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The attenuation of perceived motion smear during combined eye and head movements

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

[a] *College of Optometry, 505 J. Davis Armistead Building, University of Houston, Houston, TX 77204-2020, USA*
[b] *Department of Electrical and Computer Engineering, University of Houston, Houston, TX, USA*
[c] *Center for Neuro-Engineering and Cognitive Science, University of Houston, Houston, TX, USA*

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Abstract

The extent of perceived motion smear was compared for targets that underwent similar velocities of retinal image motion during the vestibulo-ocular reflex (VOR) in the dark, the visually enhanced VOR (VVOR), VOR suppression, and fixation. Compared to the extent of perceived motion smear during fixation, observers reported significantly less smear when the target moved either in the same direction or against the direction of the head movement during the VVOR and VOR. We also confirmed a previous finding that perceived smear is attenuated asymmetrically during VOR suppression, with attenuation occurring primarily for targets that move against the direction of the observer's head motion. The results support the hypothesis that the visual system employs extra-retinal signals that accompany eye *and* head movements to reduce the perception of motion smear for targets that move physically in the opposite direction of eye and/or head movements.

Keywords: Motion smear; VOR; VVOR; VOR suppression; Fixation; Extra-retinal signal

1. Introduction

Although movements of the eyes and head can keep the image of a moving target stable on the fovea, these movements also cause the images of *physically stationary* objects to move across the retina. Because of the substantial temporal persistence in the visual system (Bidwell, 1899; Burr, 1980; Coltheart, 1980; McDougall, 1904), the movement of an image on the retina would be expected to result in the perception of motion smear. One neural mechanism that reduces the extent of perceived motion smear is inhibitory spatio-temporal interaction between nearby moving retinal images. These interactions operate with maximal effectiveness when a sufficiently large density of elements moves across the retina (Chen, Bedell, & Ögmen, 1995; Di Lollo & Hogben, 1987; Purushothaman, Ögmen, Chen, & Bedell, 1998), and they are minimized when sparse image elements move across the retina. In the later situation, the extent of perceived motion smear approximates the value expected on the basis of visual persistence (Chen et al., 1995; Di Lollo & Hogben, 1987). Consequently, inhibitory interactions between retinal image elements are not sufficient to reduce the extent of perceived motion smear under all viewing conditions.

Previous experiments found a significantly smaller extent of perceived motion smear during various types of head-fixed voluntary eye movements than during steady fixation, for conditions in which the motion of the retinal images was equivalent (Bedell & Lott, 1996; Bedell & Yang, 2001; Bedell, Chung, & Patel, 2004). During smooth eye movements, the reduction of perceived motion smear was restricted to targets with durations longer than approximately 100 ms. For targets of shorter duration, we presume that the extent of perceived smear is limited by the physical duration of the target, rather than the duration of visible persistence.

* Corresponding author. Fax: +1 713 743 2053.
E-mail address: HBedell@Optometry.uh.edu (H.E. Bedell).

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In the experiments cited above, the motion of the test target with respect to the eye was always equal and opposite to the observers' eye movement. For example, when a stationary test target was flashed during leftward smooth pursuit at a speed of V deg/s, the relative motion between the stationary target and the eyes was equivalent to the condition in which the test target moved rightward with respect to the stationary eyes, also at V deg/s (Bedell & Lott, 1996). The reduced extent of perceived motion smear during head-fixed eye movements indicates that the visual system employs extra-retinal signals (ERSs) of eye movements, such as an efference copy signal, to improve the clarity of visual perception. Because perceived motion smear is attenuated also for targets that move in tandem with a rotating observer during the involuntary VOR (Bedell & Patel, 2005), it is reasonable to conclude that the extent of perceived motion smear can be reduced by the ERSs associated with involuntary as well as voluntary eye movements in the head.

Movements of the eyes and head frequently occur concurrently in daily life. Recently, we evaluated the effect of combined eye and head movements on the attenuation of perceived motion smear during VOR suppression, i.e., when observers fixate on a head-fixed target during full-body rotation around a vertical axis (Tong, Patel, & Bedell, 2005). VOR suppression is considered by many authors to represent a cancellation between oculomotor signals generated simultaneously by the vestibular and pursuit systems (Barnes, Benson, & Prior, 1978; Misslisch, Tweed, Fetter, Dichgans, & Vilis, 1996). Compared to the motion smear that is perceived during steady fixation, Tong et al. (2005) found a significantly smaller extent of perceived motion smear during VOR suppression, but only when the motion of the target with respect to the eye was in the *same* direction as the relative motion of an object that remains physically stationary in space. Further, because the eyes remain stationary in the head during VOR suppression, the reduction of perceived motion smear in this condition may be attributable to ERSs that indicate changes in *head* position and contribute to the perception of body orientation in the dark (Blouin et al., 1995). These considerations lead us to propose an *eye-and-head-movement* hypothesis, which states that the brain uses the ERSs that accompany eye *and* head movements to attenuate the perception of smear, selectively for targets that undergo relative motion in the opposite direction of the eye and/or head movements. Our observation that perceived smear decreases preferentially for targets that move in the opposite direction of voluntary smooth pursuit is also in agreement with this hypothesis (Tong et al., 2005).

Another possibility is that the extent of perceived motion smear is reduced for targets that move spatially in the opposite direction of *gaze movement*, rather than in the opposite direction of a separate eye or head movement. Although gaze movements can be considered as the sum of independent eye and head movements, neurophysiological evidence indicates that both cortical and subcortical neural centers contain subgroups of neurons that carry specific gaze-movement signals (Fukushima, Sato, Fukushima, Shinmei, & Kaneko, 2000; Shinmei, Yamanobe, Fukushima, & Fukushima, 2002). The possibility that the extent of perceived motion smear is reduced for targets that move in the opposite direction of gaze movement is designated the *gaze-movement* hypothesis. Although this *gaze-movement* hypothesis can account for previous results during various types of voluntary eye movements and during VOR suppression, it may not be concordant with the attenuation of perceived motion smear during the VOR (Bedell & Patel, 2005). In particular, if the gain of the VOR were less than 1.0, then a target that rotates in tandem with the observer would move in the same direction as gaze and, according to the gaze-movement hypothesis, there should be no reduction of perceived motion smear. Although perceived smear is reduced during the VOR, this evidence is insufficient to reject the *gaze-movement* hypothesis, because the gain of the VOR eye movements was not determined in the study by Bedell and Patel (2005).

In the present study we measured the extent of perceived motion smear for two combinations of eye and head movements. In the first condition, targets moved in the same or the opposite direction as the observers' physical rotation, while fixation was directed to a physically stationary target so that gaze remained approximately stable in space. Consistent with previous literature (Johnston & Sharpe, 1994; Leigh, Huebner, & Gordon, 1994), we designate this condition the visually enhanced VOR (VVOR). Results from the VVOR condition were compared to the extent of perceived smear during fixation, when the direction of gaze also was stable. The second condition represented an extension of the VOR experiment described above (Bedell & Patel, 2005) and measured the extent of perceived motion smear for targets that moved in the same and opposite directions as the observer's head movements. In this condition, the gaze moved with a speed and direction that varied inversely with the observers' VOR gain. The results from the VVOR and VOR conditions were used ultimately to test the validity of the *eye-and-head movement* and *gaze-movement* hypotheses, which make different predictions about the extent of perceived motion smear.

