



Saccades reduce latency and increase velocity of ocular accommodation

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Abstract

Horizontal vergence can be stimulated binocularly with disparity (disparity vergence) or monocularly with accommodation (accommodative vergence). The latter results from a neural cross-coupling that causes both horizontal vergence and accommodation to respond when either one is stimulated [Alpern, M., & Ellen, P. (1956). *American Journal of Ophthalmology*, 42, 289–303]. The velocity of disparity and accommodative vergence is enhanced when accompanied by saccades [Enright, J. T. (1984). *Journal of Physiology (London)* 350, 9–31; Enright, J. T. (1986). *Journal of Physiology (London)* 371, 69–89]. Based upon the coupling between accommodation and vergence, we predicted that accommodation should also be facilitated by saccades. An SRI Dual Purkinje Eyetracker was used to measure left and right eye position, and the accommodation of the left eye, in response to stimulation. Horizontal saccades were stimulated by targets separated by 2–6° and accommodation was stimulated monocularly over a range of ± 2 diopters (D). When saccades occurred within 0–400 ms following a monocular step stimulus to accommodation, latency of accommodation decreased and the associated accommodative-vergence response was synchronized with the saccade. Saccades also enhanced the velocity of accommodation and accommodative-vergence, and this facilitation increased with saccade amplitude. Transient vergence responses that are normally associated with saccades [Erkelens, C. J., Steinman, R. M., & Collewijn, H. (1989). *Proceedings of the Royal Society of London B. Biological Sciences*, 236, 441–465; Maxwell, J. S., & King, W. M. (1992). *Journal of Neurophysiology*, 68 (4), 1248–1260] did not affect accommodation when it was not stimulated by defocus. Because saccades and accommodation utilize separate plants and final common pathways, the synchronization of saccades and accommodation and the enhanced velocity of accommodation and accommodative-vergence must occur at more central sites. Possibilities include the superior colliculus, which represents both accommodation and saccades [Nagasaka, Y., & Ohtsuka, K., (1998). *Investigative Ophthalmology AVRO supplement*], vestibular nuclei which project to regions near the oculomotor nuclei [Lang, W., Buttner-Ennever, J. A., & Buttner, U. (1979). *Brain Research*, 177, 3–17], and interactions between omni pause neurons and near response cells of the mesencephalic reticular formation (MRF) [Mays, L. E., & Gamlin, P. D. R. (1995a). *Current Opinions in Neurobiology*, 5, 763–768; Mays, L. E., & Gamlin, P. D. R. (1995b). *Eye movement research: Mechanisms, processes and applications*. New York: Elsevier] which represent both accommodation and vergence [Judge, S. J., & Cumming, B. G. (1986). *Journal of Neurophysiology*, 55, 915–930; Zhang, Y., Mays, L. E., & Gamli, P. D. R. (1992). *Journal of Neurophysiology*, 67, 944–960]. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Horizontal vergence eye movements respond to a variety of stimuli including binocular disparity, accommodative-vergence, and perceived distance (see overview by Schor, Alexander, Cormack & Stevenson,

1992). Saccadic facilitation of horizontal vergence velocity has been demonstrated with natural targets that contain all of these stimulus cues (Enright, 1986; Erkelens, Steinman & Collewijn, 1989). Attempts have been made to isolate stimulus cues by viewing targets monocularly to eliminate binocular disparity while retaining blur and perceived distance cues (Enright, 1986; Erkelens et al., 1989). These studies demonstrate that saccadic facilitation of vergence velocity is dominated by disparity cues in binocular stimuli since the ampli-

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tude of inter-saccadic vergence is reduced by 75% during monocular stimulation. A remaining question is what stimuli evoke saccadic facilitation of vergence under monocular viewing conditions? Interactions between saccades and vergence could have been stimulated directly by perceived distance or blur, or indirectly by accommodative-vergence. While there have been no direct measures of accommodation during saccadic facilitation of vergence, Erkelens et al. (1989) found that the amount of saccadic facilitation of vergence obtained under monocular viewing conditions was closely related to the age (and therefore, extent of presbyopia) of the three observers, suggesting the involvement of accommodation and accommodative-vergence.

The potential facilitation of accommodation by saccades would depend upon the site of interaction. Saccades could facilitate accommodative-vergence velocity without influencing the accommodative response if the interaction occurred in the vergence plant. Alternatively, both accommodation and accommodative-vergence velocity could be enhanced by saccades if the interaction occurred at a more central site such as the near response cells, that represent both focusing and horizontal disconjugate movements of the eyes (Judge & Cumming, 1986; Zhang, Mays & Gamlin, 1992). Finally, accommodation could be facilitated indirectly as a result of saccadic facilitation of horizontal vergence and the cross-coupling between vergence and accommodation referred to as vergence-accommodation (Fincham & Walton, 1957).

We have investigated interactions between horizontal saccades and near responses of accommodation and horizontal vergence resulting from monocular stimulation of accommodation. Latencies of accommodation and accommodative-vergence were reduced and their velocities were enhanced when accommodative stimuli were accompanied by saccades. Latencies of the near responses were reduced when saccades occurred during the baseline latency period for accommodation (0–400 ms prior to the accommodative response). Velocity facilitation and latency reduction of accommodation and accommodative-vergence increased with saccade amplitude. Transient vergence responses normally associated with saccades (Erkelens et al., 1989; Maxwell & King, 1992) did not affect accommodation when it was not stimulated by defocus. This observation suggests that the saccadic enhancement of accommodation did not result from vergence driven accommodation (Fincham & Walton, 1957). The facilitation of both accommodation and vergence by saccades is consistent with the model that omnipause neurons synchronize the activity of saccades and the near response (Mays & Gamlin, 1995a,b).

2. General methods

2.1. Recording apparatus

Binocular eye movements, and the accommodative responses of the left eye were measured with the Generation V SRI Dual Purkinje Eyetracker (Crane & Steele, 1978, 1985). The optometer utilizes the Scheiner principle to monitor the conjugate focus of the eye (Crane & Steele, 1978, 1985). A Pentium computer, equipped with a Data Translation A/D and D/A board, was programmed to control data acquisition (sampling rate 200 Hz). Accommodation was monitored in the left eye. The right eye was occluded at a remote point that was optically conjugate to its entrance pupil. The occluder was positioned beyond the dichroic mirror of the SRI tracker that reflects the ocular images used to sense eye position. Horizontal position of both eyes was monitored for assessment of vergence.

The SRI recording optometer requires a large (i.e. 5 mm), stable pupil for artifact-free measures in the presence of eye movements. Measures of eye position are also facilitated by pupil dilation. Phenylephrine Hydrochloride (PHCL) 2.5% was used to dilate subjects' pupils. Although this drug has been shown to reduce the near point of accommodation (Biggs, Alpern & Bennett, 1959; Garner, Brown, Baker & Colgan, 1983; Zetterstrom, 1984), to reduce accommodative amplitude (Stephens, 1985; Mordi, Lyle & Mousa, 1986a), and to slow accommodative response times (Mordi, Tucker & Charman, 1986b), these effects might well be expected to influence the saccade and 'no-saccade' trials equally.

At the beginning of the experiment, 2–3 drops of PHCL were administered to the subjects left and right eyes. After 50–70 min, the pupils were sufficiently dilated to begin the experiment, and full dilation was maintained for at least 1.5 h, well longer than any experimental session (< 1 h).

The subjects refractive correction was placed in the optical path of the left eye. Subjects were given rest periods periodically over the course of the experiment, and used Cellufresh™ eye drops if the infra-red sources of the SRI tracker caused any irritation of the cornea. The subjects head position was maintained with a combination mouth bite and forehead rest.

2.2. Stimuli

Distance cues were minimized in the current investigation by presenting monocular stimuli at a constant distance in a fronto-parallel plane at a 30 cm viewing distance. Targets of constant size in this plane deviated from the isovergence surface (Schor, Maxwell & Stevenson, 1994) by less than 0.1°. This

target configuration emphasized retinal blur as the main stimulus to both accommodation and its cross-coupling with convergence (Schor & Kotulak, 1986).

