



# Perceptual Consequences of Ocular Lens Overshoot During Saccadic Eye Movements

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**In a previous paper we compared eye globe records of saccadic eye movements (recorded with a scleral eye coil) with lens reflection records of the same eye movements (recorded with a dual-Purkinje-image eyetracker); we found evidence for considerable dynamic deviations between the two during and immediately after saccades. We ascribed these deviations to the movements of the eye's lens relative to the optical axis of the eye. This paper quantifies a predicted psychophysical effect of lens displacements during and after saccades. Two small targets, one above the other, were flashed for 2 msec in total darkness, the bottom one exactly at the end of the saccade, the top one 30 msec later. The first target appears deviated horizontally relative to the other, in a direction opposite to the saccade. Magnitude of the relative mislocalization can be up to 0.03 deg for each degree of saccadic eye movement. The result shows that the position of the visual image on the retina is affected both by position of the globe and by deviations of the lens from its normal location.**

Displacement threshold Eye movement Saccade Lens Saccadic suppression Space perception Spatial vision

## INTRODUCTION

Saccadic eye movements are the most frequent of all human behaviors, occurring 2–3 times per second throughout waking life. The microstructure of saccades, and their perceptual consequences, however, remain incompletely understood.

During saccadic eye movements the eye undergoes rapid accelerations, reaching over 20,000 deg/sec<sup>2</sup> for a 10 deg saccade (Bahill, Brockenbrough & Troost, 1981) and even greater values for larger saccades. It has generally been assumed that the eye rotates as a whole during these accelerations. With the assumption of an inelastic eye, motions of the retina across the visual image can be inferred directly from motions of the limbus or the pupil. Most methods of monitoring eye movements, and by implication the movements of images on the retina, are based on measuring the orientation of the eyeball.

We have recently described a movement of the lens relative to the globe that occurs during each saccadic eye movement, however, saccadic accelerations result in significant deviations of the lens from the optical axis (Deubel & Bridgeman, 1995). During the initial acceleration phase of the saccade, the lens lags behind the rest of the eye. It is held in place only by the fibers of the

zonule of Zinn; these fibers must be elastic to allow accommodation to take place. At the start of a saccade the zonule begins a lateral movement of about 0.2 mm for each degree of rotation. This stretches the zonular fibers and creates a lateral force on the lens, accelerating it after a delay. Peak acceleration, and peak elastic stress, occur after about one-quarter of the saccade duration. During the second half of the saccade there is an opposite peak of acceleration during which the lens movement is slowed by the elastic zonule. The lens overshoots the final eye position, and is pulled back by passive elastic forces.

The magnitudes of these effects are dependent on the elasticity of the zonule and of the lens, as well as the peaks of accelerations of the eye movement. The effects are reduced at greater accommodative distances and in older eyes, due to the increased stiffness of the accommodative system. Further, the lens of the young eye at near accommodation may be flattened by the zonule fibers during saccadic accelerations, briefly creating a more distant accommodative state. The previous accommodative state would be restored by passive forces at the end of the saccade.

There are some perceptual consequences of the instability of lens suspension that are not widely recognized. A few observations suggesting sluggish eye lens suspension were made late in the last century. First, Coccius (1888) observed the fourth Purkinje image and described a trembling of the lens with head movements. von Hess (1896) described a downward displacement of the lens with strong accommodation, which can be seen

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entoptically. This displacement, which can attain a magnitude of 0.3 mm, shows the effect of the weight of the eye lens poorly held in place by the relaxed zonula. Neither observation extended to the results of saccadic accelerations, however.

## METHOD

### *Subjects*

Five paid subjects participated in the experiment. Their ages ranged from 21 to 32 yr. It was important to run relatively young subjects, as lens slippage within the eye decreases with age (Deubel & Bridgeman, 1995). The subjects were naive with respect to the object of the study, but were experienced with the equipment from other eye-movement-related tasks, and had normal visual acuity. Results are based on 182 trials from each subject.