1.1. Predictions for VVOR condition

Because eye and head movements occur in opposite directions during the VVOR, the *eye-and-head-movement* hypothesis predicts that the extent of perceived motion smear should be reduced for long-duration targets that move both *with* and *against* the direction of the observer's rotation. In contrast, the *gaze-movement* hypothesis predicts that the extent of perceived motion smear should be quantitatively identical during the VVOR and during fixation for any direction of target motion.

1.2. Predictions for VOR condition

Because eye and head movements are also in opposite directions during the VOR, the *eye-and-head-movement* hypothesis predicts again that the extent of perceived motion smear should be reduced for long-duration targets that move *with* and *against* the direction of rotation. In contrast, the *gaze-movement* hypothesis predicts that attenuation of perceived motion smear during the VOR should occur only for targets that move opposite to the direction of gaze movement. In other words, if VOR gain is greater (or less) than unity, then according to the *gaze-movement* hypothesis, attenuation of smear should occur only for targets that move *with* (or *against*) the direction of rotation.

The *eye-and-head-movement* and *gaze-movement* hypotheses both predict that perceived motion smear will be reduced asymmetrically during VOR suppression, as we reported previously (Tong et al., 2005). In this study we also measured the extent of perceived motion smear for targets that moved in the same and opposite direction as the observer's rotation in the VOR suppression condition, to confirm the previous results in the set of observers tested here.

The quantitative relationship between eye velocity (V_E), head velocity (V_H) and gaze velocity (V_G) during the three types of movement that were examined in the current study are illustrated schematically in Fig. 1. Table 1 provides a summary of the predictions of the *eye-and-head-movement* and *gaze-movement* hypotheses for the conditions tested in our experiments.

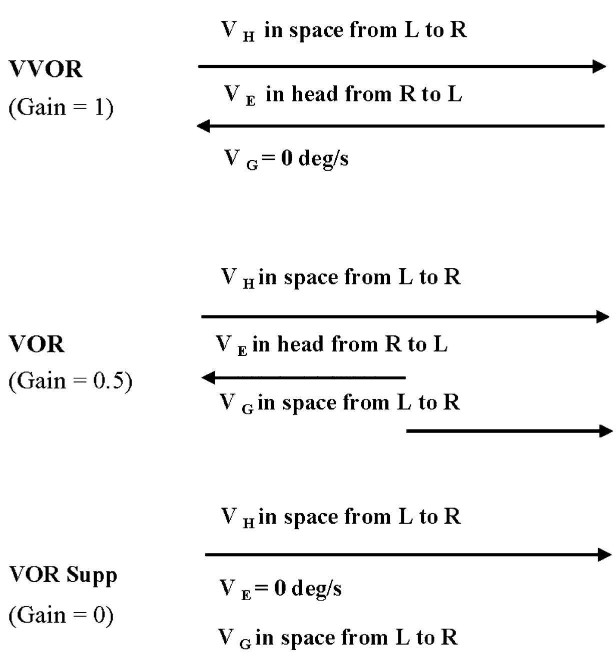

Fig. 1. Illustration of the quantitative relationship between the velocity of the head in space (V_H), the velocity of the eye in the head (V_E), and the velocity of gaze (V_G) during the visually enhanced VOR (VVOR), the vestibulo-ocular reflex (VOR), and VOR suppression (VOR Supp). The direction and length of each arrow indicates the direction and speed of the head, eye and gaze movements. Gaze velocity is represented as the vector summation between the head velocity in space and the eye velocity in the head. In the figure, the assumed values of gain (equal to $|V_E/V_H|$) for the VVOR, VOR and VOR Supp are 1, 0.5, and 0, respectively. Therefore, gaze is stationary in space during the VVOR, moves at half the speed and in the opposite direction of the head during the VOR, and at the same speed and in the same direction as the head during VOR suppression.

2. Methods

2.1. Observers

Horizontal eye and head movements and psychophysical responses were measured in five observers with normal or corrected-to-normal vision and with normal oculomotor control. The two observers who required refractive correction (S4 and S5) wore soft contact lenses. All observers gave informed consent before they participated, in compliance with the guidelines of the University of Houston Committee for the Protection of Human Subjects.

2.2. Apparatus and tasks

Horizontal whole-body rotation of the observer was achieved using a Tracoustics torsion-swing chair with a molded neck brace that held the observers' head firmly in position. The chair generated back-and-forth rotation with an averaged temporal frequency of 0.15 Hz and a peak-to-peak amplitude of 60° across observers. A chair-fixed Watson Angular Rate Sensor indicated the instantaneous angular velocity of the chair and the voltage measured across a rheostat indicated the rotational position of the chair. Horizontal eye position was monitored using an infrared limbal eye tracker (Applied Science Laboratories model 210 Eye Trac). All analogue signals were sampled at 1 kHz by a Scientific Solutions labmaster board and stored in a personal computer (PC) for later analysis. A green laser diode was reflected from a mirror galvanometer that was mounted above the observer's head and rotated along with the chair. The laser diode projected a 6′ horizontally moving test spot onto a cylindrical screen that also was attached to the observer's chair. The test spot was presented monocularly at a distance of 64 cm, with a luminance 3.5 log units above each observer's detection threshold. The duration of the test target on each trial was randomly 50, 100, 150, or 200 ms, for each of the four experimental conditions that are listed below. These durations are sufficiently brief that the presence of the target should have produced little or no disruption of the observers' ongoing eye movements. The PC controlled the presentation of the test spot and collected the signals of chair and eye movement, along with the observer's responses. Before and after each set of 40 trials, the observer fixated successively on five LEDs, spaced horizontally between ±10° to achieve calibration of the eye-position signals. Additional details about the experimental set up are provided in Bedell and Patel (2005) and in Tong et al. (2005).

2.2.1. Visually enhanced VOR (VVOR) condition

Prior to each trial, the chair was rotated away from its resting position in either the clockwise or anti-clockwise direction through a randomly chosen angle between 15° and 25°. The observer fixated on a physically stationary bright target, which was back projected onto the screen from an earth-fixed oscilloscope that was aligned with the resting position of the chair. Each presentation of the test spot was triggered to occur when the chair was within ±5° of its resting position. The test spot was presented 2° above the fixation target, and moved randomly to the left or right with a velocity between 5 and 80 deg/s. On each presentation, the trajectory of the moving test spot extended equally to the left and right of the fixation target.