The horizontal saccade stimulus (Fig. 1) consisted of three black crosses presented in a circular white 20° field. Each cross subtending 0.38° and was separated horizontally by 1, 2 or 3° at a viewing distance of 30 cm (corresponding to an accommodative stimulus of -3.33 D). The crosses were centered in a 20° aperture of the SRI visual stimulator. To eliminate the role of disparity vergence, the stimulus was viewed monocularly with the left eye. The SRI visual stimulator contains a Badal stimulus optometer that was used to stimulate accommodation. The Badal system altered the dioptric vergence subtended by the three crosses. Dioptric vergence was controlled electronically by translating a large positive lens that imaged the target at points proximal to the anterior focal point of the Badal lens. The position of this lens was controlled by the computer to adjust step changes in focus over a 4 diopter range centered about a -3.33 D midpoint.

2.3. Calibration

Right and left eye positions were calibrated simultaneously by having the subject successively fixate each of the three horizontally separated targets, three times, holding the fixation at each location for 2 s. The calibration was performed with the right eye occluded to measure its position under the same conditions as when accommodative-vergence was measured. The position-voltage gain for the right eye was measured at a later time with the right eye unoccluded to verify that the gain estimate under the occluded condition was valid. The average percentage difference between occluded and unoccluded condition gain estimates was $+7.0\%$ for LL and -0.38% for EG. The calibration

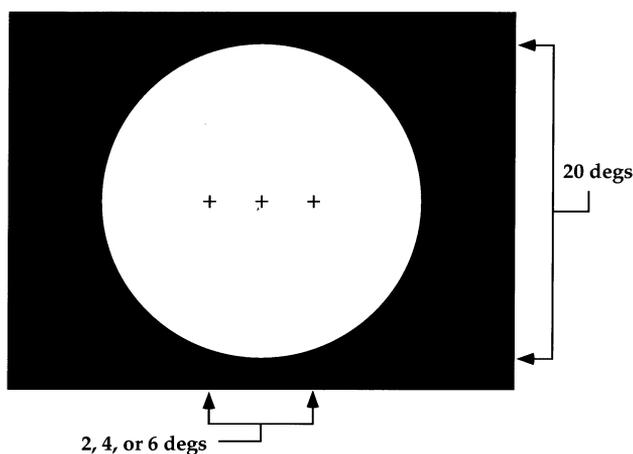


Fig. 1. Subjects view of the stimulus. Separation of crosses varied from 1 to 3°, depending on the experiment. For experiments 2 and 3, only the 4° saccade stimulus (2° separation) was used.

Table 1

Slope criteria used for determining latency and duration of left and right eye saccades, vergence and accommodation in the automated data analysis program

	Saccades	Vergence	Accommodation
Start	>25 deg/s	>3.0 deg/s	>2.0 D/s
End	<12 deg/s	<1.5 deg/s ^a	<1.0 D/s

^a Or 90% of end vergence value, if the velocity was still above criterion at the end of the trial.

utilized the same target separations used during the experiment (1, 2 or 3°: see Fig. 1). Accommodation was calibrated by having the subject fixate the center cross target and maintain clear focus, while a calibrated voltage signal was output to the SRI stimulus optometer to change the dioptric vergence of the left eye stimulus. The accommodation calibration range was $+2.0$ to -2.0 D, relative to the -3.33 D starting position determined by the 30 cm viewing distance, and the target changed focus in 0.5 D steps every 4 s. The sign notation for an increase of accommodative stimulus (ACStim) was negative (corresponding to a negative lens power) and the sign notation for an increase of accommodative response (ACResp) was positive. All calibration data were digitized and stored for off-line analysis.

2.4. Data analysis

Calibration functions were computed off-line for the position of both the left and right eyes, and for accommodation of the left eye, by plotting the stimulus values (in degrees or D, respectively) as a function of digitized values of voltage analogs of eye position and accommodation. Calibration functions were obtained by fitting a linear regression to these plots.

The data were analyzed with an automated program that applied the appropriate calibration function to the raw data. The algorithm used the velocity criteria (as calculated over five samples (25 ms sampled at 200 Hz)) shown in Table 1 to estimate latency and duration of left and right eye saccades, vergence, and left eye accommodation.

Saccade trials wherein no change in ACStim occurred (0 D trials) were analyzed separately with a slightly different version of the automated program. The analysis was identical, except that in cases where no accommodation or accommodative-vergence response was detected (by slope criteria listed in Table 1), the program would compute the mean response of accommodation and vergence over 100 ms following the end of the saccade. This was done to detect the presence of small changes in accommodation or accommodative-vergence due to the saccades.

Latency, peak velocity and duration of ocular accommodation were identified with the following criteria:

1. The algorithm searched for the first sample point after the stimulus presentation where the slope over five samples (25 ms) was greater than 1.67 D/s.
2. Starting from that point, the slope over the next 20 samples (100 ms) must be greater than 2.5 D/s.
3. The movement had to be in the correct direction.
4. The algorithm continued to loop until these three conditions were met. The first slope threshold is low and over small number of samples to obtain a reliable start time. The second slope threshold is higher and over more samples to minimize false positives.
5. Next the maximum slope was found over a 20 sample (100 ms) period by computing these slopes over the rest of the movement.
6. The end of the accommodative response was identified when both a five sample and 20 sample slope dropped below 1 D/s

Peak accommodative velocity and an estimate of vergence velocity were also computed. We were unable to calculate peak vergence velocity directly because the SRI eye tracker has a saccade overshoot artifact. This is produced by motion of the lens within the eye during a saccade which causes a brief translation of the fourth Purkinje image that is unrelated to eye rotation (Deubel & Bridgeman, 1995). This lens deviation precludes the direct computation of peak saccade or vergence velocities because different lens deviations in the two eyes could produce spurious high values for vergence velocity. Our estimate of vergence velocity during the saccade or intra-saccadic accommodative-vergence was derived from the slope of a line fit between eye position 10 ms before and 10 ms after the saccade using velocity criteria described in Table 1.

The lens motion does not affect measures of accommodation since they are based upon an analysis of retinal images rather than on the reflections from ocular surfaces (Purkinje images). We have verified this by measuring accommodation and saccades when stimulated by a change in target position while the accommodative stimulus remained unchanged. Accommodation and accommodative-vergence did not change systematically during saccades when there was no change in the accommodative stimulus. On many trials, no change in accommodation was detected by our subroutine. On other trials small increases and decreases in accommodation that averaged less than 0.25 D (see Fig. 6) were associated with both leftward and rightward 6° saccades. These changes in accommodation were not coincident with the lens artifact. When accommodation did occur, it began 60–70 ms after the saccade and peaked at about 80–100 ms or more after the saccade with an average duration of 300 ms. The lens motion artifact associated with saccades peaks in 30 ms and is completed in less than 40 ms after the saccade onset with an average duration of 30 ms (Deubel & Bridgeman,

1995). The differences in onset and duration between saccade artifact and lens accommodation indicate that the delayed changes in accommodation following the saccade were not an artifact of lens wobble.

This method for computing the slope effectively removed most of the potential transient vergence responses that are normally associated with saccades from the analysis (Erkelens et al., 1989; Maxwell & King, 1992). This study stimulated saccades ranging from 2–6° in amplitude. Saccades had durations ranging from 35 to 50 ms (Bahill, Clark & Stark, 1975; Collewijn, Erkelens & Steinman, 1997). The combined duration of these saccades and the additional 20 ms (10 ms before and 10 ms after the saccade) yields minimal temporal intervals for analyzing vergence velocity, ranging from 55 to 70 ms. Transient vergence movements associated with 5° saccades have durations ranging from 50–70 ms (Collewijn et al., 1997) indicating that our analysis interval would have excluded the majority, if not all of the transient vergence component of saccade facilitated vergence responses. Thus our procedure leads to an underestimation of the true peak velocity of vergence, and precludes measurement of the transient divergence spike that normally occurs during the intra-saccadic interval (Erkelens et al., 1989; Maxwell & King, 1992; Collewijn et al., 1997).

