Psychophysical measurements of referenced and unreferenced motion processing using high-resolution retinal imaging

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Background: Motion detection thresholds with a stationary frame of reference are significantly lower than unreferenced motion thresholds. To account for this, previous studies have postulated the existence of compensatory mechanisms, driven by the presence of a surround, that cancel the effects of eye movements. In the present study we used an adaptive optics scanning laser ophthalmoscope (AOSLO) to investigate the effects of retinal jitter due to fixation eye movements on referenced and unreferenced motion thresholds. Methods: The stimuli were produced by modulation of the AOSLO imaging beam, so that the absolute retinal position of targets was recorded. In Experiment 1 subjects made up/down motion judgments of a dark horizontal bar presented against a stationary 1-degree bright background. In Experiment 2 unreferenced motion thresholds were measured with isolated bright horizontal bars in otherwise complete darkness. In both experiments, AOSLO images for each trial were analyzed offline to extract retinal jitter and the retinal position of targets. Results: For referenced motion, the results were consistent with complete compensation for eye movements by the visual system. In the unreferenced motion case eye movements adversely affected motion judgments, although there was evidence of partial compensation for such eye movements. Conclusions: Compensatory processes completely cancel the effect of fixation jitter for referenced motion but such compensation is partial for unreferenced motion.

Keywords: referenced motion, unreferenced motion, fixation eye movements, two-frame motion, adaptive optics, adaptive optics scanning laser ophthalmoscope, high-resolution retinal imaging

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Introduction

When steadily fixating a target in space we usually perceive the position of the target as stationary. However, under such steady fixation, the eye is not physically stationary but exhibits small eye movements (Ditchburn, 1973; Steinman, 1976) so that the retinal image of the "steadily" fixated target constantly traverses the retina in a manner determined by the pattern of eye movements that comprise the fixation jitter. It has been postulated that the functional significance of such retinal jitter is to overcome the fading of retinal images that would occur if retinal images were physically stationary on the retina (Riggs, Ratliff, Cornsweet, & Cornsweet, 1953). If this retinal image jitter is considered as motion noise, one might predict that in order to discriminate the true motion of a target, the true target motion must be greater than the spurious motion produced by retinal jitter (Murakami, 2004). If so, minimum motion thresholds should be far greater than 1 arcmin because the components of eye movements comprising fixation eye movements include fixation tremors (<1 arcmin), microsaccades (typically around 5 to 10 arcmin), and drifts (≅10 arcmin) (Ditchburn & Foley-Fischer, 1967; Eizenman, Hallett, & Frecker, 1985; Ratliff & Riggs, 1950). However, since all targets in the field share this eye motion generated component of motion, a relative motion judgment might be much more sensitive.

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The human visual system is indeed extremely sensitive at making judgments of relative motion. Under optimal stimulus conditions subjects are able to discriminate target motions smaller than the diameter of a foveal cone photoreceptor (Legge & Campbell, 1981; Nakayama & Tyler, 1981; Westheimer, 1978). In order to achieve this high degree of motion sensitivity, the visual system must employ mechanisms that can differentiate real target motion from spurious motion due to retinal jitter. Murakami (2003, 2004) and Murakami and Cavanagh (1998) showed that in the absence of a reliable reference, the visual system is unable to effectively compensate for retinal motion. Physically stationary targets then appear to move. Furthermore, Murakami (2004) showed that eye velocity was correlated with motion thresholds if the surround was absent or flickered. The results of Tulunay-Keesey and VerHoeve (1987) also lend support for the idea that spatial references play a key role in the compensation for fixation eye movements. They showed that motion thresholds for an oscillating line are significantly elevated if the background against which motion judgments are made was stabilized. Furthermore, both studies showed that minimum motion thresholds were consistently higher for conditions without a spatial reference than for the conditions with a spatial reference. Similar findings of lower minimum motion thresholds with referenced versus unreferenced conditions were reported by Legge and Campbell (1981), Levi, Klein, and Aitsebaomo (1984), Shioiri, Ito, Sakurai, and Yaguchi (2002), and Whitaker and MacVeigh (1990). These studies collectively provide strong evidence that the presence of spatial references engages mechanisms that compensate for the effects of spurious image motion produced by retinal jitter and also allude to the deleterious effects of fixation eye movements on unreferenced motion thresholds.

Previous attempts to study the relationship between motion thresholds and fixation eye movements (Murakami, 2004; Tulunay-Keesey & VerHoeve, 1987) employed eye movement tracking devices to infer retinal movement. However, many of these instruments are capable of resolving eye movements with an optimal precision of about an arcmin (Stevenson & Roorda, 2005), and their accuracy depends on the subject's fixation during calibrations. This level of resolution imposes an obvious restriction when studying the effect of small eye movements on motion thresholds, which are often smaller than 1 arcmin. In the present experiment we employed high-resolution retinal imaging using the adaptive optics scanning laser ophthalmoscope (AOSLO) (Roorda et al., 2002). The AOSLO has two advantages. The first advantage is its capacity to produce high-resolution retinal imaging at the level of a cone photoreceptor. The second advantage is that the AOSLO imaging beam can be modulated to present a psychophysical stimulus (Poonja, Patel, Henry, & Roorda, 2005). The combined effect of these two advantages was that we were able to stimulate and image the retina simultaneously, thereby providing an extremely sensitive method by which to study the effects of fixation jitter on motion judgments.

In the present study we show that referenced motion thresholds are unaffected by retinal jitter due to fixation eye movements. This independence between referenced motion thresholds and retinal jitter is produced by compensatory mechanisms that are largely visually driven and require the presence of a spatial reference. Unreferenced motion thresholds are adversely affected by retinal jitter, being higher for larger magnitudes of retinal jitter due to fixation eye movements and strongly biased by the overall drift of the eye. We also conclude that compensatory processes in unreferenced motion may be partial and speculate that only certain types of eye movements are being compensated and not others.