### *Apparatus*

Saccades were recorded with a fifth-generation dual-Purkinje-image eye tracker, based on a principle originally developed by Cornsweet and Crane (1973). The device projects a focused infrared light source into the eye, and tracks both the first Purkinje image (the reflection from the front surface of the cornea) and the fourth Purkinje image (the reflection from the back surface of the lens). As the eye rotates, the first Purkinje image moves in the same direction as the eye, while the fourth image, from the concave surface of the back of the lens, moves in the direction opposite the eye (relative to the optical axis). Thus coincident movement of both images indicates head motion, while the difference between the two image motions indicates eye rotation. Special-purpose servomechanics allow a frequency response better than 250 Hz and a noise level equivalent to about 20 sec arc r.m.s. (Crane & Steele, 1985). Unlike earlier eye trackers, the fifth-generation device can follow saccadic movements of 15 deg or more without losing the eye.

In its standard application the comparison of first and fourth Purkinje images in the eyetracker is used to differentiate lateral head motion from eye rotation. Here we use the tracker in a different way; we stabilize the head and use the two Purkinje images to differentiate movements of the globe from movements of the lens.

The signals from the Purkinje eyetracker were digitized at 500 Hz for later analysis. The Purkinje eyetracker was carefully calibrated by having the subjects sequentially fixate locations indicated by little crosses on the screen. Based on these signals, an on-line calibration routine estimated veridical eye position. The system behaved linearly in the measuring range. The computer detected saccade onset by digital differentiation of the sampled eye position signal. Saccade-related sensory events were triggered when instantaneous eye velocity exceeded 30 deg/sec. After this trigger occurred, the program activated the first LED when the eye velocity dropped to 10 deg/sec at the top of the overshoot (Fig. 1).

Experiments were controlled by an IBM-compatible 486 PC which also served for the automatic off-line

analysis of the eye movement data in which saccadic latencies, saccade start and end positions, and overshoots were determined.

The initial fixation stimulus was back-projected on a screen 2.5 m from the subject's eye. This visual target consisted of a red laser spot subtending a visual angle of 0.1 deg and appeared at a visual angle of 8 deg, to the left or the right from the center of the screen. The comparison stimuli by which we aimed to determine the effect of the eye lens deviation was an array of ultra-bright red LEDs [Fig. 1(a)]. The array consisted of a single LED as the first stimulus, and a horizontal row of seven LEDs centered above the first at a vertical offset of 0.072 deg (4.3 min arc). Angular distance between the LEDs in the top row was also 0.072 deg. The LED array was physically mounted on the wall behind the subject, but was seen through a small mirror attached to the center of the screen to allow for an effective viewing distance of 6 m, thus providing the very small angles between the LEDs.

### *Procedure*

The subject viewed the screen binocularly. Head movements were restricted by a biteboard and a forehead rest. The subject's task was to maintain fixation on the actually present target, and to track it with a saccade when it jumped across the visual field.

In each trial the subject had to initially fixate the peripheral laser spot located 8 deg left or right from the center. As it was extinguished, a saccade (with a magnitude of approx. 8 deg) was elicited by briefly illuminating the lower LED. Saccades beginning earlier than 140 msec or later than 400 msec after this target step were discarded. Peaks due to the postsaccadic lens overshoot were sought by a subroutine that was activated when the saccade was detected. It triggered a 2 msec flash in the lower LED when the eye slowed to 10 deg/sec, so that the flash occurred when the lens reached the peak of its overshoot, and triggered another 2 msec flash in one of the upper LEDs 30 msec later (Fig. 1). Flashes in all of the upper LEDs were equally probable. On-line monitoring of triggering and fourth Purkinje image records assured that the trigger caught the peak of the overshoot as reliably as possible. For control trials the first LED was triggered 30 msec after the peak of the overshoot and the second LED 30 msec later. At the end of each saccade the subject indicated whether the upper LED had flashed to the right or to the left of the lower LED, in a two-alternative forced-choice procedure. The two-alternative forced-choice methodology, combined with a parametric range of stimuli, allows us to assess bias and sensitivity separately.

