Journal of Vision (2008) 8(14):7, 1–6 http://journalofvision.org/8/14/7/

Signals of eye-muscle proprioception modulate perceived motion smear

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Achieving clear perception during eye movements is one of the major challenges that the human visual system has to face every day. Like most light sensitive mechanisms, the human visual system has a finite integration time that may cause moving images to appear smeared. By comparing the perceived motion smear during ongoing eye movements and fixation, previous studies indicated that smear is reduced by a neural compensation mechanism that uses "extra-retinal information" about eye movements. However, it is not clear whether eye-muscle proprioception (afferent input), internal copies of efferent oculomotor commands (efference copy), or both contribute to the smear reduction. The present study found that similar reductions of perceived motion smear occur during passive eye movement (which is signaled only by eye-muscle proprioception) and during active pursuit tracking (for which efference copy signals exist as well). These results reveal a novel neural contribution for maintaining visual clarity and stand in contrast to previous reports that eye-muscle proprioception makes only a minor contribution to visual perception.

Keywords: motion smear, proprioception, eye muscle, eye movement, extra-retinal signal

Citation: Tong, J., Stevenson, S. B., & Bedell, H. E. (2008). Signals of eye-muscle proprioception modulate perceived motion smear. *Journal of Vision, 8*(14):7, 1–6, http://journalofvision.org/8/14/7/, doi:10.1167/8.14.7.

Introduction

The human visual system, like most light sensitive mechanisms, has a finite integration time that may cause moving images to appear smeared to some degree. Evidence suggests that neural processes compensate partially for this smear, effectively "deblurring" the moving image (Bedell & Lott, 1996; Burr, 1980; Chen, Bedell, & Oğmen, 1995). The compensation for motion smear is context dependent, depending on the degree to which the image smear is produced by motion in the world or an eye/head movement (Bedell, Chung, & Patel, 2004; Bedell & Lott, 1996; Bedell & Patel, 2005; Bedell & Yang, 2001; Tong, Aydin, & Bedell, 2007; Tong, Patel, & Bedell, 2006). This deblurring mechanism depends on information about the eye (or head) movement itself, referred to generally as "extra-retinal information." Extra-retinal eye-movement information is available from two sources: eye-muscle proprioception (Sherrington, 1918) and internal copies of efferent oculomotor commands (Von Holst & Mittelstädt, 1971). Studies of visual perception with a steady eye in sparse visual surroundings using target localization, size- or depth-judgment tasks, suggest that the contribution of eye-muscle proprioception is either small or negligible compared with efference copy signals (Bridgeman & Stark, 1991; Gauthier, Nommay, & Vercher, 1990; Gauthier, Vercher, & Zee, 1994; Niechwiej-Szwedo et al., 2007). Based on these results, it has been suggested that proprioception has the rather limited role of providing long-term calibration of the efference copy information about eye position (Lewis, Zee, Hayman, & Tamargo, 2001; Steinbach, 1987). In the study described here, we investigated the relative contribution of these two sources of extra-retinal information to the reduction of perceived motion smear during eye movement. Similar reductions of perceived motion smear occur during passive eye movement (which is signaled only by eye-muscle proprioception) and during active pursuit tracking (for which efference copy signals exist as well), indicating an important contribution from proprioception.

Methods

Participants and experimental design

Observers with normal or corrected-to-normal vision and normal ocular motility participated. Experimental

doi: 10.1167/8.14.7 Received January 11, 2008; published October 23, 2008 ISSN 1534-7362 © ARVO

protocols were reviewed by the University of Houston Committee for the Protection of Human Subjects and written informed consent was obtained from each subject. In the first experiment, smooth passive eye movements were generated in darkness by pushing on a smooth circular wire loop (diameter = 20 mm) that rested against the upper and lower left eyelids. The loop was made of standard steel wire of 0.85-mm diameter. The observers held a handle that extended from one side of the loop and pushed it from the temporal side of the left eye, generating left-to-right eye rotations. A laser spot was presented for 150 ms at a viewing distance of 185 cm during each passive movement. Horizontal rotation of a mirror in the stimulus-deflection system of a Generation 5 SRI dual-Purkinje tracker (Crane & Steele, 1985) moved the laser spot in space at a randomly chosen speed between 20 deg/s in the opposite direction of the eye push and 40 deg/s in the direction of the passive eye movement on each trial. The resulting distributions of retinal image speeds were similar for the two directions of laser-spot motion. After each presentation, the observer adjusted the separation between two continuously visible, horizontally separated bright spots to match the extent of the perceived motion smear. For comparison, matches were obtained also when left or right motion of the laser spot (range = ±30 deg/s) occurred while the observers looked straight-ahead in darkness, without generating passive eye movements.