Methods

Experiment 1: Referenced motion

Figure 1 illustrates the stimulus used in Experiment 1. The stimulus comprised a 1×1 degree red square background within which vertical motion judgments were made of a 3×19 arcmin black horizontal bar. The background was produced by vertical and horizontal scanning of a 660-nm laser beam that also served as the imaging beam of the AOSLO (Poonja et al., 2005). The vertical scan rate of the vertical scanning mirror was 30 Hz and that of the horizontal mirror was 16 kHz. The power of the laser beam at the corneal surface was 11 μW, producing an extremely bright field of approximately one million trolands. The dark horizontal bar (motion stimulus) was created by modulation of the laser beam using an Acousto-Optic Modulator (AOM).

The high temporal resolution of the AOM (20 MHz) made it possible to modulate the LASER beam at a specified time during its horizontal sweep thereby producing a dark horizontal bar within the square raster. It was therefore possible to present the psychophysical stimulus while concurrently imaging the retina (Figure 1). The region of the dark horizontal bar within the stimulus shows up as a black horizontal strip on the resulting retinal image. In this way the position occupied by the bar on the retina could be extracted with a great degree of accuracy (a single pixel corresponding to 8 arc seconds). The two-frame motion stimulus (horizontal dark bar) was presented with one of 9 vertical displacements in a method-of-constant-stimulus procedure. The starting positions of the first bar were jittered to avoid use of positional cues. Subjects reported whether the perceived motion of the bar was upward or downward. A video sequence was recorded for each trial and the response of the subject was also recorded. Twenty-five repetitions comprised a single block and a minimum of 3 such blocks comprised a

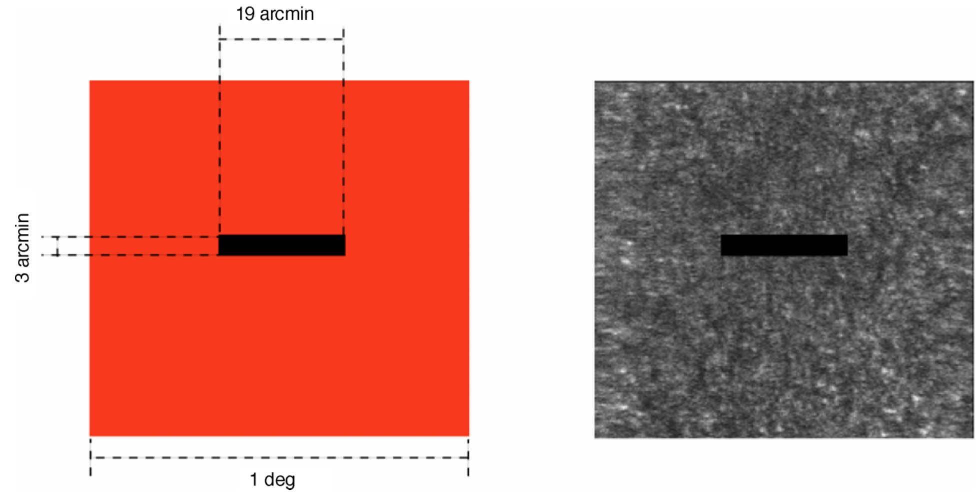

Figure 1. Left: Illustration of the 1 × 1 degree AOSLO scanning raster with horizontal bar. Subjects responded to the vertical motion of the horizontal bar against the red (660 nm) background of the imaging raster. Right: Sample image of the retina formed by the AOSLO imaging raster. Note that the dark horizontal motion stimulus shows up as a dark horizontal bar on the retinal image. The gray texture of the background represents individual photoreceptors or clusters of photoreceptors.

completed session. Each bar was presented for a single raster frame. The two bars comprising the two frame motion sequence were separated by a single blank frame or 10 blank frames, producing stimulus onset asynchrony (SOA) of 66 ms and 363 ms, respectively.

Minimum motion thresholds were extracted from the slope of the best Probit-fit cumulative normal to the data. The video sequences were analyzed offline to extract magnitude of retinal jitter between the two frames of the motion stimulus. This was achieved by computing 2-D cross-correlations of the retinal images recorded with the first and second frames of the motion stimulus. The magnitude of retinal jitter was extracted with an accuracy of a single pixel (8 arcsecs). All subjects (N = 3) were dilated prior to the experiment. Head movement was stabilized with the use of a bite bar during all conditions. Ocular aberrations were corrected before and during each experiment using a Shack–Hartman Wavefront Sensor over a 6-mm pupil (Roorda et al., 2002).

Experiment 2: Unreferenced motion

The apparatus used for Experiment 2 was the same as that in Experiment 1, but in this case the scanning beam was used to make a single bright (red) 40′ × 5′ horizontal bar presented in a dark surround. Because the AOM does not completely block the laser light, the laser itself was powered on and off to create the bright bars. The horizontal bars were presented with vertical motion using 2 randomly interleaved double-staircase procedures. A staircase procedure was used in place of the constant stimulus method because judgments were strongly biased by the drift in fixation, and the point of subjective equality (no motion) could not easily be anticipated. Psychometric functions were extracted from the staircase data and fitted with the best-fit cumulative normal. Minimum motion thresholds were extracted from the slope of the best-fit cumulative normal to the data. Again, all subjects were dilated prior to the experiment and ocular aberrations were corrected using a Shack–Hartman Wavefront sensor over a 6-mm pupil.

The method of image acquisition and extraction of retinal jitter were as described in Experiment 1; however, the cross-correlation was conducted between each motion frame and a 1 × 1 degree reference retinal image frame which was chosen from the video frames that comprised the video sequence prior to the presentation of each trial. A reference frame was required because the retinal image texture captured during the bar frames covered small, often non-overlapping areas of the retina.