2.2.2. Vestibulo-ocular response (VOR) condition

Observers were instructed to look straight ahead in a totally dark room during chair rotation. On each trial, the presentation of the test spot was triggered 80 ms after the onset of a VOR fast phase, identified using a velocity criterion from the eye-position signals that were sampled online

Table 1
Predicted extent of perceived motion smear during various eye and head movement conditions, compared to fixation

	Eye and head movement hypothesis		Gaze-movement hypothesis	
	V_{Target} & V_H same sign	V_{Target} & V_H opposite sign	V_{Target} & V_H same sign	V_{Target} & V_H opposite sign
VVOR	Reduction	Reduction	No reduction	No reduction
VOR	Reduction	Reduction	Reduction if VOR Gain > 1	Reduction if VOR Gain < 1
VOR Supp	No reduction	Reduction	No reduction	Reduction

(Bedell & Currie, 1993; Bedell & Patel, 2005). From trial to trial, the test target moved either to the left or right at a randomly selected velocity between 0 and 80 deg/s.

2.2.3. VOR suppression (VOR Supp) condition

Observers attempted to suppress their VOR eye movements by fixating on a continuously illuminated LED that was mounted on the chair-fixed screen during chair rotation. After a delay of 250–350 ms following the onset of chair rotation, the test spot was presented randomly in leftward or rightward motion, 2° above the fixation target. Otherwise, the presentations of the test spot were the same as in the VVOR condition.

2.2.4. Fixation condition

On each trial, the physically stationary observer fixated on a LED in the straight-ahead direction and triggered the presentation of the test spot. After a delay of 150–250 ms, the horizontally moving test spot appeared 2° above the fixation LED. From trial to trial, the spot's trajectory of motion was centered randomly directly above the fixation target or 5° to the left or right. Other aspects of each test spot presentation were the same as in the VVOR condition.

After each presentation, the chair was quickly brought to a stop and the observer matched the extent of perceived motion smear by adjusting the length of a bright horizontal line that was back projected onto the stationary screen, 2° below the fixation LED. For each observer, at least three blocks of 40 trials were run for each experimental condition. A schematic diagram of the presentation sequence and a typical eye movement recording for each condition are shown in Fig. 2.

2.3. Data analysis

The stored data for each trial were analyzed off-line to give the mean eye velocity, the mean chair velocity, the mean eye position with respect to the head, and the mean chair position in space for the duration of the test spot presentation. A trial was rejected if any of the following occurred: (a) the center of the moving test spot's trajectory was horizontally more than ±5° from the fovea in the VOR and VVOR conditions, (b) eye velocity was greater than 2 deg/s in the VOR suppression or fixation conditions, or (c) a saccade or blink occurred during the presentation of the test spot or within 50 ms of its onset or offset. For each accepted VVOR and VOR trial, the VOR gain was calculated as the ratio of average eye velocity to average chair (head) velocity during the interval that the test spot was presented. To foster comparison and combination of data for trials with different test-spot velocities, the matched extent of perceived motion smear was converted from units of visual angle to units of time (Bedell & Lott, 1996; Chen et al., 1995; Hogben & Di Lollo, 1985):

$$\text{Duration of perceived motion smear (s)} = \frac{\text{extent of matched smear (deg)}}{\text{retinal image velocity (deg/s)}}$$

To evaluate possible asymmetries in the extent of perceived motion smear, the trials in the VVOR, VOR and VOR suppression conditions were categorized as follows: the test target moved in the same direction as the observer's *head* movement on "Same" trials, and moved in the opposite direction as the observer's *head* movement on "Against" trials. (Note that this definition differs from our previous definition of "Same" and "Opposite" trials (Tong et al., 2005), in which the data were categorized according to the direction of the *retinal* image motion of the test target.) Statistical analysis was performed using a two-factor, repeated-measures analysis of variance (ANOVA; SuperANOVA program, Abacus Concepts, Berkeley, CA). The two factors included in this analysis were the eye movement condition, with seven levels (VVOR-Same, VVOR-Against, VOR-Same, VOR-Against, VOR Supp-Same, VOR Supp-Against, and fixation), and presentation duration, with four levels (50, 100, 150, and 200 ms). Statistical values were defined as significant when $P < 0.05$, after incorporating the Geisser-Greenhouse correction for departures from sphericity. In a separate repeated-measures analysis, the mean extent of

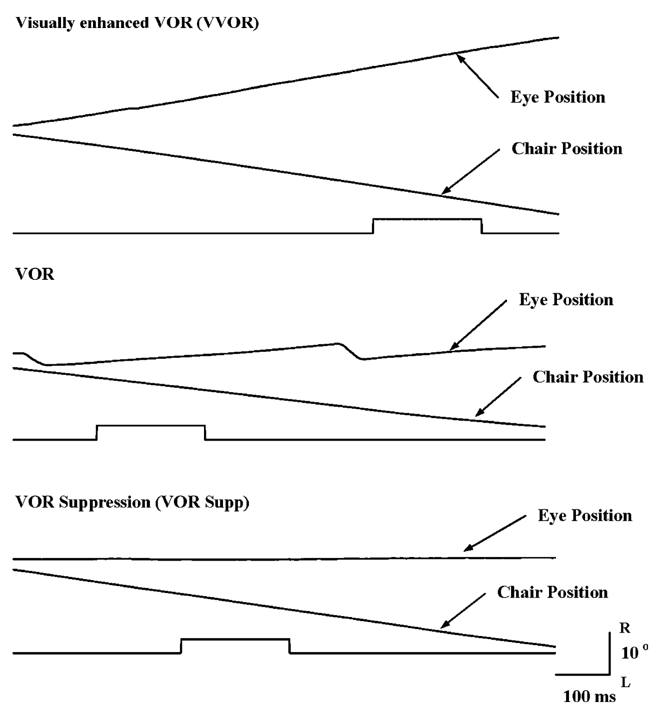

Fig. 2. Representative eye and head movement traces during the VVOR, VOR, and VOR Supp conditions. In the VVOR condition (top panel), the chair (middle trace) rotated from right to left at 21 deg/s, during which the observer maintained fixation on a physically stationary target (upper trace, $V_E = 20$ deg/s). The bottom trace indicates that the moving test target was presented to the observers (here, for 200 ms) when the chair rotated through its resting position. In the VOR condition (middle panel), the chair (middle trace) rotated from right to left at 14.5 deg/s, which induced a VOR eye movement (upper trace) with a rightward slow-phase velocity of 9 deg/s. The bottom trace indicates that the display of the moving target was triggered 70 ms after a leftward fast phase of the VOR. In the VOR suppression condition(bottom panel), the chair (middle trace) rotated from right to left at 18.8 deg/s, while the observer fixated a target that moved with the chair to keep the eye approximately stationary in the head (upper trace, $V_E \approx 0$ deg/s). The bottom trace indicates that the display of the moving test target was triggered 300 ms after the start of chair rotation. The calibration bars in the lower right corner indicate time and angular-position scales for all traces.

perceived smear in the fixation condition was compared for three visual-field locations (−5°, 0°, +5°) of the test spot at each presentation duration (Bedell & Patel, 2005).