Left and right eye positions, vergence (left minus right), and left eye accommodation traces were displayed on the computer monitor as a function of time to verify the algorithm and reject trials, if necessary. Trials were rejected if:

1. Accommodation or vergence changed by more than 50% of the start criterion (Table 1) at the time the ACStim was presented.
2. A blink occurred during the trial.
3. On a no-saccade trial, a saccade was made that was greater than 50% of the stimulus that would have occurred on a saccade trial.
4. On a saccade trial, no saccade was made, or the saccade amplitude was less than 50% of the stimulus.
5. The amplitude of the accommodative response was less than 50% of the stimulus.

2.5. Subjects

Three individuals, ages 22, 23 and 34, with normal visual and oculomotor functions, served as subjects. Two were naive as to the hypothesis under investigation (MC and EG), and the other was an author (LL). Two of the subjects (EG and LL) were able to control both the timing and amplitude of saccades in response to stimuli and to suppress saccades during no-saccade trials. Despite the instructions to not make saccades until a stimulus was presented, the third subject (MC) made inadvertent microsaccades with amplitudes up to

0.5° at unpredictable times during both saccade and no-saccade trials. When he attempted to respond to a saccade stimulus he responded with an unusual sequence of small saccades (staircase) rather than with a single large saccade. This subjects data are included in the report because they illustrate how microsaccades interact with accommodation and accommodative-vergence. However, they were analyzed with descriptive statistics separately from the other two subjects because MC was unable to control the timing and amplitude of his saccades, making it impossible to control these two parameters in his data analysis. This is not an unusual response since it has been reported in prior vergence studies (Kenyon, Cuiffreda & Stark, 1980; Erkelens et al., 1989; Maxwell & King, 1992; Oohira, 1993; Collewijn, Erkelens & Steinman, 1995). Under the 'pure/symmetric vergence' conditions described in many of these studies, small saccades often occurred, and saccade-free near responses are less typical than those containing saccades. Previous researchers have used the presence of habitual staircase saccades as an exclusion criterion for testing subjects (Collewijn et al., 1995). However, we included descriptive statistics for this subject since this behavior may be typical for some naive observers.

3. Experiment 1

Enright (1984) and Collewijn et al. (1995) have demonstrated that saccade facilitation of vergence velocity is greater when the ratio of saccade size to vergence amplitude is high. This could result from a non-linear interaction with saccade amplitude, as well as a linear interaction related to the increased duration of large compared to small saccades (Maxwell & King, 1992). In this experiment, we investigate this amplitude dependent interaction between saccades and accommodation. We also examined latencies, velocity and amplitude of accommodative-vergence associated with saccade facilitated accommodation. Subjects were asked to initiate a saccade from one fixation cross to another as soon as a change in the focus of the stimulus was detected.

3.1. Apparatus

See Section 2.

3.2. Procedure

Each trial began with a warning tone followed by a variable delay before the stimulus was presented. The subject was instructed to fixate steadily on one of the two peripheral targets (shown in Fig. 1) before initiating the trial (the central target was only used during

calibration). On 2/3 of the trials, when the stimulus changed focus, the subject was instructed to simultaneously saccade to the other peripheral cross and 'clear the stimulus' as quickly as possible. On the remaining trials (no saccade condition), a different warning tone sounded, and the subject was instructed to maintain fixation on the original cross and try to 'clear the stimulus' (or focus) as quickly as possible when the target blurred. These two types of trials were randomly interleaved with five levels of accommodation (-2.0 , -1.5 , 0 , 1.5 , 2.0 D) relative to the -3.33 D reference stimulated by the 30 cm viewing distance. The 0 D stimulus to accommodation was included as a control to determine if changes in accommodation were coupled via vergence accommodation with the divergence spike that normally occurs during saccadic version responses (Erkelens et al., 1989; Maxwell & King, 1992). Forty trials were run in each session. Three different saccade sizes (i.e. 2, 4 and 6°) were investigated in separate sessions. Each subject participated in 10–12 counterbalanced sessions.

3.3. Analysis

Mean latencies, velocities and amplitudes of accommodation and accommodative-vergence were computed for all subjects and stimulus conditions, as described in Section 2.

3.4. Results

Typical examples of eye movement and accommodation traces for the three subjects during saccade and no-saccade conditions are presented in Fig. 2A–C. These trials were chosen from the 6° saccade data set by determining the median latencies and velocities of accommodation and accommodative-vergence for each individual subject, and selecting the trials that most closely fit these median values.

Inspection of the figure reveals that for each subject, the accommodative-vergence response stimulated by monocular blur precedes the accommodation response. This finding has been reported previously (Wilson, 1973). Additionally, accommodative latencies were shorter for all subjects when associated with saccades (top and bottom panels) than in the no-saccade condition (middle panels) for at least one direction of accommodative response.

Subject EG (Fig. 2A) had a large saccade facilitation of accommodative latency for increasing direction of accommodation (left column), but none for the decreasing direction (right column). Accommodative latencies for EG (Fig. 2A) were approximately 300 ms shorter for the saccade than no-saccade condition for increases but not decreases of accommodation. He tended

to have some small saccades in the no-saccade condition (2, 4 and 6° data combined: – ACStim = 42%; + AC-

Stim = 22%), but not as many as exhibited by subject MC. Accommodative latencies for LL (Fig. 2B) were