In order to make the motion task unreferenced, extreme care was taken to remove all perceptible visual cues during the experiment by viewing the stimulus in a completely dark room. In addition, subjects viewed that raster through an aperture cut out of the central part of an eye patch to block reflected stray light from the scanning laser beam. The contralateral eye was completely occluded using another patch. The stimulus sequence was as follows: Each trial began with the subject fixating a red 1 × 1 degree raster. To initiate the presentation of the test stimuli, subjects pressed a key on a remote keypad; this was followed by a 33-ms period of darkness after which the first frame of the motion sequence was flashed. The duration of the first frame was 33 ms; however, the test stimulus (horizontal bright bar) was only visible for 1.44 ms during the first frame (The duration of the test stimulus is the number of lines comprising the test stimulus multiplied by the time per line: 60 μs × 24 lines = 1.44 ms). The second frame of the motion sequence was then flashed for 33 ms (1.44 ms for the test stimulus) following a period of darkness determined by the specific SOA condition (66 ms or 363 ms). The subject was then required to make his response while in complete darkness. The key press that recorded the subject's response triggered the presentation of the 1 × 1 degree fixation raster. Head movement was stabilized with the use of a bite bar during all conditions.

Most subjects reported the perception of the auto-kinetic effect when viewing the 1 × 1 degree fixation raster. Furthermore, subjects also reported they "felt" as though they were looking straight ahead during each trial but when the trial was over and the fixation raster re-appeared that raster was perceived to be off fixation, usually superior. Analysis of the video showed that gaze was indeed drifting downward during almost every trial. These reports further confirmed the effectivity of the reduced environment.

Data analysis

The predicted results are illustrated in Figures 2A and 2B. The *x*-axis is a common axis that plots the bar-shift in arc minutes with respect to gaze position for all 3 types of analyses. Negative values refer to downward motion and positive values refer to upward motion of the bar. The *y*-axis plots the proportion of "upward" responses made by the subject. The psychometric functions for 3 types of analyses are plotted together for comparison.

The "spatiocentric" condition refers to the psychometric functions (PFs) derived when the motion of the bar is expressed relative to the image, i.e., the physical motion of the bar within the 1-degree red background. The "retinocentric" condition refers to the PFs derived when the motion of the bar is expressed relative to the retina, i.e., how much the bar moved relative to the retina. To illustrate this point, consider the situation where the bar moves downward in space by a given amount. If the retina also moved downward by the same amount during this period, then the motion of the bar with respect to the retina will be zero, i.e., the bar will stimulate the same part of the retina. Figure 3 further illustrates the difference between bar motion in the image and bar motion on retina. The smaller black arrow indicates the magnitude and direction of movement of the horizontal bar with respect to the image. The larger black arrow indicates the magnitude and direction of movement of the retina. This can be inferred from the displacement of a bright cluster of photoreceptors (dashed circles) from Frame 1 to Frame 2 of the two-frame motion stimulus (this refers to the actual retinal displacement that occurred between the two frames). The difference between these two motions represents the movement of the bar with respect to the retina. It is this difference that we report as retinocentric

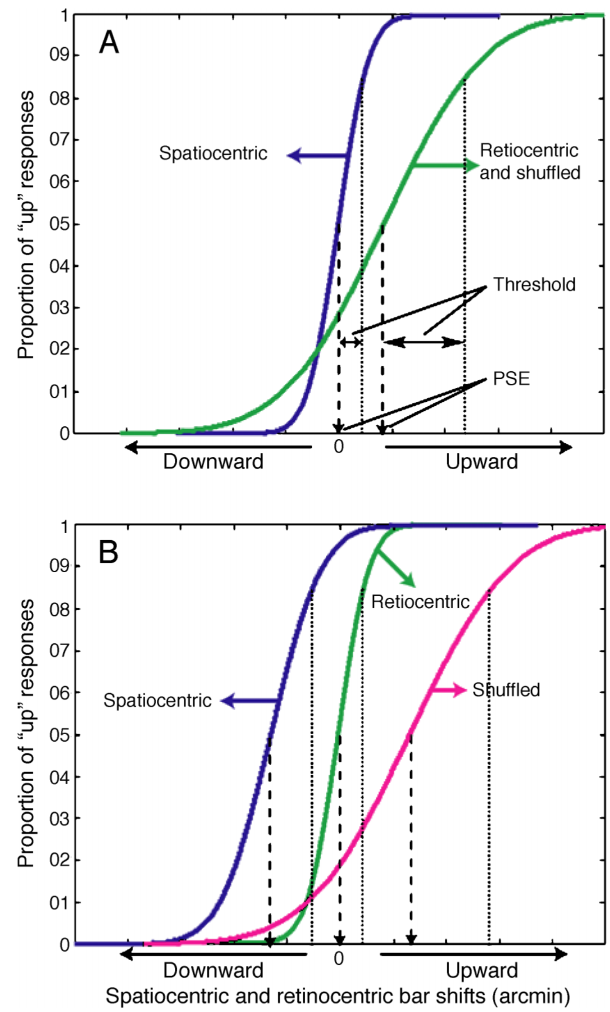

Figure 2. Psychometric curves predicted for two possible scenarios. The *x*-axis plots the motion of the bar in either spatiocentric or retinocentric coordinates. Negative values refer to "downward" motion and positive values refer to "upward" motion. The *y*-axis plots the proportion of "upward" responses. The "spatiocentric" curve depicts the performance of subjects when considering how much the bar moved within the image. The "retinocentric" curve depicts the performance of subjects when considering how much the bar moved relative to the retina. (A) Complete compensation—spatiocentric slopes will be steeper than retinocentric curves, with the Spatiocentric PSE being closer to zero. Retinocentric and "shuffled" curves should have similar slopes. (B) No compensation—retinocentric slopes will be steeper than Spatiocentric and "shuffled" curves, with the Retinocentric PSE being closer to zero. See text for explanation of "shuffled" curves.