### *Calibration and data analysis*

Each session started with a calibration procedure in which the subject sequentially fixated 10 positions arranged on a circular array of 8 deg radius. The eyetracker behaved linearly within 8 deg around the central fixation. Overall accuracy of the eyetracker

for static fixation positions was better than 0.1 deg. Dynamically, however, the eyetracker records artifactual overshoots at the end of each saccade. In a previous paper (Deubel & Bridgeman, 1995) we demonstrated that these artifacts are not due to the dynamic properties of the Purkinje eyetracker itself which were verified by recording eye position simultaneously with a Skalar search coil system and the Purkinje eyetracker, for both the human eye and an artificial eye provided with the Purkinje tracker. Rather, the findings suggested that the overshoots are a consequence of the movement of the eye lens relative to the optical axis of the eye.

To determine direction of gaze, an off-line computer program searched the eye position record for the end of the overshoot and then calculated mean eye position over a 40 msec time window. The eye movement analysis program calculated latencies and start and landing positions of all saccades occurring in each trial.

## RESULTS

Percentages of "rightward" estimates of the position of the second (upper) LED with respect to the (lower) LED flashed at the overshoot peak are given in Fig. 2, as a function of the actual horizontal stimulus distance. Negative displacement values indicate the upper LED being located to the left of the lower LED. The data are presented separately for the five subjects. The solid curves provide the data for rightward saccades, the dashed curves those for leftward saccades. As can be seen from the systematic separation between the two curves, all subjects perceived an illusory lateral displacement of the two images that was systematically influenced by the direction of the saccade. So, for rightward saccades the upper stimulus tended to be seen to the right of the lower LED. In our previous paper we analyzed in detail, by means of standard optical theory, the effects of eye lens displacements and rotations on the retinal image (Deubel

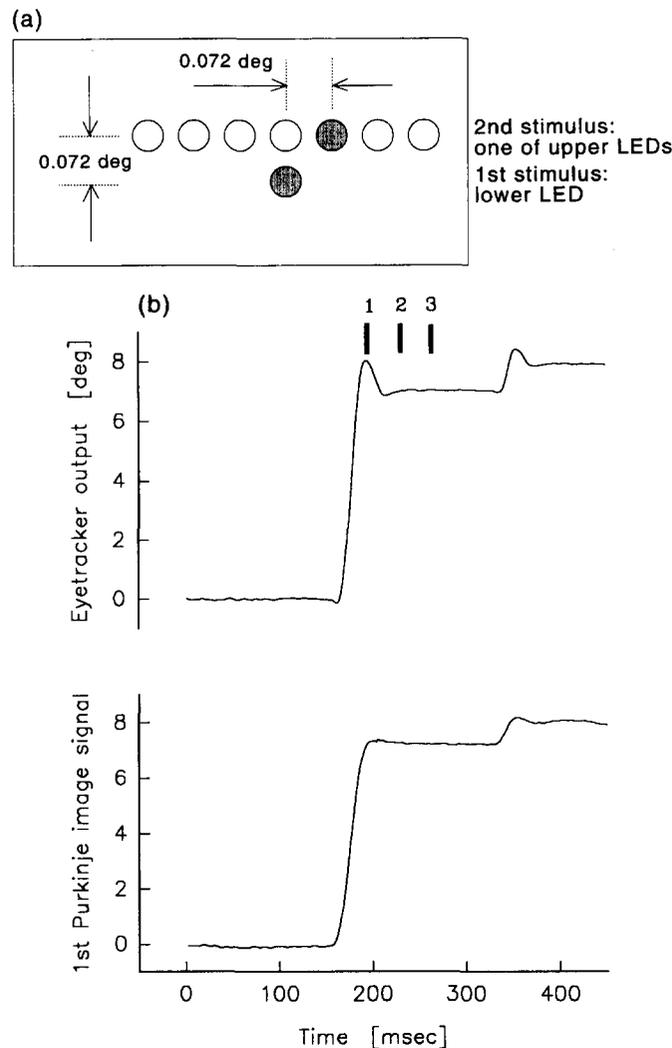


FIGURE 1. (a) Arrangement of the stimulus array. (b) Saccades of 8 deg magnitude recorded with the fifth-generation dual-Purkinje-image eyetracker. Upper trace: eyetracker signal during a saccadic eye movement. The signal represents the difference between fourth and first Purkinje image reflections. The lower trace: first Purkinje image signal (reflection from front of cornea) during the same saccade. The upper trace shows overshoots occurring in large as well as small (corrective) saccades. Overshoots are seen only in the fourth Purkinje image signal. The small vertical bars in the upper diagram indicate the moment of appearance of the 2 msec test flashes. In the main experiment the targets were flashed approximately at the time of the overshoot peak (1) and 30 msec later (2). In the control experiment target flashing occurred 30 and 60 msec after overshoot peak (2 and 3).