3. Results

3.1. Perceived motion smear at different visual-field locations during fixation

Because of the variability in the horizontal eye position at the instant the test spot was triggered during VVOR (primarily because of variability in when the target was triggered) and VOR trials (primarily because of variability in the VOR gain), the data for these two conditions were analyzed only for those trials on which the trajectory of the test spot was centered within ±5° of the fovea (see above; also Bedell & Patel, 2005).[1] The appropriateness of this criterion was examined by comparing the extent of perceived motion smear for moving test spots with trajectories centered at −5°, 0°, and +5° in the visual field in the fixation condition. Fig. 3 shows the average extent of perceived motion smear for each visual-field location and test-spot duration. A repeated-measures ANOVA indicated that the target duration significantly affects the extent of perceived motion smear ($F_{[df=3,12]} = 68.04$, $P = .0002$) but that visual-field location exerts no significant effect within the tested range ($F_{[df=2,8]} = 0.29$, $P = 0.648$). No significant interaction occurs between the visual-field location and test-spot duration ($F_{[6,24]} = 0.37$, $P = 0.72$). Consequently, the data for these different visual-field locations in the fixation condition were pooled together for the subsequent analyses.

3.2. The extent of perceived motion smear during the VVOR, VOR, VOR suppression and fixation conditions

The extent of perceived motion smear on each trial in the VVOR, VOR and VOR suppression conditions was pooled separately according to whether the motion of the test target was in the "Same" or "Against" direction compared to the observer's head and body rotation. Fig. 4 illustrates the extent of perceived motion smear, averaged across observers, for the seven different test conditions as a function of the test-spot duration. The data of the individual observers are presented in Table 2. A repeated-measures ANOVA on the observers' average matches in each condition indicates a significant effect of target duration on the extent of perceived motion smear ($F_{[df=3,12]} = 69.06$, $P = 0.0002$). Although there is no significant main effect of the test condition ($F_{[df=6,24]} = 1.98$, $P = 0.185$), a

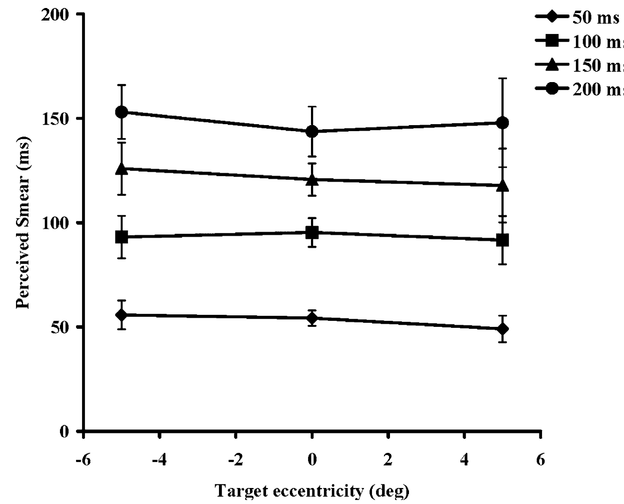

Fig. 3. The extent of perceived motion smear for targets of four durations, presented at different visual-field locations in the fixation condition. The trajectory of the moving test spot was centered at −5°, 0°, or +5° in the visual field. Each data point represents the average of five observers and the error bars represent ±1 SEM.

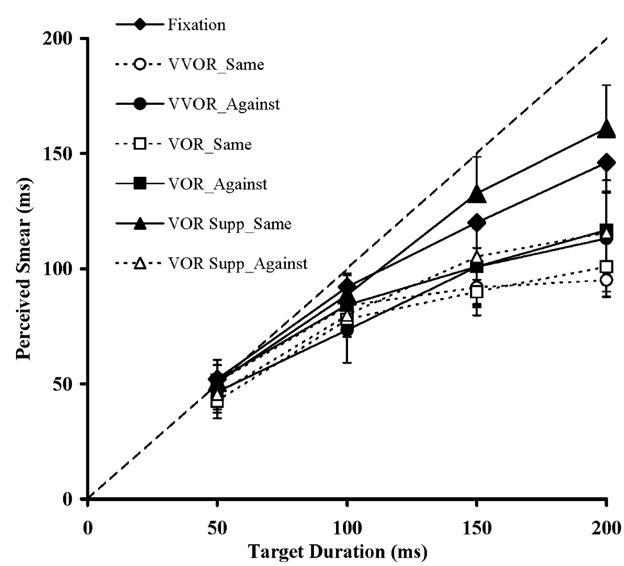

Fig. 4. The extent of perceived motion smear as a function of test-target duration during the VVOR, VOR, VOR suppression (VOR Supp), and fixation conditions. In the VVOR, VOR and VOR suppression conditions, the results are categorized according to whether the test target moved in the 'Same' direction or 'Against' the direction of the head movement. Each data point represents the average of five observers and the error bars represent ±1 SEM, across observers.

significant interaction exists between the test-spot duration and the test condition ($F_{[df=18,72]} = 3.81$, $P = .036$). This interaction indicates that the extent of perceived motion smear varies among the different test conditions, but only when the test target is of long duration.

Contrary to the gaze-movement hypothesis (Table 1), perceived motion smear is less for both directions of target motion during the VVOR condition, compared to Fixation

[1] This analysis ensured that the comparison of perceived smear in the different experimental conditions was for targets at similar retinal image locations. Because the function of the VOR and VVOR is to minimize retinal image motion across the entire retina (e.g., Angelaki, Zhou, & Wei, 2004; Robinson, 1977), extra-retinal eye and head movement signals would be expected to exert a similar influence on perceived motion smear for targets imaged at more peripheral retinal locations.

Table 2
Individual data for perceived motion smear during the Fixation, VVOR, VOR and VOR Supp conditions

	Fixation (ms)	VVOR same (ms)	VVOR Against (ms)	VOR same (ms)	VOR Against (ms)	VOR Supp same (ms)	VOR Supp Against (ms)
Duration 50 ms							
S1	35	51	18	41	33	42	34
S2	54	54	27	32	35	39	35
S3	64	56	60	42	54	67	60
S4	58	46	82	54	82	35	70
S5	49	48	46	43	54	35	30
	52 ± 5	51 ± 2	47 ± 11	42 ± 4	52 ± 9	51 ± 8	46 ± 8
Duration 100 ms							
S1	58	78	30	67	54	87	57
S2	100	71	55	72	57	84	71
S3	114	86	55	72	57	84	71
S4	91	77	100	74	126	108	99
S5	99	107	107	94	104	60	67
	92 ± 9	84 ± 6	74 ± 14	78 ± 5	84 ± 14	89 ± 9	80 ± 10
Duration 150 ms							
S1	77	94	36	75	43	85	64
S2	139	87	72	83	91	140	104
S3	138	68	107	102	113	141	135
S4	117	90	140	101	134	182	126
S5	128	121	148	90	130	116	97
	120 ± 11	92 ± 9	101 ± 21	90 ± 5	102 ± 17	113 ± 16	105 ± 12
Duration 200 ms							
S1	99	117	42	81	61	108	65
S2	161	96	83	75	100	141	103
S3	160	78	99	136	129	185	103
S4	139	81	176	110	160	217	137
S5	172	103	165	102	133	153	105
	146 ± 13	95 ± 7	113 ± 25	101 ± 11	117 ± 17	161 ± 19	116 ± 18

