

Asymmetry of perceived motion smear during head and eye movements: Evidence for a dichotomous neural categorization of retinal image motion

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Abstract

We measured perceived motion smear when retinal image motion was created either by a physically moving object or by movement of the eyes or head. Consistent with previous reports, the extent of perceived motion smear during an eye or head movement is less than that produced by physical object motion when the eyes are stationary. Moreover, perceived smear is substantially smaller when the motion of the retinal image is in the same direction as the eye or head movement compared to when image motion is in the opposite direction. These results imply that extra-retinal signals associated with eye and head movements contribute to a reduction of perceived motion smear, thereby fostering perceptual clarity. We hypothesize that the visual system uses a simple dichotomous strategy in applying these extra-retinal signals, based only on the *direction* of retinal image motion with respect to the ongoing eye or head movement.

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1. Introduction

Movements of the eyes and head allow humans to shift their gaze or track an object of interest, but these movements can also cause the images of stationary objects in the world to move across the retina. This motion of the retinal image could lead to errors of perceived direction for visual targets and, because of visual persistence (Coltheart, 1980), would be expected to make physically stationary objects appear smeared in the direction of motion (Bidwell, 1899; Burr, 1980; McDougall, 1904). One mechanism known to

mitigate perceived direction errors is a comparison in the brain between retinal image location and extra-retinal signals of eye and head movement (Bridgeman, 1995; Mergner, Nasios, Maurer, & Becker, 2001; von Holst & Mittelstaedt, 1971). Extra-retinal eye-movement signals also have been implicated in improving perceived clarity during eye movements, as the extent of perceived motion smear is substantially less when retinal image motion is produced by a stationary target during eye movement than when comparable image motion results from a physically moving target during steady fixation (Bedell, Chung, & Patel, 2004; Bedell & Lott, 1996).

Here, we present evidence that the reduction of perceived motion smear during an eye or head movement is selective for retinal image motion in the direction of this movement. Based on our results, we hypothesize

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that the brain adopts a dichotomous strategy to deal with the motion smear that occurs during object, eye, and head movements. In particular, we propose that extra-retinal signals attenuate perceived smear for retinal image motion in the *direction* that is consistent with the image motion from a physically stationary object. Retinal image motion in the opposite direction is assumed to result from a moving object and the perception of motion smear is not attenuated. Our results also indicate that a single brain mechanism is *not* responsible for reducing perceived motion smear and for updating the direction of visual targets during eye and head movements.

2. Methods

2.1. Experiment 1

In a totally dark room, the observer sat in a Tracoustics torsion-swing chair with a molded neck brace that held the head firmly in position. Visual stimuli were presented monocularly at a distance of 64 cm on a cylindrical screen that was attached to the observer's chair (Fig. 1). On each trial of the *VOR-suppression condition*, the

chair, observer, and screen rotated together to the left or right. Instantaneous angular velocity was measured using a Watson Angular Rate Sensor, attached to the chair. To suppress reflexive vestibulo-ocular (VOR) eye movements, the observer fixated on a continuously illuminated, green light-emitting diode (LED) that was mounted on the screen. Horizontal eye position was monitored using an Applied Science Laboratories model 210 Eye Trac. On each trial, the observer pushed a joystick button after the rotation of the chair began. Between 200 and 300 ms later (i.e., longer than the latency of VOR suppression: Johnston & Sharpe, 1994), a bright, horizontally moving, 6' spot was projected 2° above the fixation LED. The moving spot was produced by a green laser diode, mounted above the observer's head and reflected from a galvanometer-mounted mirror that moved with the observer's chair. The luminances of the LED and laser spot were 3.2 log units above each target's detection threshold, measured for a 50 ms flash.