Horizontal and vertical eye positions were recorded at 120 Hz using a Generation 5 SRI dual-Purkinje tracker. This eye tracker compares the locations of the first and fourth Purkinje images, thereby minimizing the influence of any eye translation that may accompany an eye push. Visual input to the right eye was blocked by placing an occluder in that eye's optical path. A representative recording of eye position is shown in Figure 1.

In the second experiment, observers matched the extent of perceived motion smear after each 150-ms presentation of a bright moving spot, presented during rightward smooth pursuit. The experimental setup was described in a previous publication (Tong et al., 2007). In a totally dark room, the observers tracked a bright dot that moved from left to right for 1 s at a speed of 8 deg/s. A bright test spot was displayed for 150 ms, after a 400- to 450-ms delay from motion onset. The test spot moved across the visual field at 8 deg/s *relative* to the pursuit target, either leftward or rightward. For comparison, perceived smear was assessed also during steady fixation for test spots that produced similar velocities of retinal image motion. During both the pursuit and fixation trials, the bright spot (2 log units above its detection threshold) moved along a trajectory that was horizontally symmetrical with respect to the pursuit or fixation target and vertically 0.5 deg above it. In this experiment, observers adjusted the length of a bright horizontal line to match the extent of perceived motion smear after each trial.

Prior to the two main experiments, observers first performed a control experiment (Sogo & Osaka, 2002) to verify the accuracy of eye tracker recordings during passive eye rotation. While the observer made a smooth passive eye movement from left to right in the dark, a bright laser spot was flashed twice in the same spatial location for 8 ms per flash with a 150-ms interval between flashes. After each trial, the observer adjusted the separation between two spots to match the perceived distance between the two flashes. For the 4 observers whose results are presented below, the angular eye rotations determined from the SRI dual Purkinje image eye tracker well matched the perceived separation of the two flashes with a ratio between 1.08 ± 0.07 and 1.1 ± 0.13 (*SE*). Three other subjects were excluded from the study because their matches deviated by more than 10% (range = 23–130%) of the change in retinal image location that was predicted from the eye-tracker recordings.

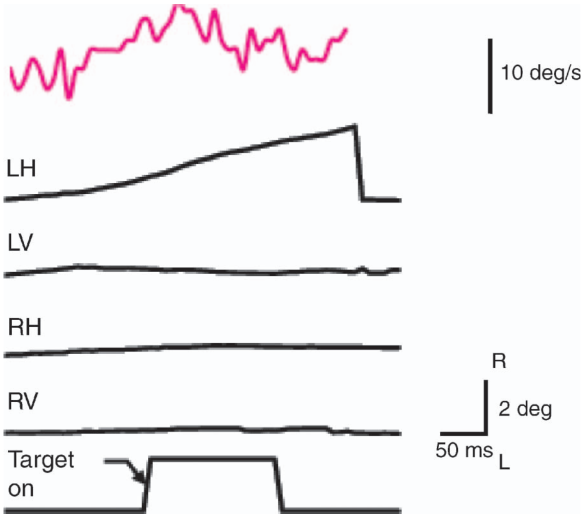

Figure 1. The horizontal (H) and vertical (V) positions of both eyes (L and R) on one trial in the passive-eye-movement experiment for the observer who exhibited the biggest difference in perceived smear between passive-eye-movement and eye-still trials. The red trace at the top represents the horizontal velocity of the left eye. The timing of the laser target is shown in the bottom trace. Note that only the left eye moves during the eye push, indicating that efferent oculomotor commands do not contribute to the observed horizontal motion of the left eye.