when the presentation duration is 150 ms or longer (Fig. 4, Table 3). Although the head and eyes moved in opposite directions with essentially the same average speed in the VVOR condition (average gain $= 1.03 \pm 0.25$, when the targets were presented for 200 ms), the variability in VVOR gain led to residual gaze movement on some of the trials. According to the *gaze-movement* hypothesis, these gaze-movements should have resulted in a directional decrease of perceived motion smear on some of the VVOR trials. However, when the VVOR results were categorized according to whether the gaze velocity was faster or slower than 2 deg/s, a repeated-measures ANOVA across observers indicated no significant difference in the extent of perceived motion smear ($F_{[1,4]} = 0.062$, $P = .82$). This analysis also showed no significant interaction between the category of gaze velocity and the test-target duration on perceived motion smear ($F_{[3,12]} = 1.07$, $P = .38$). In a final, follow-up analysis we included only the trials on which the velocity of gaze during the VVOR and during fixation was slower than 2 deg/s. Despite the similar low velocities of gaze in the two conditions, the mean extent of perceived smear was significantly smaller during the VVOR condition than during fixation, for a target duration of 200 ms (VVOR: 104 ± 13 ms, Fixation: 146 ± 13 ms; $F_{[1,4]} = 15.07$, $P = 0.02$).

In contrast to the VVOR condition, the average gain during the VOR condition was only 0.54 ± 0.34. This value of VOR gain is consistent with some previous reports (e.g., Herman, Maulucci, & Stuyck, 1982; Mizukoshi, Kobayashi, Ohashi, & Watanabe, 1983) and may be attributed in part to a temporal frequency of chair oscillation that is below the optimal range for stimulation of the semi-circu-

Table 3
Comparison between the extent of perceived motion smear during Fixation and during the VVOR, VOR and VOR Supp conditions, for target motion in the same direction and against the direction of head movement

	Target duration 50 ms	Target duration 100 ms	Target duration 150 ms	Target duration 200 ms
VVOR Same	$F_{[df=1,72]} = 0.01$, $P = 0.42$	$F_{[df=1,72]} = 1.27$, $P = 0.15$	$F_{[df=1,72]} = 13.30$, $P = 0.02^{*}$	$F_{[df=1,72]} = 45.12$, $P = 0.001^{*}$
VVOR Against	$F_{[df=1,72]} = 0.50$, $P = 0.21$	$F_{[df=1,72]} = 6.08$, $P = 0.053$	$F_{[df=1,72]} = 6.34$, $P = 0.015^{*}$	$F_{[df=1,72]} = 18.97$, $P = 0.011^{*}$
VOR Same	$F_{[df=1,72]} = 1.58$, $P = 0.14$	$F_{[df=1,72]} = 3.66$, $P = 0.08$	$F_{[df=1,72]} = 15.08$, $P = 0.017^{*}$	$F_{[df=1,72]} = 35.47$, $P = 0.003^{*}$
VOR Against	$F_{[df=1,72]} = 0.003$, $P = 0.50$	$F_{[df=1,72]} = 1.15$, $P = 0.15$	$F_{[df=1,72]} = 5.33$, $P = 0.02^{*}$	$F_{[df=1,72]} = 15.08$, $P = 0.017^{*}$
VOR Supp Same	$F_{[df=1,72]} = 0.02$, $P = 0.39$	$F_{[df=1,72]} = 0.24$, $P = 0.26$	$F_{[df=1,72]} = 2.90$, $P = 0.09$	$F_{[df=1,72]} = 3.67$, $P = 0.08$
VOR Supp Against	$F_{[df=1,72]} = 0.66$, $P = 0.19$	$F_{[df=1,72]} = 2.64$, $P = 0.10$	$F_{[df=1,72]} = 3.67$, $P = 0.08$	$F_{[df=1,72]} = 15.91$, $P = 0.015^{*}$

* Statistically significant.

lar canals (Leigh & Zee, 1991). Because the VOR gain was less than 1.0, in the VOR-Same condition the test target moved in the same direction as both the observers' gaze and head movement and, according to the *gaze-movement* hypothesis, no reduction of perceived motion smear would be expected (also see Table 1). However, Fig. 4 and Table 2 show that the extent of perceived smear is attenuated in both the VOR-same and VOR-against conditions, if the duration of the target is 150 ms or longer. The results therefore demonstrate a bi-directional attenuation of perceived motion smear during the VVOR and VOR when compared to the fixation condition, in agreement with the predictions of the eye-and-head movement hypothesis (Table 1).

In agreement with the results of our previous investigation (Tong et al., 2005), during VOR suppression the extent of perceived motion smear is similar to that during Fixation, when the test spot moves in the same direction as the eye and head movement. In contrast, the extent of perceived motion smear in the VOR-suppression Against condition is significantly less than in the Fixation condition, when the test-spot duration is 200 ms (Table 3).

3.3. Perceived motion smear in the same and against conditions during head and eye movements

In contrast to the VOR-suppression condition, in which the eyes essentially do not move with respect to the head, the eyes and head move in opposite directions during the VVOR and VOR conditions. The finding that perceived motion smear is reduced during the VVOR and VOR conditions compared to Fixation, for target motion in both the "Same" and "Against" directions, indicates that ERSs for both head and eye movements contribute to the reduction of perceived motion smear. However, a post-hoc analysis showed that the mean extent of perceived motion smear is significantly less in the "Same" VVOR and VOR conditions than in the "Against" VVOR and VOR conditions, for a target duration of 200 ms ($F_{[df=1,72]} = 9.83$, $P = .031$). Recall that in the "Same" VVOR and VOR conditions, the target moves against the direction of eye movement. Consequently, only the ERS associated with the observers' eye movements should be involved in reducing the extent of perceived motion smear. Similarly, in the "Against" VVOR and VOR conditions, the target moves against the direction of head movement and only the ERS associated with head movement should be involved in reducing perceived smear. The smaller extent of perceived smear in the "Same" compared to the "Against" VVOR/VOR conditions therefore suggests a greater efficiency of the ERS for eye than head movement in attenuating the extent of perceived motion smear.

Further evidence for a differential contribution of the ERSs for eye and head movement to the attenuation of perceived motion smear is presented in Figs. 5 and 6, which plot the extent of perceived smear on all 200-ms duration trials in the VVOR and VOR conditions as a function of the observers' eye and head velocities. These data show that the extent of perceived motion smear decreases systematically as the observers' eye velocity increases, in both the VVOR-Same (Fig. 5B, $r = -0.471$, $P < 0.001$) and VOR-same (Fig. 6B, $r = -0.253$, $P = 0.012$) conditions. In contrast, even though the observers' mean estimates of perceived smear are smaller than in the Fixation condition, the trial-by-trial estimates show no relationship with head velocity in the VVOR-Against condition (Fig. 5A, $r = 0.083$, $P = 0.32$) and a weaker relationship in the VOR-Against condition (Fig. 6A, $r = -0.222$, $P = .022$). These differences between the extent of perceived smear in the same and against directions remained apparent in the VVOR and VOR conditions when the results of the individual observers were analyzed separately.