On each trial, the spot moved at a randomly chosen observer-relative velocity between 5 and 45°/s. Across trials, the velocity of the chair ranged from 10 to 60°/s. The trajectory of the moving spot extended equally to the left and right of the fixation LED and

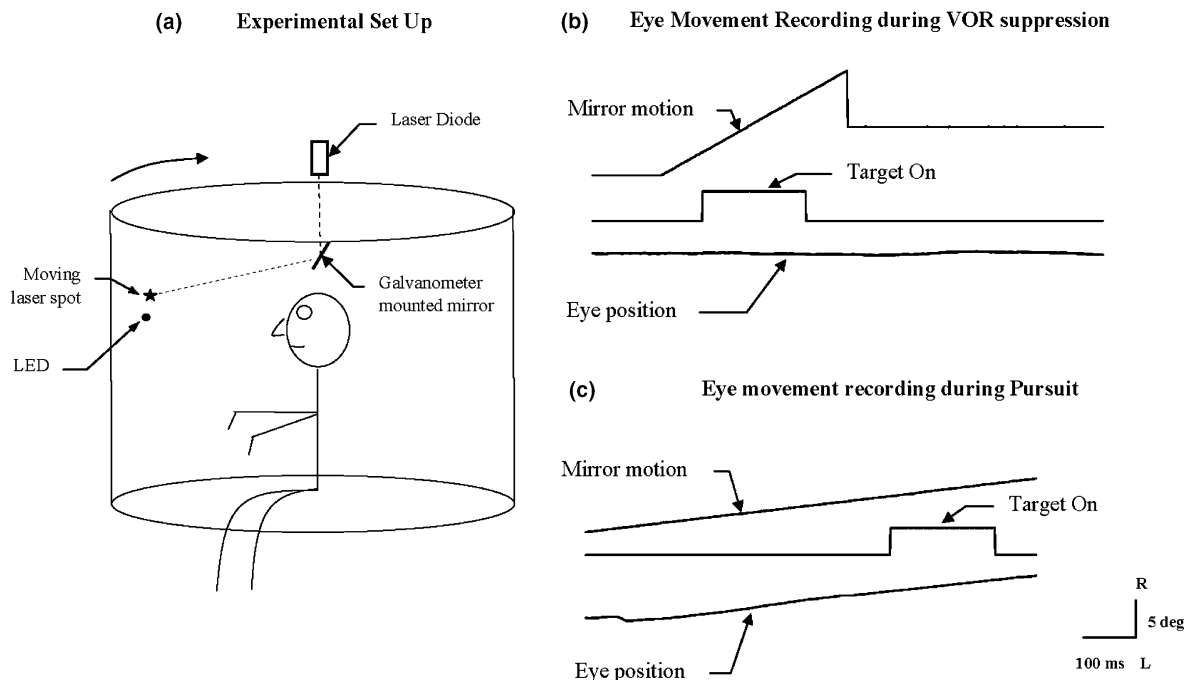


Fig. 1. Experimental set up and representation of the events on each trial. (a) Diagram of the experimental set up for experiment 1. (b) In the VOR-suppression condition, retinal image motion was produced by a laser spot that was projected from a galvanometer-mounted mirror (upper trace) onto a screen that rotated with the observer (rotation at 30°/s to the right in this trial). The middle trace indicates when the moving laser spot was visible to the observer. The bottom trace shows that the observer suppressed vestibulo-ocular eye movements and maintained an approximately constant horizontal eye position with respect to the screen. The sequence of events was similar in the fixation condition, except that the observer did not undergo rotation. (c) The bottom trace shows the observer's horizontal eye position during pursuit tracking of the laser spot (moving at 8.7°/s in this trial), after reflection from a galvanometer-mounted mirror (upper trace). The middle trace shows when the screen-stationary LED was presented during pursuit. The calibration bars in the lower right corner indicate time and angular-position scales for the traces in (b) and (c).

its duration on each trial was randomly either 50, 100, 150, or 200 ms. Following each presentation of the moving spot, the chair was stopped 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. At least three blocks of 40 trials were run for each of five normal observers, three of whom were naïve. A personal computer controlled presentation of the targets and collected the signals of chair and eye movement, along with the observer's responses.

On each trial in the *pursuit condition*, the stationary observer tracked a projected laser spot that moved either to the left or right at a random velocity between 5 and 30°/s. Between 500 and 600 ms after the onset of motion, a stationary green LED flashed 2° below the moving spot for 50, 100, 150, or 200 ms. Because of the observer's pursuit eye movement, this LED generated horizontal retinal image motion in the 'SAME' direction (e.g., temporalward motion of the image in the left eye during leftward pursuit), that extended symmetrically on either side of the fovea. After each presentation of the LED, the observer adjusted the length of a back-projected horizontal line to match the extent of perceived smear. Trials in the *fixation condition* were identical to those in VOR-suppression condition, except that the observer's chair remained physically stationary.