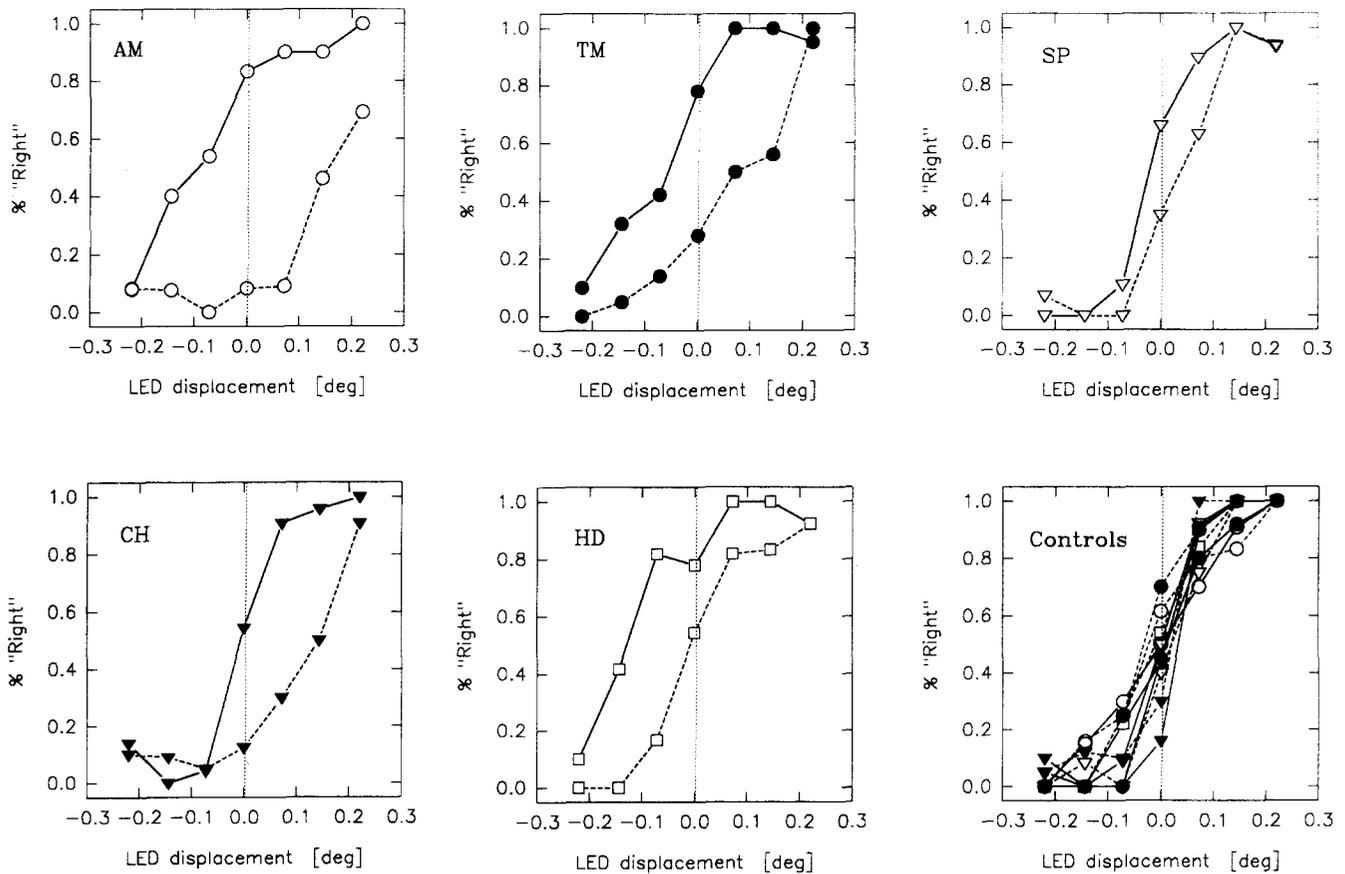


FIGURE 2. Percentages of "rightward" estimates of the position of the second (upper) LED with respect to the (lower) LED flashed at the overshoot peak, given as a function of the actual horizontal stimulus distance. Negative displacement values indicate the upper LED being located left of the lower LED. — Rightward saccades. --- Leftward saccades. Each graph shows the results for one subject. Control trials for flashes after the saccade for all subjects are in the lower-right graph; all of them show similar perceptions for both directions.

& Bridgeman, 1995, Appendix). The analysis showed that for a biconvex lens a lateral deviation of the lens will result in a lateral deviation of the image in the same direction. Thus a rightward lens overshoot (such as occurs with a rightward saccade) will shift the image on the retina to the right, leading to a perceived leftward shift of the previously presented lower LED flashed during the overshoot. As expected, the data from the control experiments with later LED flashing exhibited no systematic biases.

The data were used to compute the mean estimation bias, i.e. the displacement between the two successive stimuli that would be required for the subjects to indicate rightward and leftward displacements with equal probability. These biases are presented in Fig. 3 in relation to the mean overshoot size  $s$  of the eyetracker signal, for each of the five subjects. Positive values of  $s$  indicate rightward overshoots. The results show that overshoot size as measured with the Purkinje eyetracker and