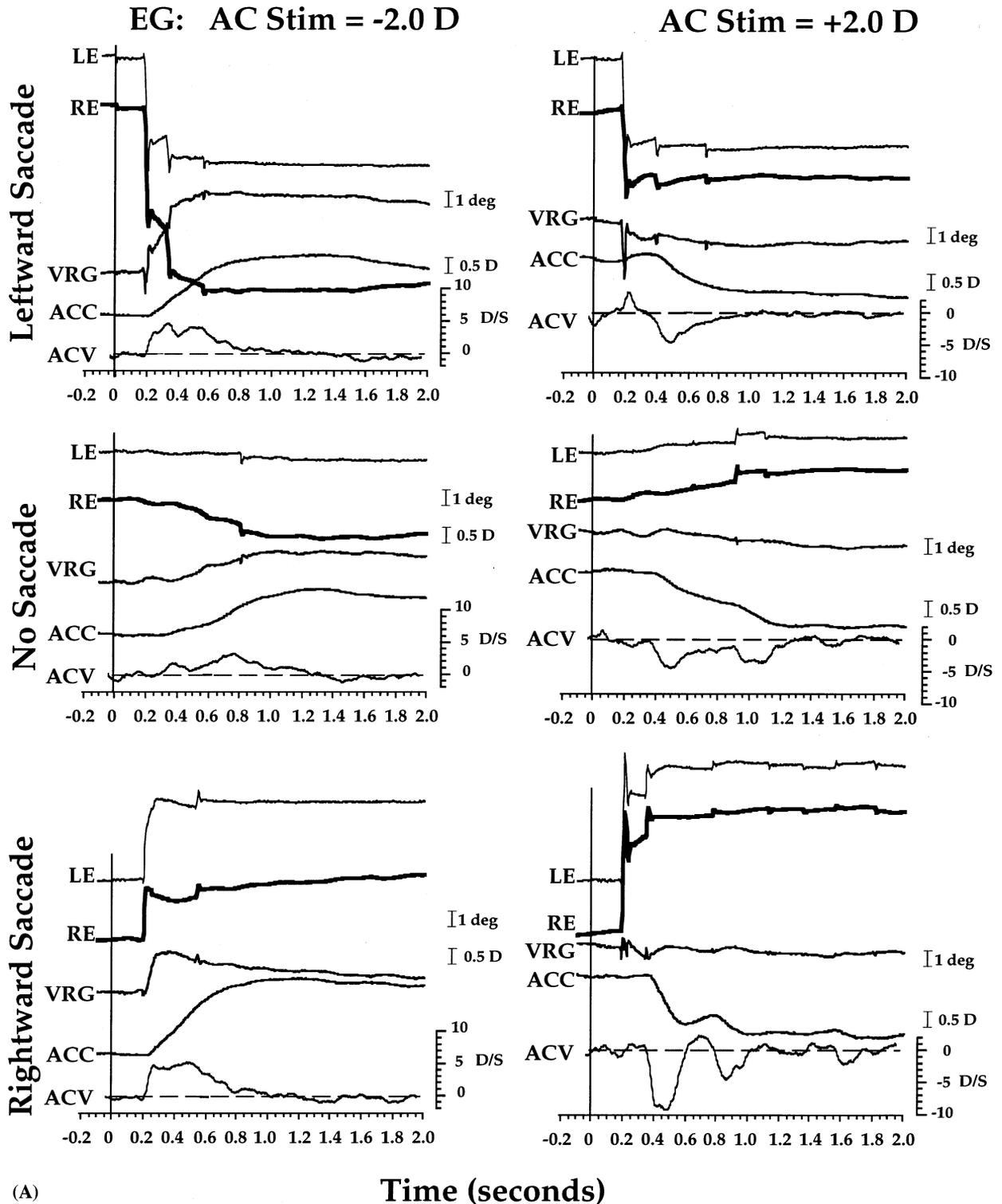


Fig. 2. Typical examples of eye movement and accommodation traces for three subjects during 6° saccade (top and bottom panels) and no-saccade (middle panels) conditions (left panel, trials requiring increased accommodation; right panel, trials requiring *decreased* accommodation). Time 0 corresponds to ACStim onset. The following conventions apply: LE, left (viewing) eye position; RE, right (non-viewing) eye position; VRG, vergence position (LE-RE); ACC, accommodation (D); ACV, accommodation velocity (D/s) derivative of ACC (21st order digital FIR filter with a low-pass, 12.5 Hz cut-off). These recordings illustrate changes of responses but not the absolute magnitudes.

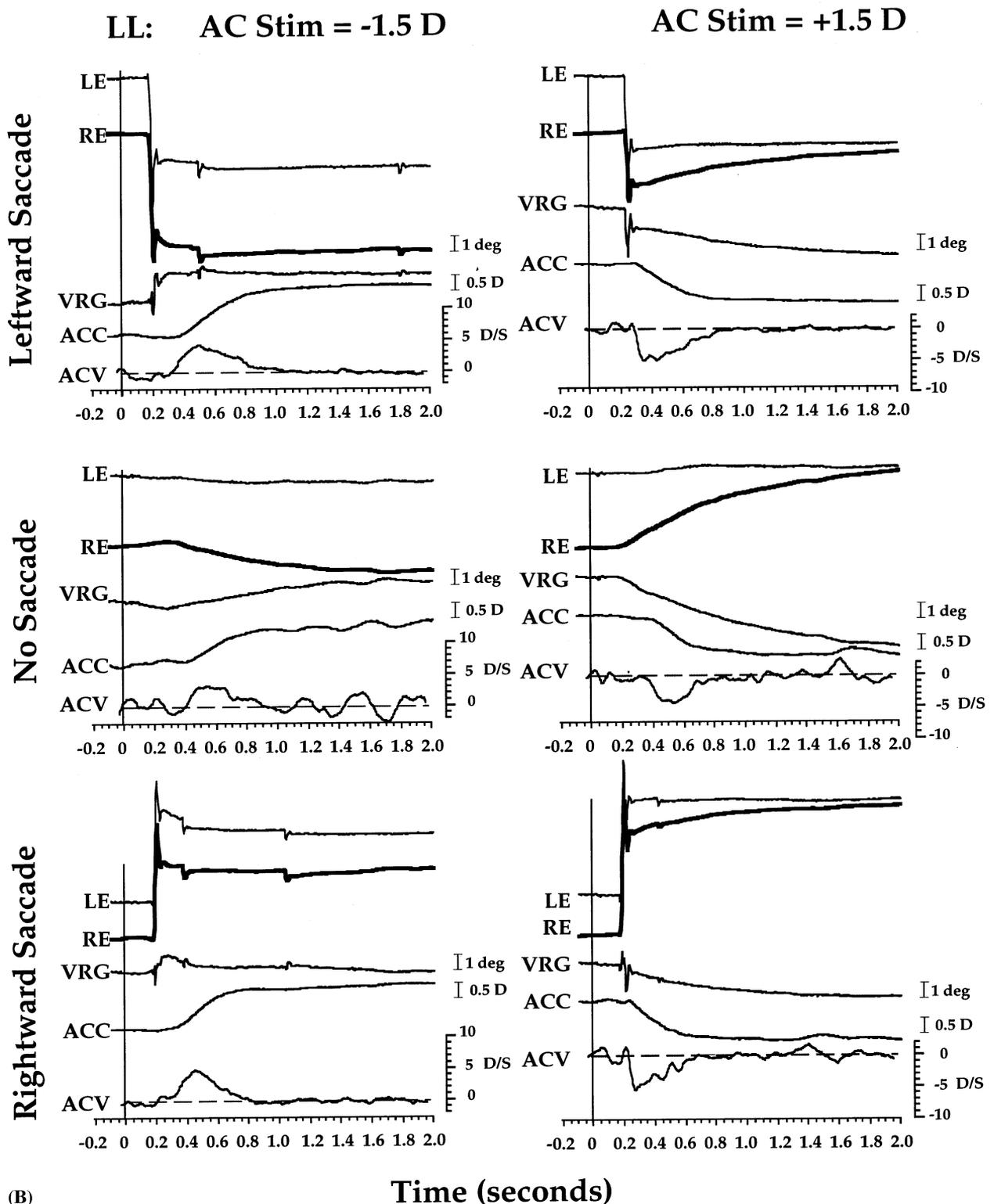


Fig. 2. (Continued)

approximately 100 ms shorter for the saccade than no-saccade conditions for both directions of accommodation. This subject was able to suppress small saccades effectively (percentage of saccades in the no-saccade

condition for 2, 4 and 6° data combined: - ACStim = 15%; + ACStim = 0%). Accommodative latencies for MC (Fig. 2C) were 100 ms shorter for the saccade than no-saccade condition for decreases of accommodation,

and his latencies for increasing accommodation were similar in the no-saccade condition and the saccade condition. The latency facilitation shown by MC for decreasing accommodation was primarily the result of

differences in the no-saccade condition for increasing and decreasing accommodation. In the no-saccade condition, MC had longer latencies for decreases compared to increases in accommodation. Unlike subjects LL and