Eye-movement records were examined off line and trials were rejected if any of the following occurred: (a) eye-velocity gain was less than 0.5 during pursuit, (b) eye velocity was greater than 2°/s during VOR-suppression or fixation, 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 VOR-suppression and pursuit trial, chair and eye-movement velocity were averaged across the duration of the target presentation. To allow the data for different velocities of the target to be compared, the extent of matched smear was converted from units of visual angle to units of duration (Bedell et al., 2004; Bedell & Lott, 1996; Chen, Bedell, & Ögmen, 1995; Hogben & Di Lollo, 1985), using the equation:

Duration of perceived smear

$$= \frac{\text{extent of matched smear (}^\circ\text{)}}{\text{retinal image velocity (}^\circ\text{/s)}}.$$

2.2. Experiment 2

Four of the five observers from experiment 1 participated. Stimuli were generated on a Hewlett-Packard 1311B oscilloscope, subtending 8° by 6° at the observer's viewing distance of 2 m. Viewing was monocular in a dimly lit room. In the *pursuit condition*, the observer tracked a target that moved smoothly to the left or right

across the face of the oscilloscope at 5°/s. Between 400 and 475 ms after the onset of the moving pursuit target, a 0.7' bright spot appeared 1° above or below it for a duration of 200 ms. This spot moved physically on the oscilloscope at a velocity of 5, 8, or 11°/s in either the same or the opposite direction as the moving pursuit target. In the *fixation condition*, the bright spot moved randomly to the right or left at 5, 8, or 11°/s, along a trajectory 1° above or below the stationary fixation target. In both the pursuit and fixation conditions, the luminance of the moving spot was 1.5 log units above its detection threshold, which was dim enough to eliminate visible phosphor persistence (Bedell & Lott, 1996; Groner, Groner, Muller, Bischof, & Di Lollo, 1993). As in experiment 1, above, the observer adjusted the length of a bright horizontal line presented 1° above or below the stationary fixation target to match the extent of perceived motion smear on each trial.

The experimental protocols were reviewed by the University of Houston Committee for the Protection of Human Subjects. Written informed consent was obtained from the observers in both experiments before they participated.

3. Results and discussion

3.1. Experiment 1

Consistent with previous reports (Bedell et al., 2004; Bedell & Lott, 1996), the average matches of the five normal observers indicate that the extent of perceived motion smear is greater during fixation than pursuit, when the duration of the target is longer than 100 ms (Fig. 2: $F_{[1,36]} = 7.85$, $P = 0.038$, at a duration of 150 ms; $F_{[1,36]} = 60.24$, $P = 0.0002$, at a duration of 200 ms).

The extent of perceived motion smear on VOR-suppression trials was analysed separately according to whether the motion of the retinal image was in the 'SAME' or the 'OPPOSITE' direction as the rotation of the observer's head and body on that trial. Specifically, temporalward motion of the left eye's retinal image is in the 'SAME' direction and nasalward motion of the left eye's retinal image is in the 'OPPOSITE' direction, when the observer rotates to the left. The extent of perceived smear when the target's retinal image moved in the 'SAME' direction as the rotation of the observer during VOR suppression is similar to that in the pursuit condition, for all durations of the target ($F_{[3,12]} = 0.19$, $P = 0.67$). On the other hand, the extent of perceived smear when the target's retinal image moved 'OPPOSITE' to the direction of head and body rotation is similar to that in the fixation condition ($F_{[3,12]} = 0.053$, $P = 0.82$). The extent of perceived motion smear on the 'SAME' and 'OPPOSITE' trials in the VOR-suppression