perceived stimulus displacement correlate well. The mean magnitude of the psychophysical effect calculated from these data is 0.062 deg for each degree of overshoot. The bias in estimates could not have been due to mislocalization accompanying the main saccade, because it is in the direction opposite the saccade.

Since we assume that the observer's judgement is

directly related to eye lens movement, we should be able to predict for each trial the deviation of perceived target direction from overshoot size. Unfortunately, however, a trial-by-trial correlation of overshoot size with the psychophysical effect is not meaningful because of the small amount of psychophysical information collected in each forced-choice trial. The small variability in the saccade trials [Fig. 3(a)] indicates that the overshoots were very consistent across trials.

## DISCUSSION

Our findings provide converging evidence for the idea that the overshoots in the Purkinje image tracker records reflect movements of the lens relative to the rest of the eye during saccades.

The results presented in Fig. 3 indicate that the size of the angular displacement of a target due to the lens deviation is 0.062 deg psychophysical error per degree of overshoot as determined with the Purkinje eyetracker. Analysis of the optical properties of the human eye reveals that a target displacement of 0.062 deg is equivalent to a retinal image displacement of 0.075 mm (see Deubel & Bridgeman, 1995, Appendix). If an angular relative displacement of the lens axis with respect to the optical axis of the eye is assumed, our former theoretical