motion. In this case, the magnitude of movement of the retina is much larger than the movement of the bar with respect to the image, so the predicted response will be in opposite directions for spatiocentric and retinocentric frames of reference. Psychometric functions were generated separately for these two frames of reference. Spatiotopic functions were generated directly from the constant stimuli used, and Retinotopic functions were

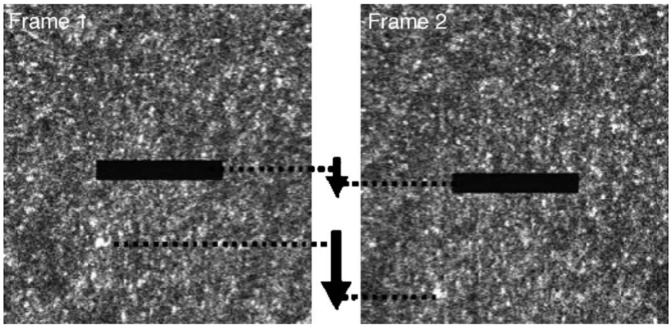

Figure 3. Two sample AOSLO images showing the positions occupied by the horizontal bars during the two-frame motion sequence. The shorter black arrow indicates the displacement of the horizontal bar relative to the image (downward)—spatiocentric motion. The longer black arrow indicates the magnitude of retinal displacement inferred from the change in position of a cluster of photoreceptors (dashed circles) from Frame 1 to Frame 2 (downward). In this case, the magnitude of retinal displacement is larger than the magnitude of displacement of the horizontal bar with respect to the image. Therefore, the direction of displacement of the bar relative to the retina (Retinocentric motion) is upward.

generated by calculating the retinal image motion on each trial and binning these motions.

Figure 2A represents the predicted results for each PF if the visual system completely compensated for the retinal jitter that occurred during each trial, i.e., it responds to bar motion in the image. If this were the case, the PFs derived for the "spatiocentric" analysis would be steeper than that of the "retinocentric" PFs. The reason for this is that including the effects of eye movements in the analysis when such compensation has already been achieved by the visual system will be tantamount to adding eye movement noise. This will elevate motion thresholds and therefore produce a flatter PF slope. In order to estimate the effect of adding such noise, we conducted a third analysis referred to as "shuffled." The logic of the "shuffled" analysis was as follows: If the visual system completely compensated for its eye movements, then repeating the retinocentric analysis for randomly assigned eye movements will produce PFs with slopes that are similar when compared to the PFs obtained if the analysis was conducted for eye movement specific to each trial. In both cases, the amount of eye movement noise added will be similar because they belong to the same distribution of eye movements. Another test for the frame of reference used by the visual system is to examine the PSE (point of subjective equality) of the PFs for each type of analysis. The PSE refers to the displacement of the bar that is perceived as being stationary by the subject. If subjects used a spatiocentric reference (i.e., how much the bar moved in space), then the expected PSE for the "spatiocentric" PFs should be close to zero bar motion in space. However, if the subjects used a retinocentric frame of reference (i.e., how much the bar moved on the retina), then the PSE for the "retinocentric" PFs should be closer to zero than the "spatiocentric" curves.

Figure 2B depicts the predicted results if the visual system did not compensate for the effects of the fixation jitter on each trial. If no compensation occurred, the slope of the "retinocentric" analysis should be steeper than that of the "spatiocentric" analysis because the visual system responds not to the physical motion of the bar, but to how much and in which direction the bar moved relative to the retina. Consequently, the "retinocentric" curve should also be steeper than that of the "shuffled" analysis and the PSE of the "retinocentric" PFs should tend to zero motion of the bar on the retina.

Results

Results for Experiment 1 are plotted in Figure 4. The x and y axes are as in Figure 2, described above. Results for the 66-ms and 363-ms SOAs are plotted in the left column and right columns, respectively, for 3 subjects. The standard deviation or slope of the psychometric functions is listed adjacent to their respective legends. For each SOA, the "spatiocentric" curve is consistently steeper (mean across subjects for 66-ms and 363-ms SOA: 1.47 and 1.51 arcmin) than the "retinocentric" curve (mean across subjects for 66-ms and 363-ms SOA: 2.35 and 5.64 arcmin). Furthermore, the "shuffled" curve has a fairly similar slope as that of the "retinocentric" curve (mean across subjects for 66-ms and 363-ms SOA: 3.183 and 6.38 arcmin). In most cases, the PSE for the "spatiocentric" curves is closer to zero than that of the "retinocentric" curves across SOA, thereby suggesting that the PSE is consistent with spatiocentric coordinates rather than retinal coordinates. Regardless of the SOA, the slope for the "spatiocentric" curve is fairly similar, but slopes of the "retinocentric" and "shuffled" curves are much flatter for the longer SOA. We hypothesize that the above trend could be accounted for by larger magnitude of eye movement that occurred with the longer SOA.

Figure 5 plots the distribution of fixation eye movement for the 66- and 363-ms SOA for each subject. The x-axis plots the gaze shift in arc minutes. Positive values indicate an upward gaze shift and negative values a downward gaze shift. The y-axis plots the number of trials in which a given gaze shift occurred. It is evident that with the longer SOA, the vertical gaze shift distribution is skewed to larger "downward" shifts in addition to exhibiting larger standard deviations. These observations are consistent with the hypothesis that the flatter slopes obtained with the "retinocentric" and "shuffled" analyses are due to the increased retinal (gaze) movements that occurred with the longer SOA. Of further interest was that despite the increase in eye movement variability, minimum motion thresholds (Spatiocentric curves) are comparable for the two SOA conditions.