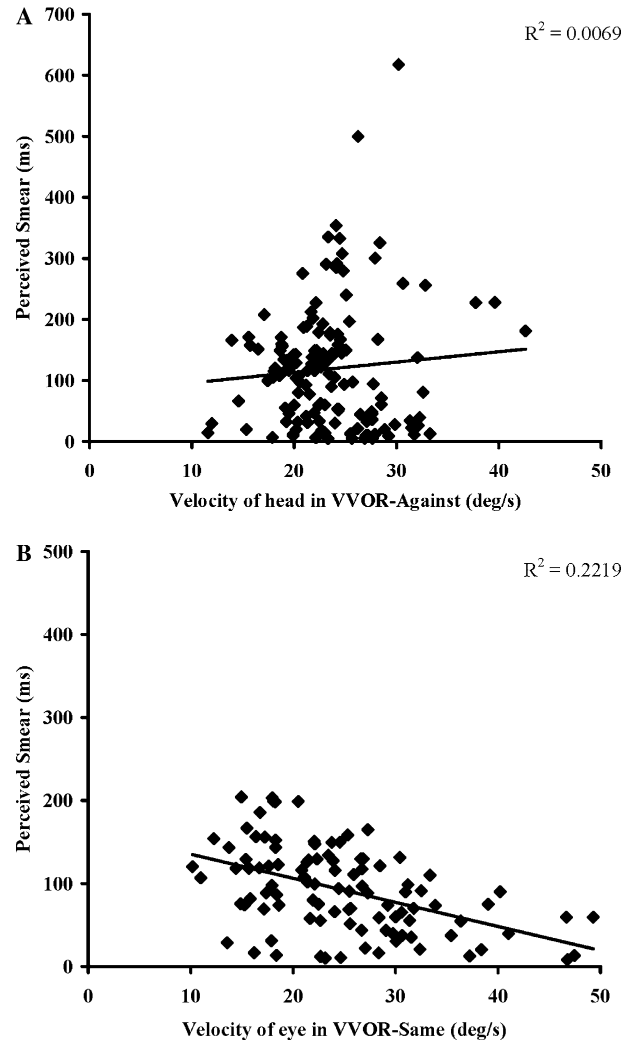

Fig. 5. (A) The extent of perceived smear as a function of the observers' head velocity, on individual 'Against' motion trials in the VVOR condition. (B) The extent of perceived smear as a function of the observers' eye velocity, on individual 'Same' motion trials in the VVOR condition. Note that in the 'Same' motion trials, the eye velocity is against the direction of target motion. Only the data for a target duration of 200 ms are presented.

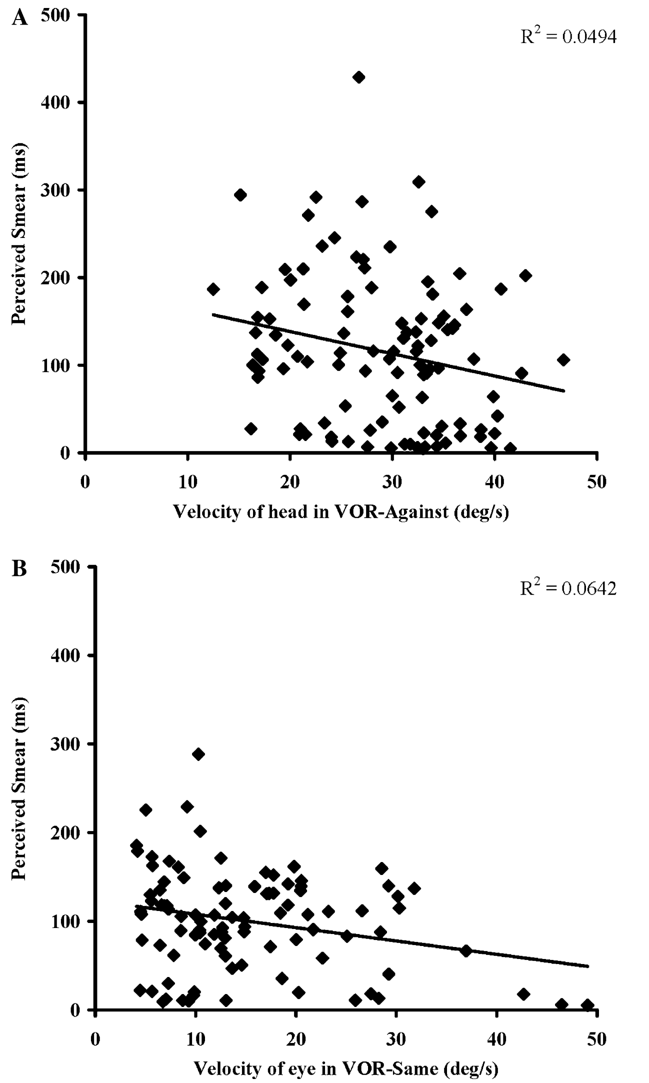

Fig. 6. (A) The extent of perceived smear as a function of the observers' head velocity, on individual 'Against' motion trials in the VOR condition. (B) The extent of perceived smear is shown as a function of the observers' eye velocity, on individual 'Same' motion trials in the VOR condition. As in VVOR condition, in the 'Same' motion trials of the VOR condition, the eye velocity is against the direction of target motion. Only the data for a target duration of 200 ms are presented.

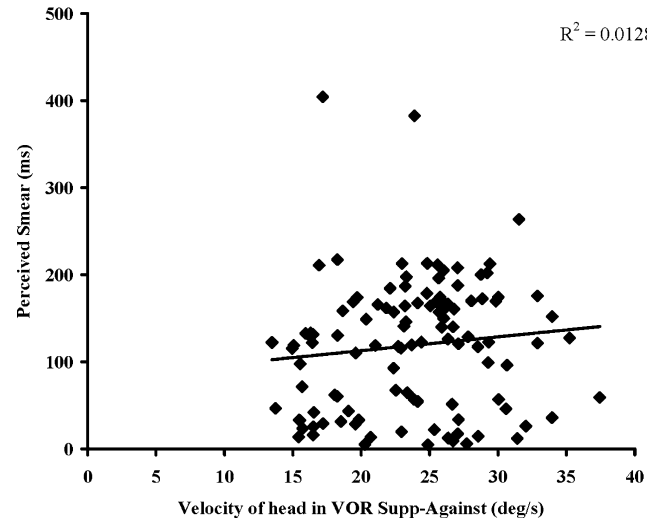

Fig. 7. The extent of perceived smear as a function of the observers' head velocity, on individual 'Against' motion trials in the VOR suppression (VOR Supp) condition. Only the data for a target duration of 200 ms are presented.