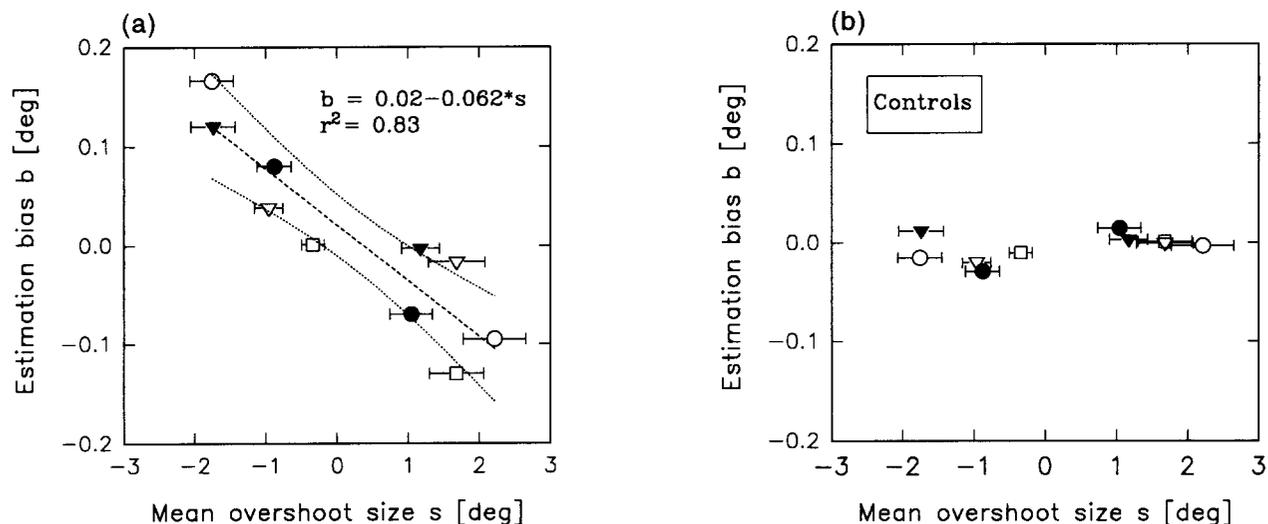


FIGURE 3. Estimation biases for saccade trials (a) and control trials (b), calculated from the psychometric functions given in Fig. 2. The data are shown as a function of the mean overshoot size  $s$  for the individual subject and saccade direction. Positive values of  $s$  indicate rightward overshoots as occurring with rightward saccades. The figure also shows the result of a regression analysis. Confidence intervals are plotted for  $P < 0.05$ .

calculations predict that a Purkinje signal overshoot of only 0.62 deg would already be accompanied by this size of retinal image displacement. However, the fact that the visual displacement effects determined in our experiment are only 62% of the theoretical prediction does not come unexpectedly. A possible technical reason for this discrepancy is that it is not possible to trigger the test flashes exactly at the moment of the overshoot peak. Rather, triggering is more often a few msec too early or too late. This small error is unavoidable, as the peak is very sharp, and it will tend to decrease the measured effect. Further, small forward glissades as frequently occur at the ends of saccades diminish the effect.

The effect is not a mislocalization of visual targets due to extraretinal signals affecting localization in the absence of a visual context. Rather, the flashes were intentionally bright enough to create brief afterimages that the subject could inspect after the saccade. We sought a physical effect on the retina, not an illusion of localization. It is unlikely that the effect was biased by changing extraretinal signals, for Martin (1972) has shown that relative retinal location is the dominant factor in localization of two targets presented within 200 msec.

If the psychophysical effect demonstrated in Fig. 2 and Fig. 3 is so clear, why has it not been seen before in the dozens of studies on localization during saccades? The probable answer is that the effect can be seen in only a very narrow time window; the trigger must occur within a few msec of the peak of the overshoot for the reversal of apparent direction to be seen. We concentrated all of our observations (except control trials) in this narrow window to resolve the effect. The reason we found the reversal of apparent direction, then, is that our previous work had told us where to look.

Our data provide additional evidence that the lens does not accelerate as fast as the eye at either end of a saccade,

because the elasticity of the zonular fibers limits the magnitude of acceleration for brief periods. The Purkinje image eyetracker displays overshoots at the ends of saccades and small backshoots at the beginnings of saccades (Fig. 1) not because of an instrument artifact, but because the image is actually moving in that way. The dynamical difference between the first and fourth Purkinje image records reflects lens motion relative to the globe.

From our observations we expect to find up to 0.03 deg of retinal shift per degree of saccade: the question remains open whether this shift will scale linearly with saccade sizes larger than we presented. Saccades of 12 deg or more should lead to remarkable effects, considerably larger than the radius of the central fovea. These could have important effects in the brief interval at the end of a large saccade, and lead to the idea that one of the functions of saccadic suppression of displacement (Bridgeman, Hendry & Stark, 1975) is to prevent perception of retinal displacements that cannot be compensated or recalibrated by even the most sophisticated efference copy or extraocular muscle proprioception.

The normal pattern of post-saccadic glissades is in a direction that would minimize the effects of simultaneously occurring overshoots. It is possible that the glissades evolved partly to compensate for some of the lens overshoot effect. The visual system cannot evolve to eliminate the overshoots themselves, for they are consequences of zonular elasticity that are essential for accommodation. Indeed, both accommodation and overshoots decrease in magnitude with age (Deubel & Bridgeman, 1995).

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