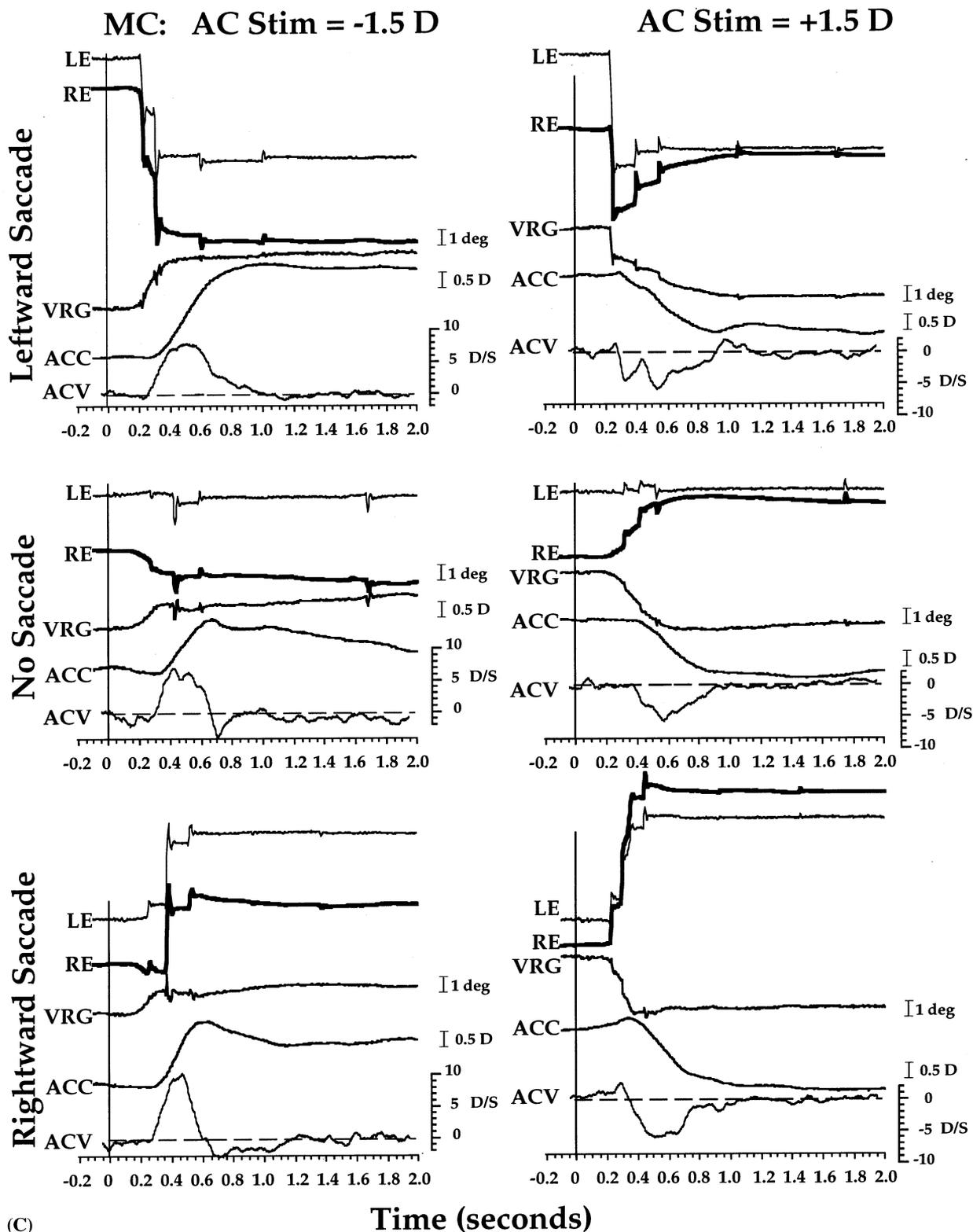


Fig. 2. (Continued)

EG, MC was unable to suppress small saccades during the no-saccade condition (percentage of saccades occurring in the no-saccade condition for 2, 4 and 6° data combined: $-ACStim = 64\%$; $+ACStim = 93\%$). Compare the no-saccade conditions for MC (Fig. 2C: middle panels) with those for subject LL (Fig. 2B). The typical pattern of staircase saccades is evident for MC in the middle panel of Fig. 2C but not for LL in the middle panel of Fig. 2B.

The velocities of accommodation and accommodative-vergence for EG and LL were greater when associated with saccades than in the no-saccade condition. In the example shown for EG, (see Fig. 2A), velocity for increasing accommodation was 3 D/s without saccades and 4.5–5 D/s for the saccade condition. A striking example of saccade facilitation is shown for EG whose accommodative velocity was 9 D/s for decreasing accommodation with a rightward saccade. In the example shown for LL, (see Fig. 2B), velocity for relaxing accommodation (right panel) was 4.5 D/s for the no-saccade condition and 6 D/s for the saccade condition. Saccadic facilitation of accommodative velocity was less apparent for MC (Fig. 2C), who was unable to suppress involuntary saccades during the no-saccade trials. Although the latency of his decreasing accommodative response was reduced with saccades, the velocity was the same as for the no-saccade condition. The velocity of his accommodative response in the no-saccade condition (6–7 D/s) was greater than that for EG or LL in their saccade-facilitated conditions. It is possible that velocity enhancement was prevented by a saturation limit of the accommodation plant. Figure 2C does illustrate some saccadic facilitation of accommodative response velocity (8–10 D/s) for MC when accommodative stimulus was increased.

Figure 3 presents bar graphs of the mean latencies for combined data of EG and LL. Latency of accommodation (left panels) and accommodative-vergence (right panels) are represented for the three saccade sizes for leftward (LW), rightward (RW) and no saccade conditions. Responses to 1.5 and 2 D stimuli were combined. Accommodation latencies were shorter for the saccade than no-saccade conditions, and this effect increased with saccade size. Asterisks and *P* values indicate significant differences between the saccade and no-saccade latencies at the $P < .05$ level. We used a repeated measures ANOVA to test for differences in the response latency between the saccade and no-saccade conditions while accounting for the correlations among measurements within each subject. These were done separately for leftward and rightward saccades. Comparison of the left and right panels of Fig. 3 illustrate that when accommodation stimulus increased ($-$ lens) saccades also reduced latencies for accommodative-vergence. However, when accommodation decreased ($+$ lens) saccades reduced latencies more for

accommodation than accommodative-vergence. This difference was observed for individual subjects as well as for the group data shown in the figure. The mean accommodation and accommodative-vergence latencies for the three subjects are presented in Table 2.

Facilitation of accommodative latency varied idiosyncratically with direction of accommodative response and direction of saccades. Latency was reduced in the saccade condition with increases in accommodation for EG, decreases in accommodation for MC, and both directions of accommodation for LL. Similar trends were observed for saccadic facilitation of the latency for accommodative vergence. These changes were unrelated to the resting focus of accommodation for these subjects (1.25 D for EG; 0.1 D for MC and 0.0 D for LL), all of which were two or more diopters less than the baseline reference accommodative stimulus (-3.33 D).

Figure 4A presents frequency histograms of the delay of accommodative-vergence relative to saccade onset. The delay was calculated from the difference between saccade onset and accommodative-vergence onset to illustrate the synchrony of these motor responses, collapsed across saccade size, for individual subjects. The light hatched bars indicate trials in which the latency of accommodation was shorter than the latency in the no saccade condition minus 2 standard deviations. These represent express accommodation responses that have clearly been facilitated by saccades. The dark bars indicate delays associated with accommodative responses of longer latencies that fell within 2 standard deviations of the normal latency in the no saccade condition. Positive values indicate trials where vergence responses started before the saccade was initiated, and negative values indicate that the saccade started first. Normally, the latency for accommodation and accommodative-vergence is greater than the latency for saccades (Wilson, 1973). Infrequent examples of negative values are contained in all but one of the histograms. More frequently, saccade facilitation was indicated by the clustered peaks of the latency distributions for accommodative-vergence near zero, indicating that the onset of saccades and accommodative-vergence were approximately synchronous. The accommodative vergence associated with express accommodative responses are more tightly clustered around zero delay or synchronous responses than are the responses associated with longer latencies. Synchronization for EG and LL occurred for both increases and decreases of accommodation. There was also limited synchronization for MC for the decreasing accommodation responses. The most frequent responses by MC were positive values, indicating accommodative-vergence preceded saccades, possibly as a result of his early inadvertent saccades. On average, accommodative-vergence latencies were 25 ms shorter than saccadic latencies. The distributions of

Table 2
Accommodation and accommodative-vergence latencies, velocities, and amplitudes for individual subjects in Experiment 1^a

	Latency (ms)				Velocity (D/s), (deg/s)				Amplitude (D), (deg)			
	Saccade		No sacc		Saccade		No sacc		Saccade		No saccade	
	–Lens	+Lens	–Lens	+Lens	–Lens	+Lens	–Lens	+Lens	–Lens	+Lens	–Lens	+Lens
<i>Accommodation</i>												
EG	285 (9.17)	327 (9.24)	334 (11.09)	389 (6.25)	4.83 (0.24)	–5.50 (0.22)	3.73 (0.16)	–4.66 (0.27)	1.65 (0.07)	–1.37 (0.04)	1.44 (0.07)	–1.36 (0.06)
LL	324 (5.91)	332 (6.93)	387 (10.54)	383 (10.63)	4.60 (0.08)	–4.39 (0.10)	3.63 (0.11)	–4.32 (0.09)	1.41 (0.03)	–1.37 (0.03)	1.60 (0.04)	–1.37 (0.02)
MC	285 (4.63)	325 (5.85)	307 (5.28)	392 (9.89)	7.06 (0.21)	–6.88 (0.20)	7.40 (0.27)	–6.90 (0.29)	1.87 (0.05)	–1.66 (0.04)	1.72 (0.06)	–1.63 (0.04)
<i>Accommodation-vergence</i>												
EG	183 (7.31)	199 (4.93)	234 (16.3)	187 (3.75)	11.45 (0.62)	–7.48 (0.26)	7.12 (0.49)	–5.49 (0.31)	2.13 (0.26)	–0.82 (0.05)	1.60 (0.09)	–0.77 (0.07)
LL	165 (2.19)	183 (4.28)	258 (13.48)	191 (7.99)	11.28 (0.36)	–8.61 (0.36)	5.49 (0.26)	–5.91 (0.22)	2.04 (0.21)	–2.47 (0.14)	1.67 (0.29)	–2.43 (0.20)
MC	176 (2.60)	194 (2.65)	170 (3.64)	205 (4.15)	11.22 (0.42)	–20.70 (0.45)	10.66 (0.37)	–17.00 (0.37)	1.77 (0.07)	–4.09 (0.08)	1.50 (0.07)	–4.38 (0.15)

^a Reported values are collapsed across saccade amplitude and direction. Values in parentheses are S.E.M.