Data analyses

The extent of perceived motion smear was converted from units of visual angle to a duration in ms by dividing the length of smear (deg) by the retinal image speed (deg/ms). In the first experiment, an eye-push trial was rejected if any of following happened: (1) the horizontal speed of the left eye was below 3 deg/s; (2) the vertical speed of the left eye was more than 2 deg/s; (3) the duration of the passive eye movement did not extend throughout the duration of stimulus presentation; or (4) the eye-tracking signal was lost before or during the stimulus presentation. In the second experiment, a pursuit trial was rejected if either of the following occurred: (1) pursuit gain was lower than 0.8 or higher than 1.2, or (2) a saccade or blink occurred during the presentation of the test spot or within 50 ms of its onset or offset. On average, approximately 77% and 49% of eye-movement trials were rejected in the first and second experiments, respectively.

Results

Analysis indicated that, for each observer, the occluded right eye remained essentially stable while the left eye was moved passively (see Figure 1). The average horizontal velocities of the right eye ranged from 0.34 ± 0.13 deg/s to 0.94 ± 0.26 deg/s for three of the observers. Because of mechanical interference between the two channels of the SRI Eyetracker, the interpupillary distance of the fourth observer was too small to obtain reliable eye recordings of both eyes simultaneously.

Previous studies indicated that the neural compensation for motion smear is asymmetrical, occurring preferentially for relative motion of the target in the opposite direction of eye movement (Tong et al., 2006, 2007). As discussed in these papers, we interpret this asymmetrical compensation to reflect a preference by the visual system to perceive targets as clear only if the targets are interpreted as potentially stationary in the world. Here, we determined the extent of perceived motion smear for three conditions:

1. when the laser target moved *with* the direction of eye push,
2. when the laser target moved *against* the direction of eye push, and
3. during motion of the target with no eye push.

The results show a significant difference among these conditions (see Figure 2A; repeated-measures ANOVA: $F_{[2,6]} = 9.54$, $p = 0.025$). Specifically, the duration of perceived motion smear is approximately 40 ms less when the spot moves *against* compared to *with* the direction of passive eye movement ($F_{[1,6]} = 15.32$, $p = 0.015$) or compared to when the eye remains stationary ($F_{[1,6]} = 13.24$, $p = 0.019$). In contrast, when the laser spot moves *with* the direction of passive eye movement, the extent of perceived motion smear is similar to that during no eye push ($F_{[1,6]} = 0.076$, $p = 0.73$). The selective reduction of perceived smear during *against* motion is not attributable to an effect of the laser spot on the observers' passive eye movements, as paired t tests indicate no significant difference in passive eye velocity according to the direction of laser-spot motion (range of p values across observers = 0.08–0.97). The scatter plots of the data of the four individual observers in Figure 2B indicate that the extent of perceived smear decreases with increasing eye velocity when the target moves against the direction of eye movement, which is consistent with previous studies (Tong et al., 2006, 2007).

In the second experiment, the same observers reported the extent of perceived motion smear during smooth pursuit and fixation. In agreement with previous studies (Tong et al., 2006, 2007), Figure 3A indicates that the extent of perceived motion smear is significantly smaller