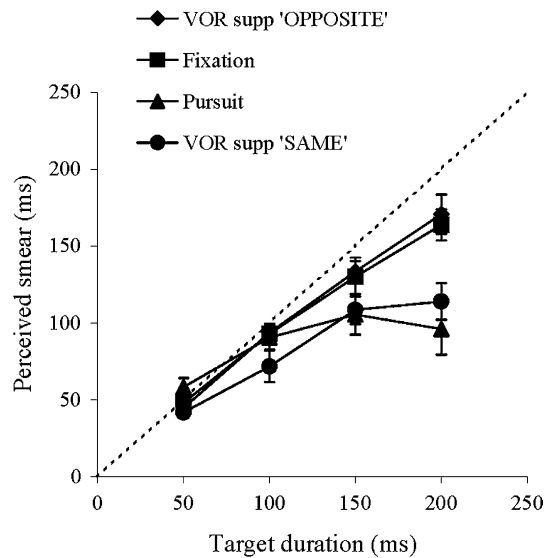


Fig. 2. Extent of perceived motion smear during fixation, pursuit, and VOR-suppression in experiment 1. The extent of perceived smear is plotted as a function of target duration in the fixation and pursuit conditions, and for retinal image motion of the target in the 'SAME' and 'OPPOSITE' direction of observer motion in the VOR-suppression condition. Each data point represents the average of five observers ± 1 SE.

condition differ significantly for each duration of the target except for 50 ms (range of $F_{[1,36]}$ values = 6.27, $P = 0.05$, at a duration of 100 ms to 42.53, $P = 0.0008$, at a duration of 200 ms).

Because the *physical* motion of the target was opposite to the direction of head and body rotation on the 'SAME' trials in the VOR-suppression condition, the velocity of the target's motion *in space* was generally slower than on 'OPPOSITE' trials and, on some trials, was close to 0°/s. Consequently, the significantly smaller extent of perceived smear on 'SAME' compared to 'OPPOSITE' trials might be attributable to a preferential reduction of smear on the trials when the target is approximately stationary in space. However, a plot of the perceived extent of smear on the 'SAME' trials as a function of the target's velocity in space shows no evidence that the minimum extent of smear occurs for target velocities near 0°/s (Fig. 3). Rather, it is apparent in Fig. 3 that the extent of perceived smear on 'SAME' trials decreases with the velocity of the retinal image motion (target velocity in space—observer velocity). No similar relationship exists between the extent of perceived smear and image velocity on 'OPPOSITE' trials during VOR-suppression. The outcome of this analysis indicates that the mechanism responsible for attenuating perceived motion smear operates independently of the mechanism that determines perceived stability of a visual target during eye and head movements.

The retinal image motion of the target was very similar in the fixation and pursuit conditions. Similarly, the only difference in retinal stimulation on the 'SAME' and

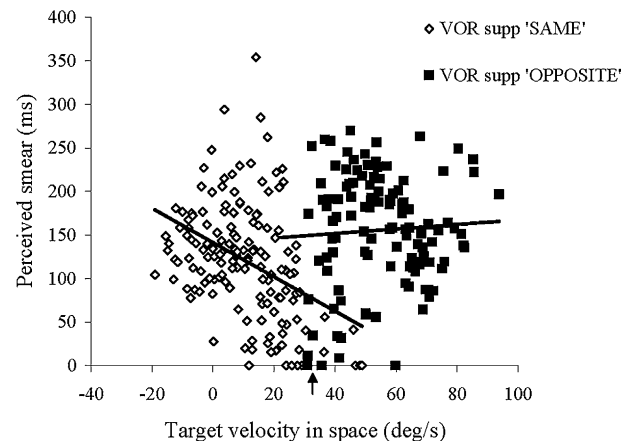


Fig. 3. The extent of perceived smear is shown as a function of the target's physical velocity in space, on individual 'OPPOSITE' (filled symbols) and 'SAME' trials (unfilled symbols) in the VOR-suppression condition. Only the data for a target duration of 200 ms are presented. Positive values on the x axis indicate movement of the target in space in the direction of observer rotation; negative values indicate movement of the target in the opposite direction. The physical velocity of the target in space was obtained by summing the velocity of the target with respect to the screen and the observer's velocity of rotation. The vertical arrow below the x axis represents the mean velocity of observer rotation for all of the acceptable trials in this condition. The best fitting lines to the data from the 'SAME' and 'OPPOSITE' trials are shown.