The *eye-and-head-movement* hypothesis predicts that the ERS associated with head movement is responsible for the attenuation of perceived motion smear in the VOR-suppression condition, because little or no eye movement occurs with respect to the head. In accordance with this prediction, statistical analysis reveals no significant differences between the attenuation of perceived motion smear in the VVOR, VOR and VOR-suppression "Against" conditions ($F_{[df=2,8]} = 0.133$, $P = 0.75$). Further, as shown in Fig. 7, the trial-by-trial estimates of perceived motion smear have no significant relationship with the velocity of head movement in the VOR-suppression "Against" condition ($r = 0.11$, $P = 0.23$), in agreement with the results shown for the VVOR and VOR "Against" conditions in Figs. 5A and 6A. The observed dependency of perceived motion smear on eye velocity in the VOR and VVOR conditions, but not on head velocity in the VOR, VVOR, and VOR-suppression conditions suggests that different neural strategies are used to apply the ERSs associated with eye vs. head movements.

4. Discussion

A number of previous investigations demonstrated that the extent of perceived motion smear is greater for motion of the retinal image that occurs during fixation than during an eye and/or head movement, if the duration of the target exceeds approximately 100 ms (Bedell & Lott, 1996; Bedell & Patel, 2005; Bedell & Yang, 2001; Bedell et al., 2004; Chen et al., 1995; Tong et al., 2005). In agreement with these previous studies, the present experiments show that the extent of perceived smear during fixation and during eye and/or head movements diverges systematically up to a target duration of at least 200 ms.

Recently, we reported that the extent of perceived motion smear is reduced asymmetrically for long-duration targets during either smooth pursuit or VOR suppression (Tong et al., 2005). The reduction of perceived smear, compared to when analogous motion of the retinal image occurs during steady fixation, is attributed to the action of ERSs associated with eye and/or head movements. Our interpretation of the observed asymmetry is that ERSs attenuate perceived motion smear primarily for targets that move in the opposite direction of an eye or head movement, such that the motion of the retinal image is consistent *in direction* with that produced by a stationary object in space.

A goal of this study was to determine whether the ERSs that attenuate perceived motion smear are associated specifically with eye or head movements, or if the relevant

ERS is related to gaze movement. The *gaze-movement* hypothesis can account for the reported attenuation of perceived smear during various voluntary eye movements (Bedell & Lott, 1996; Bedell & Yang, 2001; Bedell et al., 2004), but it is inconsistent with the bi-directional reduction of perceived smear that we observed for targets presented in the VVOR and VOR conditions of this study. In particular, even though the direction of gaze is nearly stationary in both the VVOR and fixation conditions, our results indicate that the extent of perceived smear is less during the VVOR for targets that move in either the "Same" direction or "Against" the direction of head movement. In the VOR condition, the predictions of the gaze-movement hypothesis depend on the VOR gain. However, according to this hypothesis, smear reduction should occur only for one direction of target motion and not the other. The observed bi-directional reduction of perceived smear in the VOR condition is therefore inconsistent with the gaze-movement hypothesis. On the other hand, a bi-directional reduction of perceived smear in both the VVOR and VOR conditions is consistent with the *eye-and-head-movement* hypothesis, because opposite head-in-space and eye-in-head movements (if VOR gain >0) occur in both of these conditions.

The attenuation of perceived smear in the VVOR and VOR "Same" conditions, in which the target moves in the same direction as the movement of the head, varies according to the velocity of eye movement in the head. Previously, Bedell and Lott (1996) failed to find a significant change in the duration of perceived motion smear, when the velocity of a pursuit target increased from 4 to 12 deg/s. The absence of a significant relationship between the attenuation of perceived smear and eye velocity during pursuit may have resulted from the slower and more limited range of eye velocities that they investigated, compared to the range of eye velocities examined in the VVOR and VOR conditions of this study. Tong et al. (2005) measured the extent of perceived smear during pursuit, for eye velocities that ranged from 5 to 36 deg/s. Fig. 8 plots the extent of perceived smear as a function of the eye movement velocity on individual trials from this previous study, for a target duration of 200 ms. Despite substantial scatter, the extent of perceived motion smear decreases as the velocity of eye movement increases [$r = -0.17$, $P = 0.02$]. Consequently, the results obtained during single voluntary (smooth pursuit) and involuntary (VOR) eye movements, as well as during the interaction between voluntary and involuntary (VVOR) movements all show an attenuation of perceived smear that increases with eye velocity, for targets that move in the opposite direction of the eye movement. Based on the similarity of the results in these conditions, we suggest that the extra-retinal eye movement signals that contribute to the reduction of perceived motion smear arise at a relatively low neural level, after the eye velocity signals for voluntary and involuntary eye movements are combined.

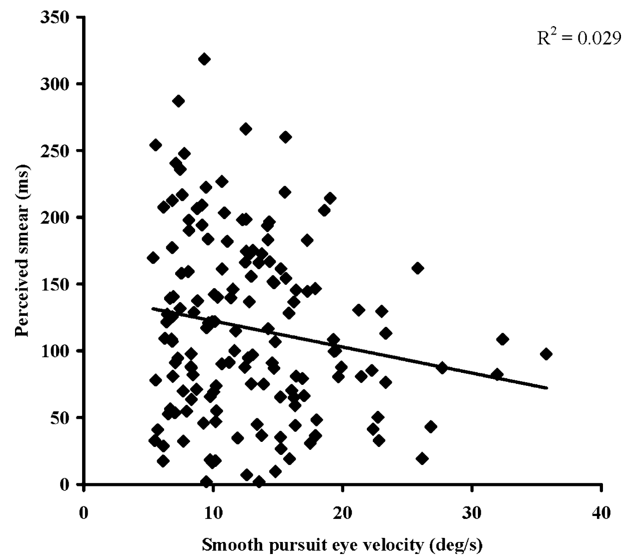

Fig. 8. The extent of perceived smear as a function of eye velocity on individual trials, when the test target moved against the direction of pursuit eye movement. Data are for a target duration of 200 ms, from Tong et al. (2005).

The reduced extent of perceived motion smear for targets that move *against* the direction of head movement in the VVOR and VOR conditions provides evidence that ERSs for head movement also play a role in maintaining the clarity of visual perception. Compared to the relationship between the extent of perceived smear and eye velocity in the "Same" direction-of-motion conditions, the attenuation of perceived smear in the "Against" conditions is related less obviously to the velocity of head movement, at least within the range between approximately 12 and 45 deg/s. The reduction of perceived motion smear in the VOR-suppression "Against" condition, which is similar to that observed in the VOR and VVOR "Against" conditions, also fails to show a relationship with head velocity. In addition, when the velocities of eye and head movement are comparable, the extent of perceived smear in the VVOR and VOR conditions is slightly but significantly less for long-duration targets in the "Same" compared to the "Against" conditions. Previously, Tong et al. (2005) reported a smaller mean extent of perceived smear during pursuit than in the VOR suppression-against condition (96 ± 17 ms vs. 114 ± 12 ms, for a 200 ms target duration), even though the velocities of pursuit eye movements were much lower than the velocities of head movement. These observations indicate that the ERSs associated with eye movements are more effective in reducing the extent of perceived motion smear than the ERSs associated with head movements, and suggest that distinct neural mechanisms are responsible for these two types of ERSs.