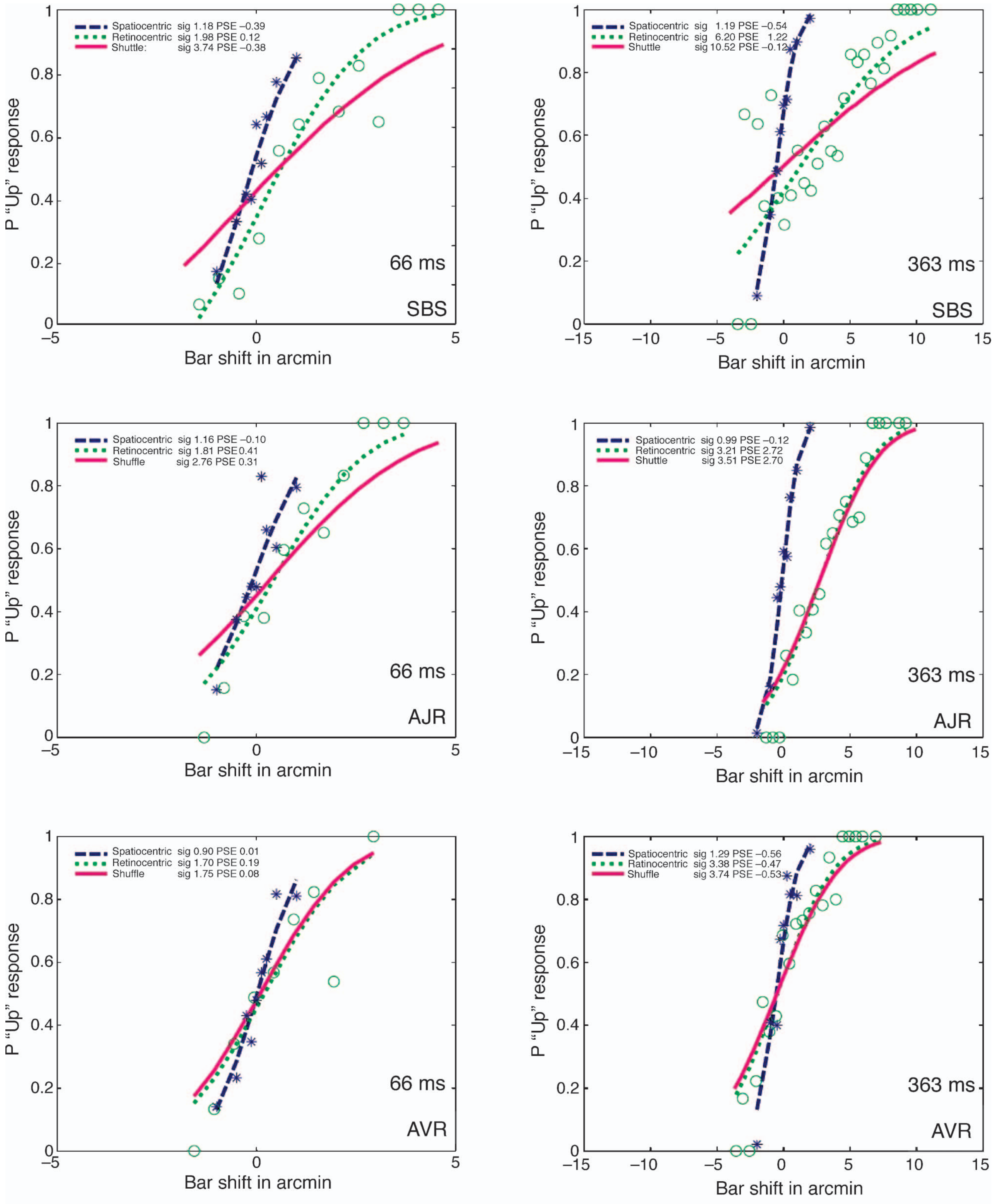

Figure 4. Referenced motion condition: psychometric functions (PFs) are plotted for 3 subjects across two SOA conditions (66 and 363 ms). The slopes of the “spatiocentric” curves (dashed line) are steeper than both “retinocentric” and “shuffled” curves regardless of the SOA condition. Furthermore, the PSE of “spatiocentric” curves are generally closer to zero when compared with the “retinocentric” and “shuffled” analyses. The slopes of the “retinocentric” and “shuffled” curves are on average similar across SOA conditions.