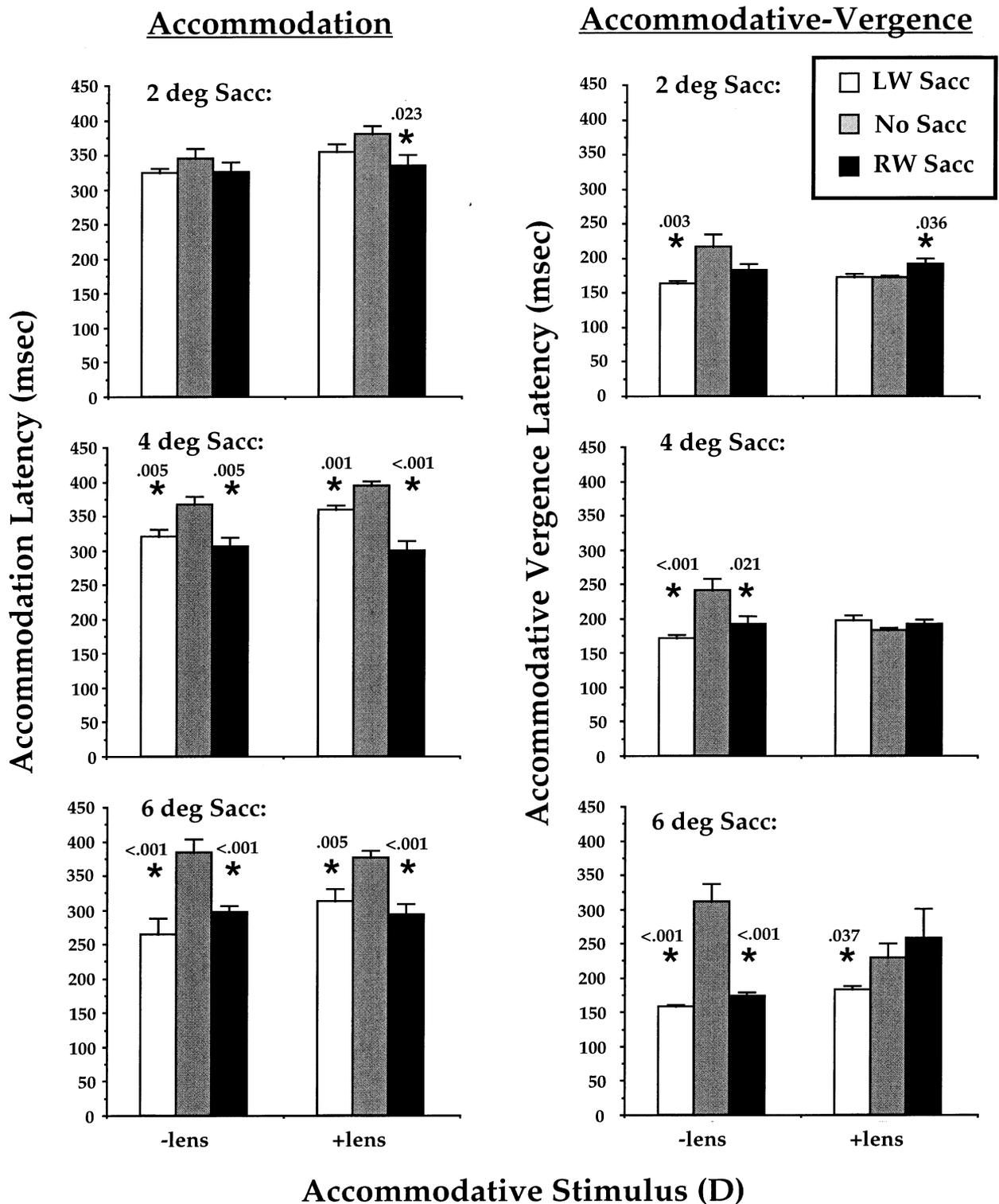


Fig. 3. Mean latencies for subjects EG and LL for accommodation (left graphs) and accommodative-vergence (right graphs) for 2, 4 and 6° saccades. Leftward saccades (LW), left/white bars; rightward saccades (RW), right/black bars; no-saccade condition, middle/gray bars. Error bars indicate +1 S.E.M. Asterisks and *P* values indicate significant differences between the saccade and no-saccade latencies at the 0.05 level.

delays were bimodal for EG. One response mode was synchronous and the other was negative for decreasing accommodative stimuli and positive for increasing ac-

commodative stimuli. The predominant positive response exhibited by MC could have resulted from a serial strategy in response to our multiple task of

accommodation and gaze shift. Accommodation could have been initiated first followed by a gaze shift. The synchronous responses exhibited by LL and EG suggest parallel processing of the two tasks (correcting eye position and reducing blur). Indeed EG reported that at times he could perform both tasks at once and at other times he focused first and made the saccade later.

Figure 4B presents frequency histogram of the delay of accommodation response relative to saccade onset. The delay was calculated from the difference between saccade onset and accommodation onset, collapsed

across saccade size for individual subjects. The histograms examine the similarity of the delay distributions of accommodation for comparison with delay distributions of accommodative-vergence, relative to saccades, as shown in Fig. 4A. The light hatched bars indicate trials in which the latency of accommodation was shorter than the latency in the no saccade condition minus 2 standard deviations. These represent express accommodation responses that have clearly been facilitated by saccades. The dark bars indicate delays associated with accommodative responses of longer la-

