

search Program award 003652-0185-2001 from the State of Texas. A portion of our results was presented at the May, 2002 ARVO meeting in Sarasota, FL.

References

Abadi, R. V., Whittle, J. P., & Worfolk, R. (1999). Oscillopsia and tolerance to retinal image motion in congenital nystagmus. *Investigative Ophthalmology and Visual Science, 40*, 339–345.

Barnes, G. R., Benson, A. J., & Prior, A. R. (1978). Visual-vestibular interaction in the control of eye movement. *Aviation Space and Environmental Medicine, 49*, 557–564.

Bedell, H. E. (2000). Perception of a clear and stable visual world with congenital nystagmus. *Optometry and Visual Science, 77*, 573–581.

Bedell, H. E., & Bollenbacher, M. A. (1996). Perception of motion smear in normal observers and individuals with congenital nystagmus. *Investigative Ophthalmology and Visual Science, 37*, 188–195.

Bedell, H. E., Chung, S. T. L., & Patel, S. S. (2004). Attenuation of perceived motion smear during vergence and pursuit tracking. *Vision Research, 44*, 895–902.

Bedell, H. E., & Currie, D. C. (1993). Extraretinal signals for congenital nystagmus. *Investigative Ophthalmology and Visual Science, 34*, 2325–2332.

Bedell, H. E., & Johnson, C. A. (1984). The perceived size of targets in the peripheral and central visual fields. *Ophthalmic and Physiological Optics, 4*, 123–131.

Bedell, H. E., Klopfenstein, J. F., & Yuan, N. (1989). Extraretinal information about eye position during involuntary eye movement: optokinetic afternystagmus. *Perception and Psychophysics, 46*, 579–586.

Bedell, H. E., & Lott, L. A. (1996). Suppression of motion-produced smear during smooth pursuit eye movements. *Current Biology, 6*, 1032–1034.

Bedell, H. E., & Yang, J. (2001). The attenuation of perceived motion smear during saccades. *Vision Research, 41*, 521–548.

Bidwell, S. (1899). *Curiosities of light and sight*. London: Swan Sonnenschein.

Bridgeman, B. (1995). A review of the role of efference copy in sensory and oculomotor control systems. *Annals of Biomedical Engineering, 23*, 409–422.

Bowen, R. W., Pola, J., & Matin, L. (1974). Visual persistence: Effects of flash luminance, duration and energy. *Vision Research, 14*, 295–303.

Castet, E. (1994). Effect of the ISI on the visible persistence of a stimulus in apparent motion. *Vision Research, 34*, 2103–2114.

Castet, E., Lorenceau, J., & Bonnet, C. (1993). The inverse intensity effect is not lost with stimuli in apparent motion. *Vision Research, 33*, 1697–1708.

Chaudhuri, A. (1990). A motion illusion generated by afternystagmus suppression. *Neuroscience Letters, 118*, 91–95.

Chen, S., Bedell, H. E., & Ögmen, H. (1995). A target in real motion appears blurred in the absence of other moving targets. *Vision Research, 35*, 2315–2328.

Di Lollo, V., & Bishoff, W. F. (1995). Inverse-intensity effect in duration of visible persistence. *Psychological Bulletin, 118*, 223–237.

Di Lollo, V., & Hogben, J. H. (1985). Suppression of visual persistence. *Journal of Experimental Psychology: Human Perception and Performance, 11*, 304–316.

Duffy, F. H., & Burchfiel, J. L. (1975). Eye-movement-related inhibition of primate visual neurons. *Brain Research, 89*, 121–131.

Freeman, T. C. A., Sumnall, J. H., & Snowden, R. J. (2003). The extra-retinal motion aftereffect. *Journal of Vision, 3*, 770–771.

Fukushima, J., Akao, T., Takeichi, N., Kurkin, S., Kaneko, C. R. S., & Fukushima, K. (2004). Pursuit-related neurons in the supplementary eye fields: Discharge during pursuit and passive whole body rotation. *Journal of Neurophysiology, 91*, 2809–2825.

Goldstein, H. P., Gottlob, I., & Fendick, M. G. (1992). Visual remapping in infantile nystagmus. *Vision Research, 32*, 1115–1124.

Haber, R. N., & Standing, L. G. (1970). Direct estimates of apparent duration of a flash followed by visual noise. *Canadian Journal of Psychology, 24*, 216–229.

Hansen, R. M., & Skavenski, A. A. (1977). Accuracy of eye position information for motor control. *Vision Research, 17*, 919–926.