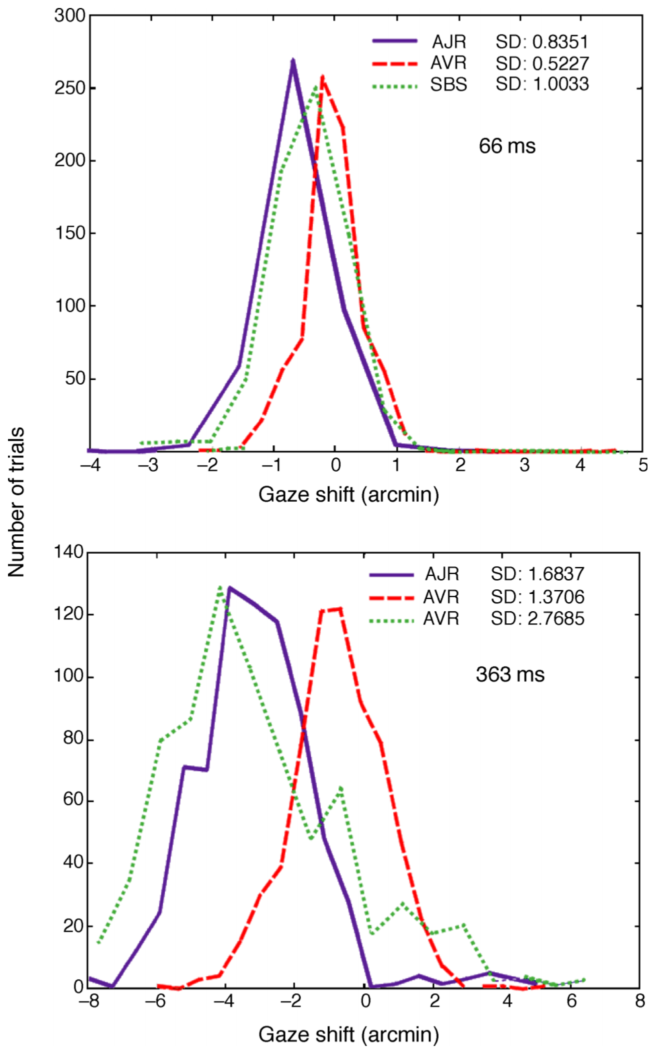

Figure 5. The above figure plots the gaze shift distribution for the referenced condition (Experiment 1) for 3 subjects across 66-ms and 363-ms SOA. The *x*-axis plots gaze shift in arc minutes with positive values indicating upward gaze shifts and negative values indicating downward gaze shifts. The *y*-axis plots the number of trials a given gaze shift occurred. Standard deviations of each distribution appear adjacent to the legend.

The results for Experiment 2 are plotted in Figure 6. The *x* and *y* axes are the same as in Figure 4. For the 66-ms SOA condition, the "retinocentric" curve is steeper than the "spatiocentric" curve across all subjects (AJR: 1.64 vs. 1.88 arcmin, AVR: 1.62 vs. 2.37 arcmin, SBS: 2.62 vs. 3.21 arcmin). However, this trend was not evident in the 363-ms SOA condition. The "retinocentric" curve for all subjects was flatter than the "spatiocentric" curve even though it was consistently steeper than the "shuffled" curve. Furthermore, in most subjects, the PSE is consistent with retinal coordinates, rather than spatiocentric coordinates. Thus by considering how much the bar moved with respect to the retina, improved performance when compared to the "shuffled" curve but not when compared to the "spatiocentric" curve. This trend is not completely consistent with the prediction of no-compensation (Figure 2B) but rather depicts a trend that suggests a partial compensation for eye movements. One complicating factor is that the psychometric functions are not always monotonic (see SBS and AJR data for 363 ms), so that the fits may underestimate the psychometric function slopes at their steepest point.

To obtain a clearer understanding of the references used by subjects when making motion judgments with or without a spatial reference, the data of Experiments 1 and 2 were plotted as indicated in Figures 7A and 7B. The *x*-axis plots the shift of the bar in the image and the *y*-axis plots the shift of the gaze position. Positive values indicate upward motion or gaze and negative values indicate downward motion or gaze. The vertical line extending from zero abscissa represents zero motion of the bar in the image. The diagonal line extending from the left vertex of the *x* and *y* axes has a slope of 1. This represents the line of zero motion of the bar with respect to the retina, i.e., if the bar in the image moved down in space while the gaze shifted downwards by the same magnitude, the movement of the bar on the retina will be zero. The plus symbols (+) represent subjects' "up" responses and the circles (o) represent "down" responses.

It follows that if the motion of the bar were based on how much the bar moved with respect to the image, then the subjects "up"/"down" responses should segregate on either side of the vertical line (zero image motion line). However, if the motion of the bar was based on how much the bar moved with respect to the retina, then "up"/"down" responses of the subject should segregate along the diagonal line (zero retinal motion line). This intuitive plot revealed that for the referenced motion condition (Experiment 1) "up"/"down" responses clearly segregated along the zero image motion line (Figure 7A). This observation is consistent with a system that bases the judgment of motion independent of eye movement. However, in the case of unreferenced motion (Experiment 2), "up"/"down" responses segregated along an oblique axis although not necessarily along the zero retinal motion line (Figure 7B). This trend suggests that compensation of fixation eye movements by the visual system in unreferenced conditions was not all or none but rather partial.

Discussion

The present study provides strong evidence that the visual system is exceptionally robust to the effects of fixation eye movements on motion judgments, provided such motion judgments are made in the presence of spatial references. However, when motion judgments are unreferenced, the effects of fixation eye movements adversely affect motion thresholds.