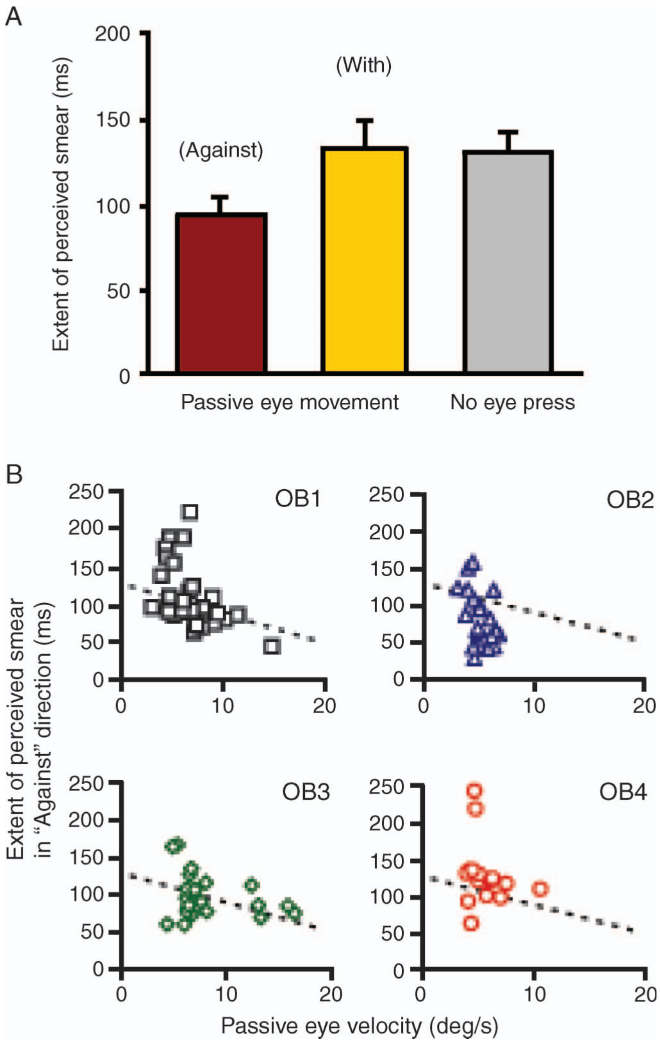

Figure 2. Results of the passive-eye-movement experiment. (A) The extent of perceived motion smear is categorized according to whether the test target moved in the opposite ("Against" condition) or the same direction ("With" condition) as the passive eye movement or moved while the eyes remained still in the dark. Each bar represents the average of four observers and the error bars represent 1 *SEM*, across observers. (B) The extent of perceived smear as a function of the observers' passive eye velocity, on individual "Against" motion trials. Each observer's data are presented in a different panel. The same dashed line appears in each panel and represents the regression line fit to the aggregate data of all the observers ($y = -3.99x + 129.26$; $r^2 = 0.064$).

when the target moves *against* the direction of an ongoing pursuit eye movement compared with when the target moves in the same direction as pursuit ($F_{[1,6]} = 8.35$, $p = 0.036$) or during fixation ($F_{[1,6]} = 10.62$, $p = 0.024$). Figure 3B shows that the relationship between the eye speed during pursuit and the extent of perceived smear is qualitatively similar to that shown during passive eye movement in Figure 2B. Although the slopes fit to the four observers' aggregate data differ by a factor of 2.5 in the first and second experiments (Figures 2B and 3B), a linear regression analysis using a dummy variable showed no significant difference between the results ($t_{[df=161]} = 1.09$, $p = 0.28$).[1] Further, the slopes of the lines fit to the two data sets are closer quantitatively (slope during passive eye movement = -6.39; slope during pursuit = -10.32; $t_{[df=97]} = 0.39$, $p = 0.70$) if the eye velocities in the passive eye-movement condition are restricted to be in the same range as those sampled during pursuit.