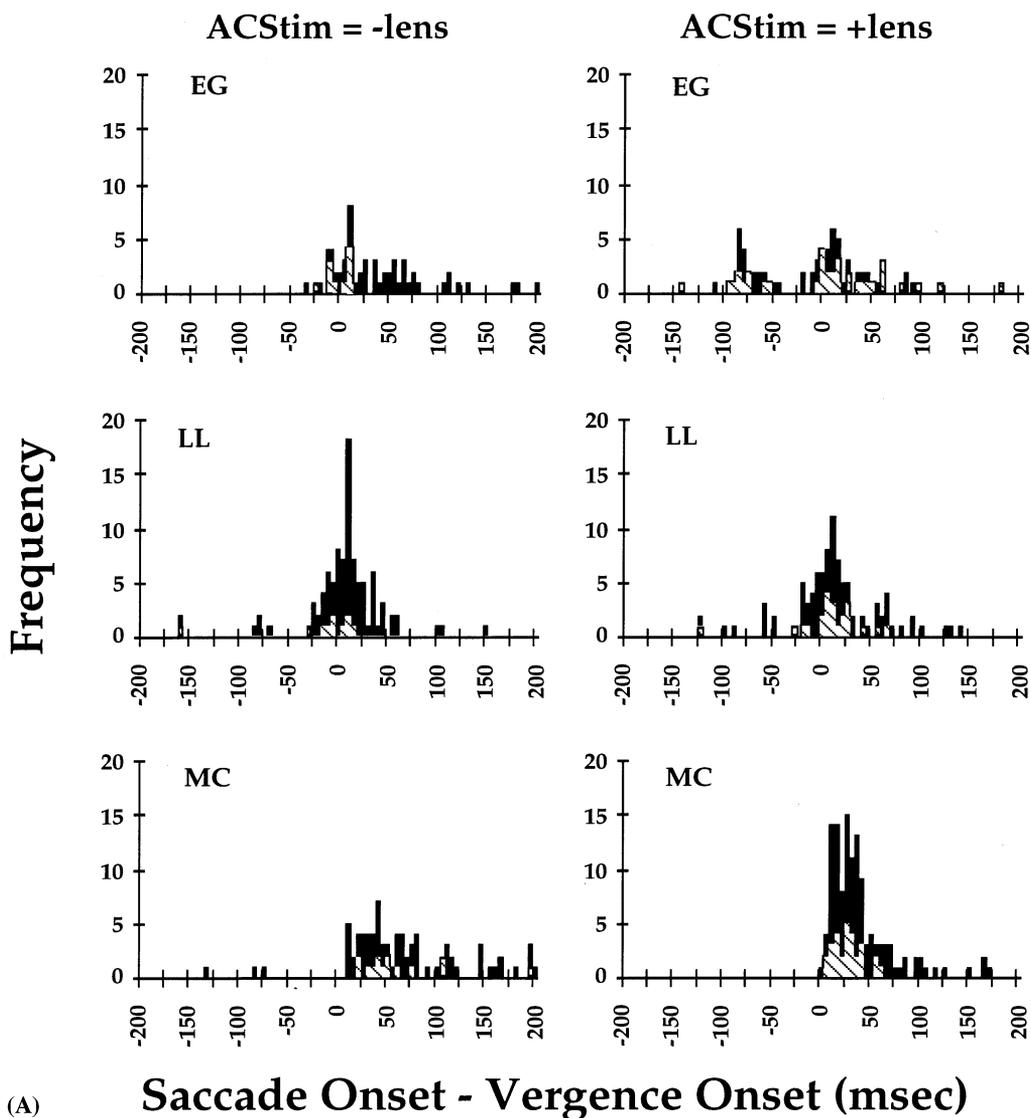
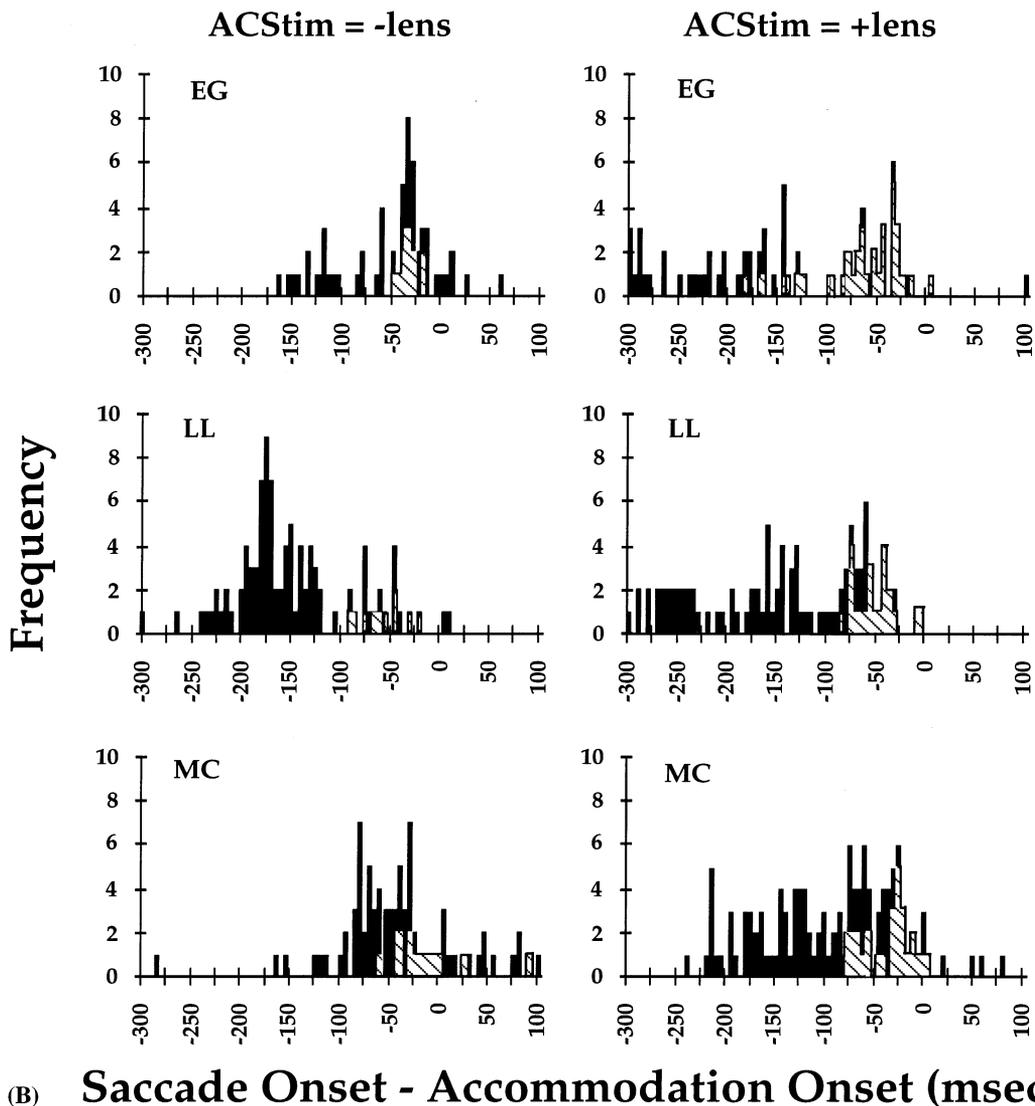


Fig. 4. (A) Delay of accommodative-vergence relative to saccade onset. Delay was computed from differences between saccade latency and accommodative-vergence latency. Frequency (number of occurrences) of the delay for individual subjects for two directions of accommodation (left panel, trials requiring a increase in accommodation; right panels, trials requiring a decrease in accommodation). Hatched pattern indicates trials in which latency of accommodation was shorter than the latency in the no saccade condition, minus 2 standard deviations. Data combined for all saccade sizes. (B) Delay of accommodation relative to saccade onset. Delay was computed from difference in saccade latency and accommodation latency. Frequency (number of occurrences) of delays for individual subjects for two directions of accommodation (left panel, trials requiring a increase in accommodation; Right panels, trials requiring a decrease in accommodation). Hatched pattern indicates trials in which the latency of accommodation was shorter than the latency in the no saccade condition minus 2 standard deviations. Data combined for all saccade sizes.



(B) **Saccade Onset - Accommodation Onset (msec)**

Fig. 4. (Continued)

tencies that fell within 2 standard deviations of the normal latency in the no saccade condition. Positive values indicate trials where accommodative responses started before the saccade was initiated, and negative values indicate that the saccade started first. The majority of responses are negative indicating that saccades usually preceded the accommodative response. The express accommodative responses tend to be clustered around a 50 ms delay from the saccadic response and delays are longer for accommodative responses associated with longer latencies.

The time lag of accommodation from accommodative-vergence is illustrated by the peaks of the light hatched parts of the delay histograms for accommodation (Fig. 4B) and accommodative-vergence (Fig. 4A) which differ by approximately 50 ms for EG, 75 ms for LL, and 75 ms for MC. The temporal lag of accommodation response from its associated accommodative-ver-

gence has been attributed to the neuromuscular delay of the ciliary body and plant delay of accommodation (Wilson, 1973). The distributions of delay histograms for accommodation and accommodative-vergence have similar ranges but they differ in kurtosis (peaking). The delays for accommodation (Fig. 4B) were more evenly distributed and less kurtotic than the delays for accommodative-vergence (Fig. 4A). Similar observations were made by Wilson (1973) who interpreted the differences in means and standard deviations of latencies as indicating that independent cell populations contribute to the activity of accommodation and accommodative-vergence.

Figure 5 presents mean velocities of accommodation (left panels) and accommodative-vergence (right panels) for subjects EG and LL associated with three saccade sizes for leftward (LW), rightward (RW) and no saccade conditions. Velocities for both accommodation

and accommodative vergence were higher for the saccade than the no-saccade condition for both of these subjects, and this effect increased with saccade size.