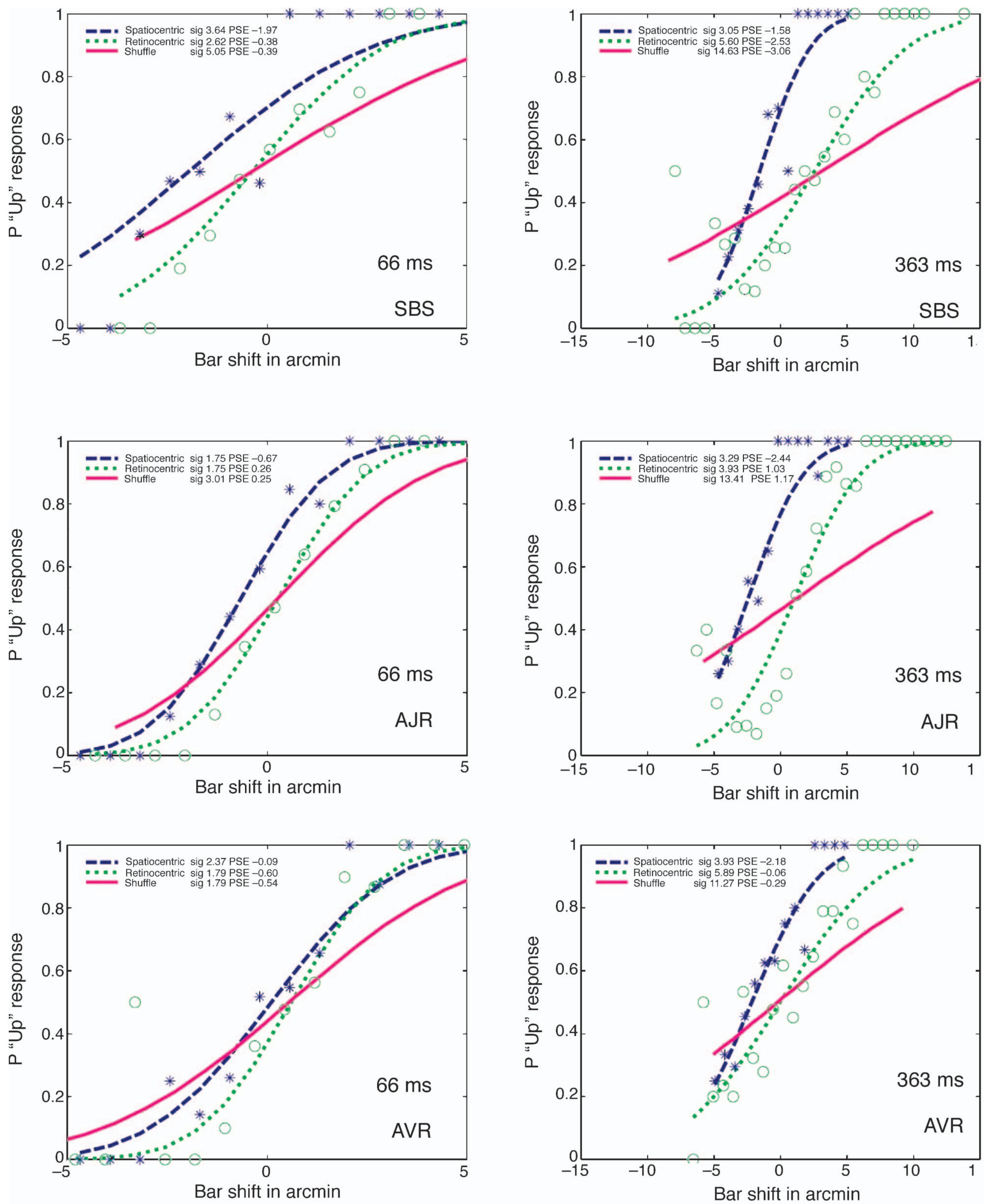

Figure 6. Unreferenced motion condition: Psychometric functions are plotted for 3 subjects across 66-ms and 363-ms SOAs. The slopes of the “retinocentric” analyses are comparable to those of the “spatiocentric” analyses especially for the short SOA. “Retinocentric” slopes are consistently steeper than “shuffled” curves regardless of the SOA. The PSE of the “retinocentric” curves are on average closer to zero when compared with the “spatiocentric” curves.

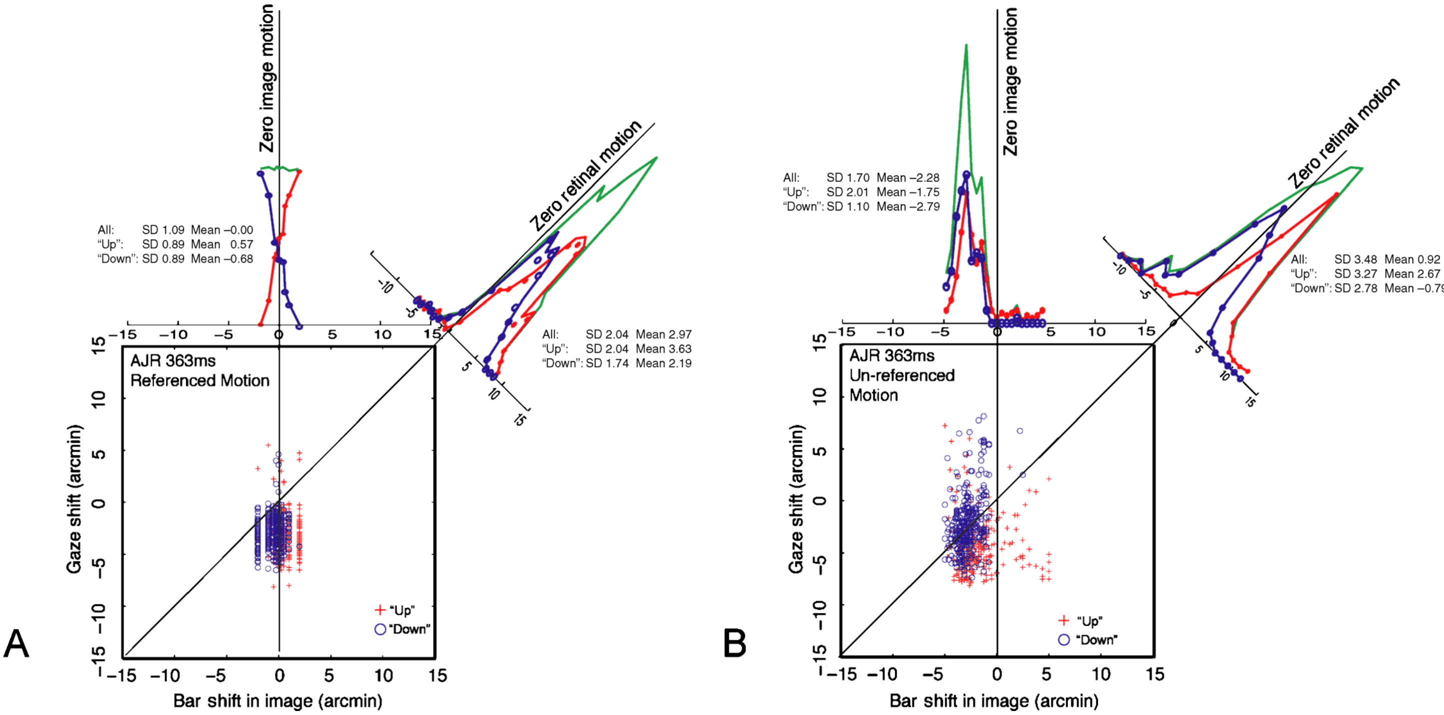

Figure 7. The "up" (+)/"down" (o) responses for subject AJR are plotted as a function of the movement of the bar in the image (*x*-axis) and the shift of the gaze position (*y*-axis) for the 363-ms SOA condition under REFERENCED (A) and UNREFERENCED (B) conditions. Positive values along the *x* and *y* axes represent upward motion/gaze and negative values represent downward motion/gaze. The vertical line extending from the zero abscissa (ZERO IMAGE MOTION) represents ZERO motion of the bar in the image, i.e., zero spatiocentric motion of the bar, and the diagonal line extending from the vertex with a slope of 1 (ZERO RETINAL MOTION) represent ZERO motion of the bar on the retina, i.e., zero retinocentric motion of the bar. The distributions of the "up" and "down" responses and their respective means and standard deviations are indicated at the top and right corner of each plot.