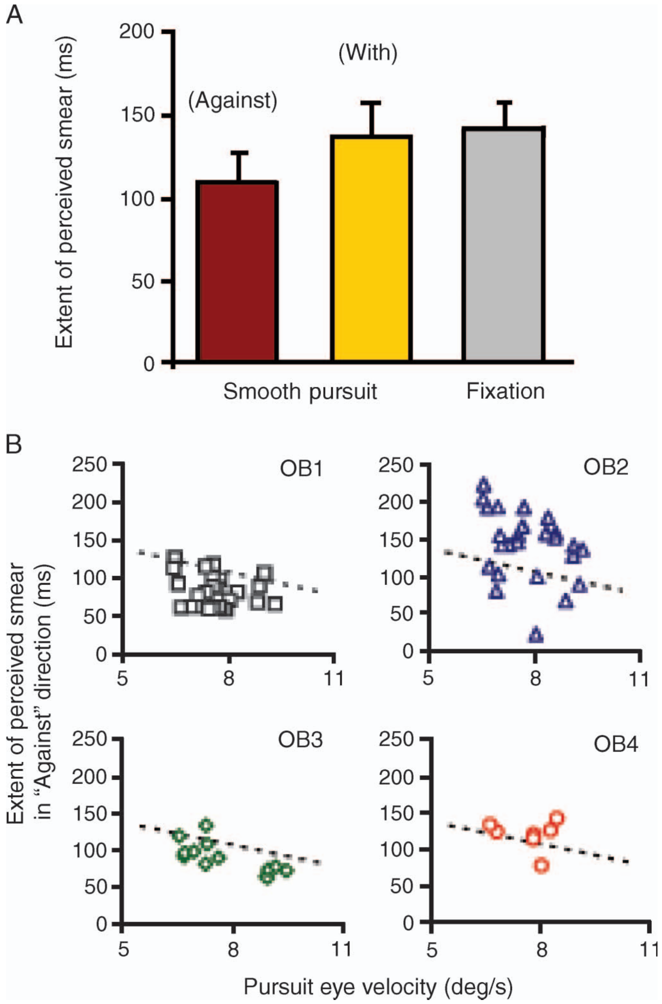

Figure 3. Results of the smooth pursuit experiment. (A) The extent of perceived motion smear is categorized according to whether the test target moved in the opposite ("Against" condition), or the same direction ("With" condition) as the smooth-pursuit eye movement, or moved during steady fixation. Each bar represents the average of four observers and the error bars represent 1 *SEM*, across observers. (B) The extent of perceived smear as a function of the observers' pursuit eye velocity, on individual "Against" motion trials. Each observer's data are presented in a different panel. The same dashed line appears in each panel and represents the regression line fit to the aggregate values of perceived motion smear as a function of pursuit eye velocity for all of the observers ($y = -10.32x + 189.80$; $r^2 = 0.044$). Note that Figures 2B and 3B have different horizontal scales.

The extent of perceived motion smear in the "no-eye-push" condition in the first experiment is similar to that in the "fixation" condition in the second experiment ($t_{[df=3]} = 0.68$, $p = 0.54$). The similarity of these results indicates that the characteristics of the matching stimuli used in the two experiments (two separated dots in Experiment 1 vs. a line in Experiment 2) have no significant impact on the results. We therefore compared the efficacy of extra-retinal signals in reducing perceived motion smear in each experiment by calculating the difference between the smear reported in the "no-eye-push" (or "fixation") and the "against" eye-movement conditions and then dividing this difference by the extent of perceived motion smear during the "no-eye-push" or "fixation" condition. This analysis revealed that the efficacy of extra-retinal signals during smooth pursuit (mean = 22%) is not significantly different from the efficacy during passive eye movement (mean = 27%, paired t-test: $t_{[df=3]} = 0.46$, $p = 0.68$).

Discussion

According to Hering's law of equal innervation (Hering, 1977), we should observe a conjugate rotation of the occluded right eye if oculomotor command signals contributed in any way to the rotation of an observer's left eye (Bridgeman & Stark, 1991; Ilg, Bridgeman, & Hoffmann, 1989). Because passive rotations of the left eye were not accompanied by similar movements of the right eye, we conclude that only afferent proprioceptive signals accompany the passive eye movements in the first experiment. These proprioceptive signals are likely responsible for the reduced extent of perceived motion smear during passive eye rotation compared to the perceived motion smear when the eye remains still. Recent electrophysiological recordings revealed that monkey primary somatosensory cortex contains neurons that carry tonic and phasic information about eye position, derived exclusively from eye-muscle proprioception (Wang, Zhang, Cohen, & Goldberg, 2007). The current results may reflect modulation by the activity in these or similar neurons on the representation of retinal motion smear in the primary visual cortex (Geisler, 1999).

The present results are not consistent with a significantly stronger contribution of efference copy signals than eye-muscle proprioception in maintaining visual clarity. A possible explanation for the high efficacy of proprioceptive signals in the present study is that motion smear is generated when the eye position is changing. On the contrary, the relative contribution of eye-muscle proprioception to visual perception was evaluated previously with the eyes in a constant position (Bridgeman & Stark, 1991; Gauthier et al., 1990, 1994; Niechwiej-Szwedo et al., 2007). Previous studies of perceived motion smear during active eye movements, such as pursuit (Bedell & Lott, 1996), saccades (Bedell & Yang, 2001), and vergence (Bedell et al., 2004), attributed the reduction of perceived motion smear to the influence of extra-retinal signals, such as efference copy signals. However, eye-muscle proprioception and efference copy signals were not evaluated separately in these studies. Because the reduction of perceived motion smear during passive eye movement is similar to that during pursuit, we cannot rule out the possibility that proprioception alone is sufficient to reduce the extent of perceived smear. On the other hand, it is also possible that a combination of eye-muscle proprioception and efference copy signals is used to foster visual clarity. Recent studies showed that vestibular signals and extra-retinal eye-movement signals contribute to the reduction of perceived motion smear during passive head movements (Bedell & Patel, 2005; Tong et al., 2006). Taken together, the evidence from the present and previous studies suggests that the brain combines all of the available sources of extra-retinal signals to foster visual clarity during eye and head movement, with a significant contribution from proprioception.