As indicated in our previous study (Tong et al., 2005), the extent of perceived smear is reduced primarily when the motion of the target with respect to the eyes is against the direction of a voluntary eye movement. This asymmetric reduction of perceived smear represents a useful strategy for maintaining relatively clear vision during voluntary eye movements, such as pursuit and saccades, when perceived smear would be expected to result from the relative motion between the eyes and physically stationary objects in the background. On the other hand, relative motion of a target in the same direction as a voluntary eye movement indicates that the target is moving physically in the world. Because motion smear can facilitate the detection and discrimination of target motion (Burr & Ross, 2002; Geisler, 1999; Tong, Aydin, & Bedell, in press), it would be counterproductive for ERSs to attenuate smear perception in this situation.

The relative motion of a target in the direction opposite a head movement also is consistent with a target that is stationary in space, and it is reasonable to anticipate that the extent of perceived smear would be attenuated. Conversely, because a target that moves in the same direction as a head movement *during VOR suppression* must be moving physically, no attenuation of perceived smear would be expected. Both our previous (Tong et al., 2005) and present results during VOR suppression are consistent with these expectations.

When we move in daily life, a combination of head and eye movements typically minimize the retinal image motion produced by physically stationary objects. However, the VOR gain required to eliminate the retinal image motion for a physically stationary object varies systematically with the viewing distance (Bigeur & Prablanc, 1981; Hine & Thorn, 1987; Jones, 1985). Specifically, in order to eliminate motion of the retinal image, the VOR gain needs to be higher when viewing at near, compared to at distance. Just such a modulation of VOR gain according to the viewing distance has been reported (Bigeur & Prablanc, 1981; Clement & Maciel, 2004; Jones, 1985). When the VOR gain increases appropriately for near viewing, physically stationary targets at greater distances will undergo relative motion in the same direction as the head movement. Similarly, when the VOR gain is appropriate for viewing at distance, then physically stationary objects at near will undergo relative motion in the direction opposite the head movement. Because human observers shift gaze frequently between distance and near, an attenuation of perceived smear for target motion in *both* directions represents a simple strategy by which the brain can maintain visual clarity for physically stationary objects at all viewing distances when the eyes and the head move in opposite directions.

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References

Angelaki, D. E., Zhou, H. H., & Wei, M. (2004). Foveal versus full-field stabilization strategies for translational and rotational head movements. *Journal of Neuroscience, 23*, 1104–1108.

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

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., & Patel, S. S. (2005). Attenuation of perceived motion smear during the vestibulo-ocular reflex. *Vision Research, 45*, 2191–2200.

Bedell, H. E., & Yang, J. (2001). The attenuation of perceived image smear during saccades. *Vision Research, 41*, 521–528.

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.

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

Bigeur, B., & Prablanc, C. (1981). Modulation of the vestibule-ocular reflex in eye-head orientation as a function of target distance in man. In A. F. Fuchs & W. Becker (Eds.), *Progress in oculomotor research: Proceedings of the International Conference on Oculomotor Research* (pp. 525–530). New York: Elsevier/North Holland.

Blouin, J., Vercher, J. L., Gauthier, G. M., Paillard, J., Bard, C., & Lamarre, Y. (1995). Perception of passive whole-body rotations in the absence of neck and body proprioception. *Journal of Neurophysiology, 74*, 2216–2219.

Burr, D. C. (1980). Motion smear. *Nature, 284*, 164–165.

Burr, D. C., & Ross, J. (2002). Direct evidence that "speedlines" influence motion mechanisms. *Journal of Neuroscience, 22*, 8661–8664.

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.

Clement, G., & Maciel, F. (2004). Adjustment of the vestibulo-ocular reflex gain as a function of perceived target distance in humans. *Neuroscience Letters, 366*, 115–119.

Coltheart, M. (1980). Iconic memory and visible persistence. *Perception & Psychophysics, 27*, 183–228.

Di Lollo, V., & Hogben, J. H. (1987). Suppression of visible persistence as a function of spatial separation between inducing stimuli. *Perception & Psychophysics, 41*, 345–354.

Fukushima, K., Sato, T., Fukushima, J., Shinmei, Y., & Kaneko, C. R. (2000). Activity of smooth pursuit-related neurons in the monkey periarcuate cortex during pursuit and passive whole-body rotation. *Journal of Neurophysiology, 83*, 563–587.

Geisler, W. S. (1999). Motion streaks provide a spatial code for motion direction. *Nature, 400*, 65–69.

Herman, R., Maulucci, R., & Stuyck, J. (1982). Development and plasticity of visual and vestibular generated eye movements. *Experimental Brain Research, 47*, 69–78.

Hine, T., & Thorn, F. (1987). Compensatory eye movements during active head rotation for near targets: effects of imagination, rapid head oscillation and vergence. *Vision Research, 27*, 1639–1657.

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

Johnston, J. L., & Sharpe, J. A. (1994). The initial vestibulo-ocular reflex and its visual enhancement and cancellation in humans. *Experimental Brain Research, 99*, 302–308.

Jones, G. M. (1985). Adaptive modulation of VOR parameters by vision. *Reviews of Oculomotor Research, 1*, 21–50.

Leigh, R. J., & Zee, D. S. (1991). The vestibular–optokinetic system. In R. J. Leigh & D. S. Zee (Eds.), *The neurology of eye movements* (2nd ed., pp. 15–58). Philadelphia: F.A. Davis Company.

Leigh, R. J., Huebner, W. P., & Gordon, J. L. (1994). Supplementation of the human vestibulo-ocular reflex by visual fixation and smooth pursuit. *Journal of Vestibular Research, 4*, 347–353.

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

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.

Mizukoshi, K., Kobayashi, H., Ohashi, N., & Watanabe, Y. (1983). Quantitative analysis of the human visual vestibulo-ocular reflex in sinusoidal rotation. *Acta oto-laryngologica. Supplementum, 393*, 58–64.

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.

Robinson, D. A. (1977). Vestibular and optokinetic symbiosis: an example of explaining by modelling. In R. Baker & A. Berthoz (Eds.), *Control of gaze by brainstem neurons* (pp. 49–58). New York: Elsevier.

Shinmei, Y., Yamanobe, T., Fukushima, J., & Fukushima, K. (2002). Purkinje cells of the cerebellar dorsal vermis: simple-spike activity during pursuit and passive whole-body rotation. *Journal of Neurophysiology, 87*, 1836–1849.

Tong, J. L., Aydin, M., & Bedell, H. E. (in press). Direction-of-motion discrimination is facilitated by visible motion smear. *Perception & Psychophysics*.

Tong, J. L., 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*, 1519–1524.