'OPPOSITE' trials in the VOR-suppression condition was the *direction* of the retinal image motion relative to head and body rotation. Because the unequal extent of perceived motion smear in these pairs of conditions can not be attributed to differences in the retinal stimulation, or to differences in attention (Bedell et al., 2004), we conclude that extra-retinal signals are responsible for the reduction of perceived smear in the pursuit condition and in the 'SAME' trials of the VOR-suppression condition. Extra-retinal signals for eye movement are available from efferent motor commands and as afference from the extraocular muscles; extra-retinal signals for head and body rotation are available from the vestibular system (Bridgeman, 1995; Gauthier, Nommay, & Vercher, 1990; Mergner et al., 2001).

The highly dissimilar results that we obtained on 'SAME' vs. 'OPPOSITE' trials in the VOR-suppression condition led us to hypothesize that the brain uses these extra-retinal signals to attenuate perceived motion smear based on a dichotomous categorization of the retinal image motion that occurs during head and body rotation. Specifically, we suggest the brain makes the simplifying assumption that retinal image motion in the 'SAME' direction as head and body rotation is produced by a physically stationary object, which should not be perceived as smeared. On the contrary, retinal image motion in the 'OPPOSITE' direction of head and body rotation is consistent with an object that physically moves in space. Because motion smear has been shown to facilitate the detection and discrimination of target

motion (Burr & Ross, 2002; Geisler, 1999), presumably it would be inadvisable for extra-retinal signals to attenuate perceived motion smear in this direction.

If the above hypothesis represents a general strategy for dealing with the retinal image motion that occurs in the presence of eye and/or head movement, then an asymmetry in the extent of perceived motion smear should occur for retinal image motion in the ‘SAME’ vs. the ‘OPPOSITE’ direction of pursuit eye movements. The purpose of experiment 2 was to test this prediction.

3.2. Experiment 2

Unlike the pursuit condition in experiment 1, the retinal image motion produced by the target in experiment 2 could be either in the ‘SAME’ or the ‘OPPOSITE’ direction as the pursuit eye movement. As shown in Fig. 4a, the extent of perceived motion smear on the ‘SAME’ trials in the pursuit condition is significantly less than that observed during fixation ($F_{[1,6]} = 24.62$, $P = 0.0042$). In contrast, the extent of perceived smear on ‘OPPOSITE’ trials during pursuit does not differ from fixation ($F_{[1,6]} = 0.18$, $P = 0.65$). When the results are plotted in terms of the velocity of the target spot in space, the extent of perceived smear is seen to decrease on ‘SAME’ but not ‘OPPOSITE’ trials, very similarly to the VOR-suppression condition (Fig. 4b).

4. General discussion

For targets that consist of multiple, closely spaced elements, an attenuation of perceived motion smear has been accounted for on the basis of spatio-temporal interactions between the moving components of the retinal image, itself (Castet, 1994; Chen et al., 1995; Di Lollo & Hogben, 1987; Purushothaman, Ögmen, Chen, & Bedell, 1998). However, in accordance with the outcome of previous studies (Bedell et al., 2004; Bedell & Lott, 1996), the asymmetrical attenuation of perceived smear shown here for an isolated moving target indicates that a second mechanism uses extra-retinal signals to reduce perceived smear, depending on the relative direction of the eye or head movement and the retinal image motion of the target. One possibility is that this second form of attenuation occurs in extrastriate cortex, such as the middle superior temporal (MST) area, which has been reported to be active during VOR suppression (Naito et al., 2003) and exhibits responses to both retinal image motion and eye movements (Haarmeier, Their, Repnow, & Petersen, 1997).

Previously, Brenner and van den Berg (1994) reported data that are consistent with a dichotomous categorization of the retinal image motion during pursuit eye movements. In their experiment, the perceived speed of a pursued target depended almost solely on the relative velocity between this target and an untracked back-