Acknowledgments

We thank Girish Kumar for technical help. This research was supported by National Institutes of Health Grants R01 EY05068, P30 EY07551, and R01 EY12986.

Commercial relationships: none.

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Footnote

[1] In a previous study that used a wider range of pursuit velocities, the slope of the relationship between the extent of perceived motion smear and the eye velocity during pursuit is −1.95 (cf. Figure 8 of Tong et al., 2006), which is similar to the value that we observed here in the eye-push condition.

References

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

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

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

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

Bridgeman, B., & Stark, L. (1991). Ocular proprioception and efference copy in registering visual direction. *Vision Research, 31,* 1903–1913. [PubMed]

Burr, D. (1980). Motion smear. *Nature, 284,* 164–165. [PubMed]

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

Crane, H. D., & Steele, C. M. (1985). Generation-V dual-Purkinje-image eyetracker. *Applied Optics, 24,* 527. [PubMed]

Gauthier, G. M., Nommay, D., & Vercher, J. L. (1990). The role of ocular muscle proprioception in visual localization of targets. *Science, 249,* 58–61. [PubMed]

Gauthier, G. M., Vercher, J. L., & Zee, D. S. (1994). Changes in ocular alignment and pointing accuracy after sustained passive rotation of one eye. *Vision Research, 34,* 2613–2627. [PubMed]

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

Hering, E. (1977). *The theory of binocular vision*. New York: Plenum.

Ilg, U. J., Bridgeman, B., & Hoffmann, K. P. (1989). Influence of mechanical disturbance on oculomotor behavior. *Vision Research, 29,* 545–551. [PubMed]

Lewis, R. F., Zee, D. S., Hayman, M. R., & Tamargo, R. J. (2001). Oculomotor function in the rhesus monkey after deafferentation of the extraocular muscles. *Experimental Brain Research, 141,* 349–358. [PubMed]

Niechwiej-Szwedo, E., González, E. G., Bahl, B., Verrier, M. C., Wong, A. M., & Steinbach, M. J. (2007). Manipulation of extraocular muscle afference has no effect on higher order perceptual judgments. *Vision Research, 47,* 3315–3323. [PubMed]

Sherrington, C. S. (1918). Observations on the sensual role of the proprioceptive nerve supply of the extrinsic ocular muscles. *Brain, 41,* 332–343.

Sogo, H., & Osaka, N. (2002). Effects of inter-stimulus interval on perceived locations of successively flashed perisaccadic stimuli. *Vision Research, 42,* 899–908. [PubMed]

Steinbach, M. J. (1987). Proprioceptive knowledge of eye position. *Vision Research, 27,* 1737–1744. [PubMed]

Tong, J., Aydin, M., & Bedell, H. E. (2007). Direction and extent of perceived motion smear during pursuit eye movement. *Vision Research, 47,* 1011–1019. [PubMed]

Tong, J., Patel, S. S., & Bedell, H. E. (2006). The attenuation of perceived motion smear during combined eye and head movements. *Vision Research, 46,* 4387–4397. [PubMed] [Article]

Von Holst, E., & Mittelstädt, H. (1971). In P. C. Dodwell (Ed.), *Perceptual processing: Stimulus equivalence and pattern recognition* (pp. 41–71). New York: Appleton-Century-Crofts.

Wang, X., Zhang, M., Cohen, I. S., & Goldberg, M. E. (2007). The proprioceptive representation of eye position in monkey primary somatosensory cortex. *Nature Neuroscience, 10,* 640–646. [PubMed]