Heckmann, T., & Post, R. B. (1988). Induced motion and optokinetic afternystagmus: Parallel response dynamics with prolonged stimulation. *Vision Research, 28*, 681–694.

Hogben, J. H., & Di Lollo, V. (1985). Suppression of visible persistence in apparent motion. *Perception and Psychophysics, 38*, 450–460.

Jeannerod, M., & Putkonen, P. T. S. (1970). Oculomotor influences on lateral geniculate nucleus neurons. *Brain Research, 24*, 125–129.

Kawano, K., Sasaki, M., & Yamashita, M. (1984). Response properties of neurons in the posterior parietal cortex of monkey during visual-vestibular stimulation. I. Visual tracking neurons. *Journal of Neurophysiology, 51*, 340–351.

Leigh, R. J., Dell'Osso, L. F., Yaniglos, S. S., & Thurston, S. E. (1988). Oscillopsia, retinal image stabilization and congenital nystagmus. *Investigative Ophthalmology and Visual Science, 29*, 279–282.

Lott, L. A., & Bedell, H. E. (1995). Extraretinal signals for rebound nystagmus: Availability to the motor vs. perceptual systems. *Investigative Ophthalmology and Visual Science, 36*(suppl.), S351.

Lubimov, V., & Logvinenko, A. (1993). Motion blur revisited. *Perception, 22*(suppl.), 77.

McDougall, W. (1904). The sensations excited by a single momentary stimulation of the eye. *British Journal of Psychology, 1*, 78–113.

McKee, S. P., & Taylor, D. G. (1984). Discrimination of time: Comparison of foveal and peripheral sensitivity. *Journal of the Optical Society of America A, 1*, 620–627.

Misslisch, H., Tweed, D., Fetter, M., Dichgans, J., & Vilis, T. (1996). Interactions of smooth pursuit and the vestibuloocular reflex in three dimensions. *Journal of Neurophysiology, 75*, 2520–2532.

Ono, H., & Mapp, A. P. (1995). A restatement and modification of Wells–Hering's laws of visual direction. *Perception, 24*, 237–252.

Post, R. B., & Leibowitz, H. W. (1985). A revised analysis of the role of efference in motion perception. *Perception, 14*, 631–643.

Purushothaman, G., Ögmen, H., Chen, S., & Bedell, H. E. (1998). Motion deblurring in a neural network model of retino-cortical dynamics. *Vision Research, 38*, 1827–1842.

Schneider, B., Ehrlich, D. J., Stein, R., Flaum, M., & Mangel, S. (1978). Changes in the apparent lengths of lines as a function of degree of retinal eccentricity. *Perception, 7*, 215–223.

Shallo-Hoffmann, J. A., Bronstein, A. M., Morland, A. B., & Gresty, M. A. (1998). Vertical and horizontal motion perception in congenital nystagmus. *Neuro-ophthalmology, 19*, 171–183.

Thier, P., & Erickson, R. G. (1992). Responses of visual-tracking neurons from cortical area MST-I to visual, eye and head motion. *European Journal of Neuroscience, 4*, 539–553.

Tkalcevic, L. A., & Abel, L. A. (2003). Effects of stimulus size and luminance on oscillopsia in congenital nystagmus. *Vision Research, 43*, 2697–2705.

Tong, J., Patel, S. S., & Bedell, H. E. (2005). Asymmetry of perceived motion smear during head and eye movements: Evidence for a dichotomous neural categorization of retinal image motion. *Vision Research, 45*(12), 1519–1524.

Toyama, K., Komatsu, Y., & Shibuki, K. (1984). Integration of retinal and motor signals of eye movements in striate cortex cells of the alert cat. *Journal of Neurophysiology, 51*, 649–665.

Tyler, C. W. (1985). Analysis of visual modulation sensitivity. II. Peripheral retina and the role of photoreceptor dimensions. *Journal of the Optical Society of America A, 2*, 393–398.

Vanni-Mercer, G., & Magnin, M. (1982). Single neuron activity related to natural vestibular stimulation in the cat's visual cortex. *Experimental Brain Research, 45*, 451–455.

von Holst, E., & Mittelstaedt, H. (1971). The principle of reafference: Interactions between the central nervous system and the peripheral organs. In P. C. Dodwell (trans.), *Perceptual processing: Stimulus equivalence and pattern recognition* (pp. 41–71). New York: Appleton-Century-Crofts (published originally in Die Naturwissenschaften, 1950).

Whiteside, T. C. D, Graybiel, A., & Niven, J. I. (1965). Visual illusions of movement. *Brain, 88*, 193–210.