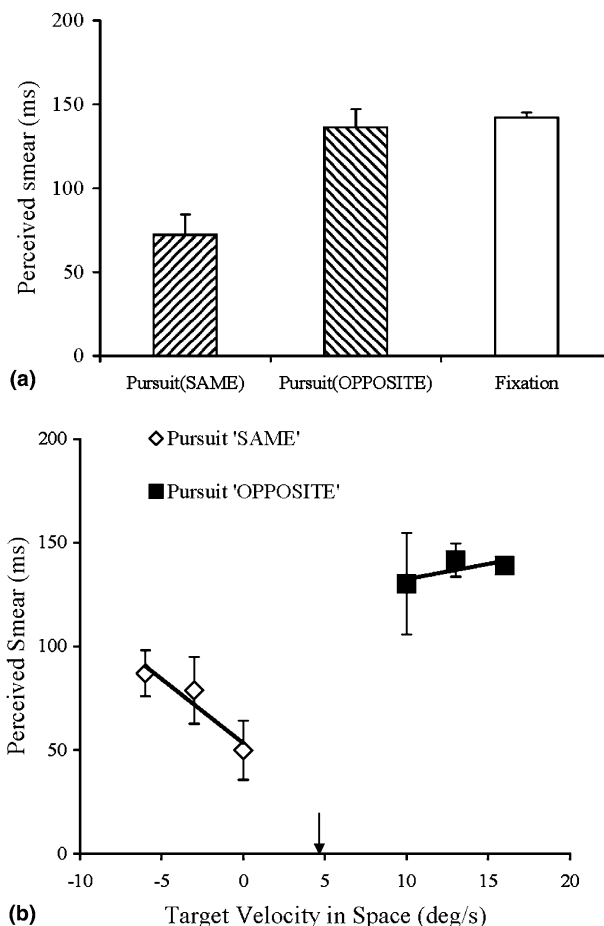


Fig. 4. The extent of perceived motion smear during fixation and pursuit in experiment 2. (a) The average extent of perceived smear is less when motion of the target's retinal image is in the ‘SAME’ direction as smooth pursuit, than when retinal image motion is ‘OPPOSITE’ to the direction of smooth pursuit, or when motion of the target occurs during steady fixation. Average data ± 1 SE are shown for five observers, for a target duration of 200 ms. (b) The average extent of perceived smear (± 1 SE) is plotted as a function of the target's physical velocity in space on ‘OPPOSITE’ (filled symbols) and ‘SAME’ trials (unfilled symbols). The mean velocity of pursuit eye movements on acceptable trials was 4.4°/s, indicated by the vertical arrow below the x axis.

ground stimulus, if the retinal image of the background moved in the direction of pursuit. A straightforward interpretation of this result is that the visual system assumes the untracked background stimulus provides a stationary reference in space. On the other hand, when the retinal image of the untracked background moved in the opposite direction from pursuit, then the perceived speed of the pursued target depended primarily on the speed of eye movement, which the visual system presumably determined on the basis of extra-retinal signals.

The similar asymmetry in the extent of perceived motion smear during VOR suppression in experiment 1 and during pursuit in experiment 2 leads to some additional conclusions. First, the reduction of perceived motion

smear does *not* require the eyes to move physically with respect to the head, as little or no eye movement occurs in the VOR-suppression condition. Evidence exists that VOR suppression can be attributed (at least partly) to an internal pursuit-like signal that opposes the neural command for the VOR (Barnes, Benson, & Prior, 1978; Misslisch, Tweed, Fetter, Dichgans, & Vilis, 1996). Therefore, one possibility is that an extra-retinal signal related to pursuit is responsible for the asymmetric reduction of perceived motion smear in *both* the pursuit and VOR-suppression conditions. However, perceived motion smear is reduced also during VOR eye movements in the dark, for targets that move physically with the observer (Bedell & Patel, 2002). Because no pursuit command is generated in this condition, the extra-retinal signal for pursuit can not be the only neural signal that leads to an attenuation of perceived smear. Although other alternatives exist, we propose that the extra-retinal signal associated with *any* eye or head movement can reduce the extent of perceived motion smear.

In summary, our results suggest that the brain adopts a simple dichotomous strategy to deal with the retinal image motion that results from various combinations of object, eye, and self movement with respect to the external world. Specifically, extra-retinal signals are applied to attenuate the extent of perceived motion smear if, during an ongoing eye or head movement, the motion of the retinal image is consistent *in direction* with that produced by a stationary object in space. On the other hand, no reduction of perceived smear occurs if motion of the retinal image occurs in the absence of an eye or head movement or if, during an eye or head movement, the direction of image motion is not consistent with a physically stationary object. This dichotomous categorization of retinal image motion would be expected to reduce the complexity of the neural circuitry and computations that are needed to generate relatively clear and accurate visual perception during movements of the eyes and head.

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