In the case of referenced motion, expressing performance with respect to how much the bar moved on the retina ("retinocentric" curves in Figure 4) was almost equivalent to correcting for randomly assigned fixation eye movement. This suggests that analyzing with a correction for the effects of fixation eye movement was equivalent to adding "noise" to motion judgments. Such a trend is consistent with mechanisms that either ignore or completely compensate for the effect of retinal jitter. Further support for such mechanisms was provided by the observation that despite an increase in the magnitude of eye movements with the longer SOA, the motion threshold ("spatiocentric" curves) did not change dramatically, even though longer SOAs were associated with larger retinal excursions. The third observation that adds impetus to this argument is depicted in Figure 7A. The "up"/"down" responses segregated along the zero image motion line and not along the zero retinal motion line, i.e., the PSE (point of subjective equality) is consistent with spatiocentric coordinates and not retinal coordinates.

However, the above observations do not seem to hold true in the case of unreferenced motion. The results show that while correcting for the eye movements due to fixation jitter ("retinocentric curves" in Figure 6) improves motion thresholds when compared to the "shuffled" curves, the thresholds were still higher than those obtained in the referenced condition, especially for the longer SOA. This observation was interesting because one would expect unreferenced "retinocentric" slopes to be equivalent to referenced "spatiocentric" slopes. The reason for this is that if fixation eye movements solely affected unreferenced motion judgments, then by removing fixation eye movements as a source of noise, we would expect the resulting slopes to be equivalent to the condition where eye movements are either ignored or compensated by the visual system. This condition is represented by the referenced motion condition. Notwithstanding this argument, the observation that the longer SOA condition produced higher motion thresholds regardless of the manner in which the PFs were analyzed suggests that eye movements adversely affected the ability to discriminate unreferenced motion. Furthermore, in Figure 7B the "up"/"down" responses segregated along an oblique axis between the zero image motion line and zero retinal motion line. In this case the PSE shifted from zero image motion toward zero retinal motion, but this shift in PSE was not complete. These observations taken together allude to the operation of partial compensation for fixation eye movements made during unreferenced motion tasks.

With regard to the issue of partial compensation, the most parsimonious explanation for partial compensation may be that certain types of eye movements executed during unreferenced conditions may be compensated by the visual system, while other types may not. An interesting yet consistent observation that was made during the unreferenced motion condition was that all subjects exhibited a slow downward drift of the eyes during the blank interstimulus periods. This was evident in the staircase trials as well as the eye movement histograms of Figure 5. Subjects were unaware that such downward drift occurred; in fact some subjects reported that they "felt" as though they were looking straight ahead at the start of each trial but when the trial was over and the fixation raster re-appeared that raster was perceived to be off fixation, usually superior. We therefore speculate that it may be possible that this downward drift may not be compensated by the visual system, whereas other types of fixation eye movements such as microsaccades may be compensated. Unfortunately, by using the present paradigm we were only capable of extracting the position of the retina when the test stimulus flashed. Therefore it was not possible to ascertain whether the shift in eye position that occurred between each motion frame was due to drifts, saccades or a combination of both. This issue might be resolved by imaging continually with invisible levels of infrared light, producing a continuous eye motion record without providing a reference frame.

The results of the present study also offer strong support for the assertions made by previous studies that the presence of a spatial reference is key to achieving effective compensation for the effects of retinal jitter due to fixation eye movements (Murakami, 2003, 2004; Tulunay-Keesey & VerHoeve, 1987). Furthermore, the results of Experiment 2 are strongly suggestive of compensatory mechanisms that are largely visually driven. This observation therefore argues against the exclusive contribution of processes such as efference copy (outflow signals) or inflow signals such as muscle proprioception (Bridgeman, 1995) as being responsible for driving such compensation. Murakami (2004) postulated a possible mechanism by which compensation could be achieved. He stated that in the presence of a spatial reference, the effects of retinal jitter due to eye movements move both stimulus and surround with the same velocity. Processes that employ a spatial differentiation of velocity will then be able to extract differential motions and therefore remove the effects of spurious motion produced by the fixation eye movements. During unreferenced motion, such spatial velocity differentiation is not possible and therefore the effects of spurious motion produced by the fixation eye movements mask spatiocentric motion of the stimulus therefore producing higher unreferenced motion thresholds. The results of Experiment 1 could be accounted for by such a system; however, the results of Experiment 2 suggest that some form of rudimentary compensation for fixation eye movements may still exist in the absence of a spatial reference and that such compensatory strategies do not seem to be visually driven.

Conclusions

The present set of experiments have shown that motion detection within a frame of reference are unaffected by retinal jitter due to fixation eye movements. This independence between referenced motion thresholds and retinal jitter is produced by compensatory mechanisms that are largely visually driven. Unreferenced motion thresholds are adversely affected by retinal jitter, especially the overall drift of the eye, being higher for larger magnitudes of retinal jitter due to fixation eye movements. Compensatory processes in unreferenced motion may be partial, with only certain types of eye movements being compensated for and not others.

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