Asterisks and *P* values indicate significant differences between the saccade and no-saccade velocities at the 0.05 level. A repeated measures ANOVA was used to

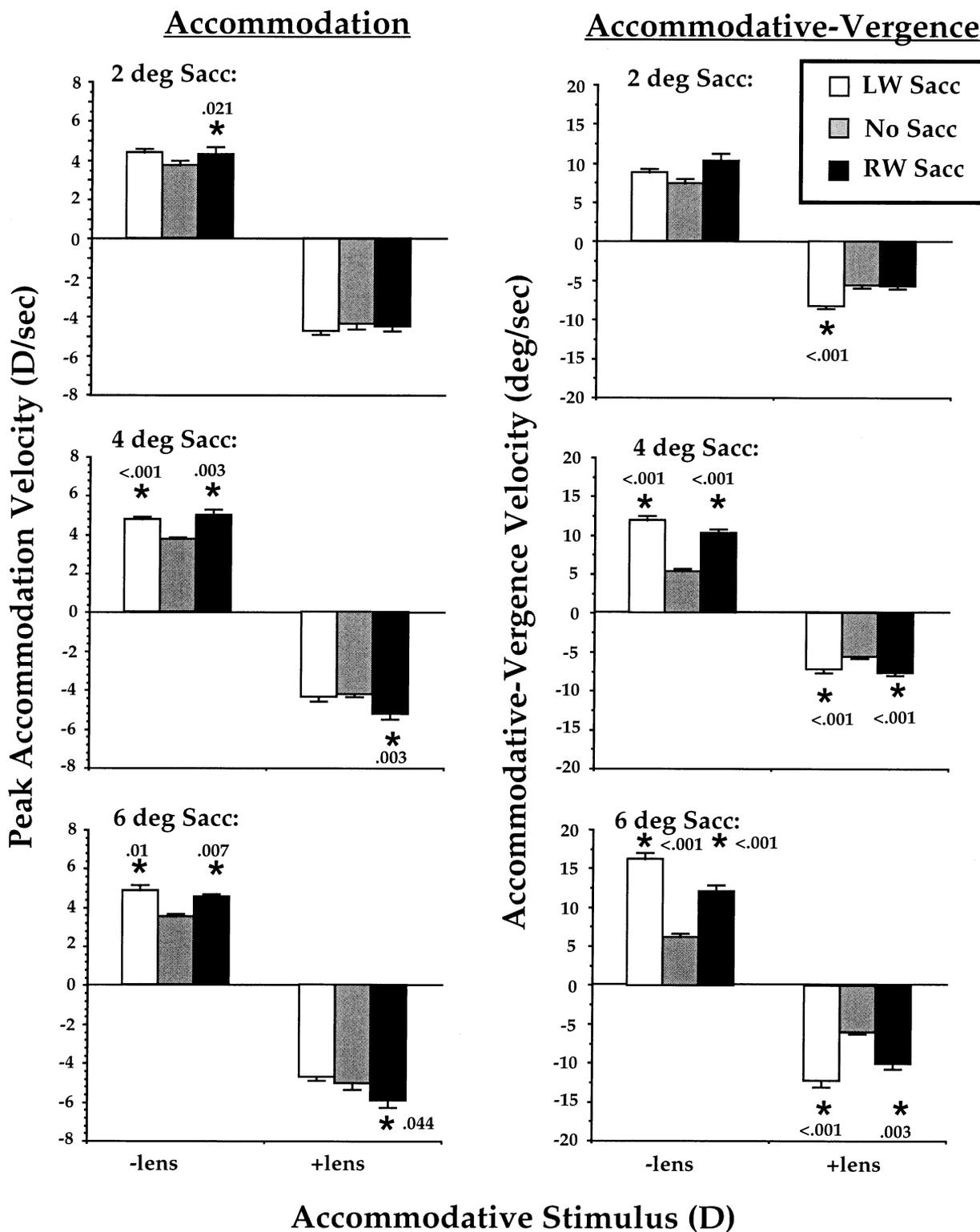


Fig. 5. Mean velocities for subjects EG and LL for accommodation (left graphs) and accommodative-vergence (right graphs) for 2, 4 and 6° saccades. Leftward saccades (LW), left/white bars; rightward saccades (RW), right/black bars; no-saccade condition, middle/gray bars. Error bars indicate +1 S.E.M. Asterisks and *P* values indicate significant differences between the saccade and no-saccade velocities at the 0.05 level.

test for differences in peak response velocity between the saccade and no-saccade conditions while accounting for the correlations among measurements within each subject. These were computed separately for leftward and rightward saccades. Mean accommodation and accommodative-vergence velocities for the three subjects are presented in Table 2. Velocity of accommodation and accommodative vergence also varied idiosyncratically with direction of accommodative response and direction of saccades. EG had greater accommodation and accommodative-vergence velocity facilitation for stimuli requiring an increase in accommodation with leftward saccades, as well as for stimuli requiring a decrease in accommodation with rightward saccades. LL had a greater velocity facilitation of both functions for stimuli requiring an increase in accommodation with rightward saccades. These differences were similar to the directional asymmetries for saccadic facilitation of accommodative-vergence reported by Enright (1986).

Figure 6 (solid regions) presents total amplitudes of accommodative response (left panels) and accommodative-vergence (right panels) for subjects EG and LL for the three saccade-size trials for leftward (LW), rightward (RW) and no saccade conditions. Asterisks and *P* values indicate significant differences between the saccade and no-saccade total amplitudes at the 0.05 level. A repeated measures ANOVA was used to test for differences in response amplitudes between the saccade and no-saccade conditions while accounting for the correlations among measurements within each subject. These were computed separately for leftward and rightward saccades. In addition, the hatched regions of Fig. 6 (right panel) depict intra-saccadic accommodative-vergence. For comparison, the portion of total accommodative-vergence completed in the same time interval is shown for the no-saccade condition (hatched region of the middle = gray bar).

The accommodation and accommodative-vergence responses to the 0 D condition are also presented in Fig. 6. As indicated in the figure, accommodation and accommodative-vergence did not change systematically during saccades when there was no change in the accommodative stimulus. Small increases in accommodation were associated with either increases or decreases in vergence indicating that there was no systematic coupling between these responses. The changes in accommodation were predominantly less than 0.25° which is within the low frequency noise fluctuations for the accommodative system (Kotulak & Schor, 1986). This observation suggests that changes in accommodation associated with saccades are not stimulated by the transient divergence spike that normally accompanies saccades (Erkelens et al., 1989; Maxwell & King, 1992). This saccade-related response interval was calculated separately for each subject and saccade size. Mean accommodation and accommodative-vergence re-

sponses, as well as intra-saccadic accommodative vergence for the three subjects are presented in Table 2.

On average, there was no change in accommodation amplitude with saccade size or saccade condition (see Table 2). This is not surprising given that the accommodative loop was closed. The total accommodative-vergence response amplitude for a stimulus requiring decreased accommodation was independent of saccade size. However, there was an increase in accommodative-vergence with saccade amplitude for accommodative stimuli in the increased direction ($-$ lens) which did not reach the significance level because of large variability. Saccade facilitated accommodative vergence amplitudes during the intra-saccadic interval (hatched area) were more striking than facilitation of the total response amplitude (solid area). As shown in Table 2, the amount of accommodative-vergence completed during the saccade (or saccade related response interval) was greater than the vergence completed during the same time interval in the no-saccade condition, and this effect increased with saccade size.

It is possible to calculate the response AC/A ratio (the gain of accommodative vergence associated with each diopter of accommodation) from these data. Accommodative vergence is expressed in units of degrees rather than the more familiar unit of prism diopters. The normal response AC/A ratio, according to Ogle Martens and Dyer (1967), is four prism diopters/D. The average response AC/A of the two main subjects EG and LL is 2.53 prism diopters/D when they had no saccades or small saccades. The AC/A was much higher when saccades were allowed (averages 3.8 prism diopters/D). While the no-saccade values are lower than the 'normal' they are not outside of the normal range of values (Ogle et al., 1967). Normally, the AC/A measures are made without monitoring saccades so that the 'normal' value could be influenced by the presence of saccades. The main point here is that the accommodative vergence values are larger when associated with saccades.

4. Experiment 2

Experiment 1 has demonstrated that facilitation of latency and velocity of accommodation and accommodative vergence, and amplitude of accommodative-vergence depends on saccade size. This section addresses the question, of whether saccade facilitation of accommodation and accommodative-vergence depends on accommodative stimulus amplitude.

4.1. Subjects

Two subjects from experiment 1 (EG and LL) participated in experiment 2.

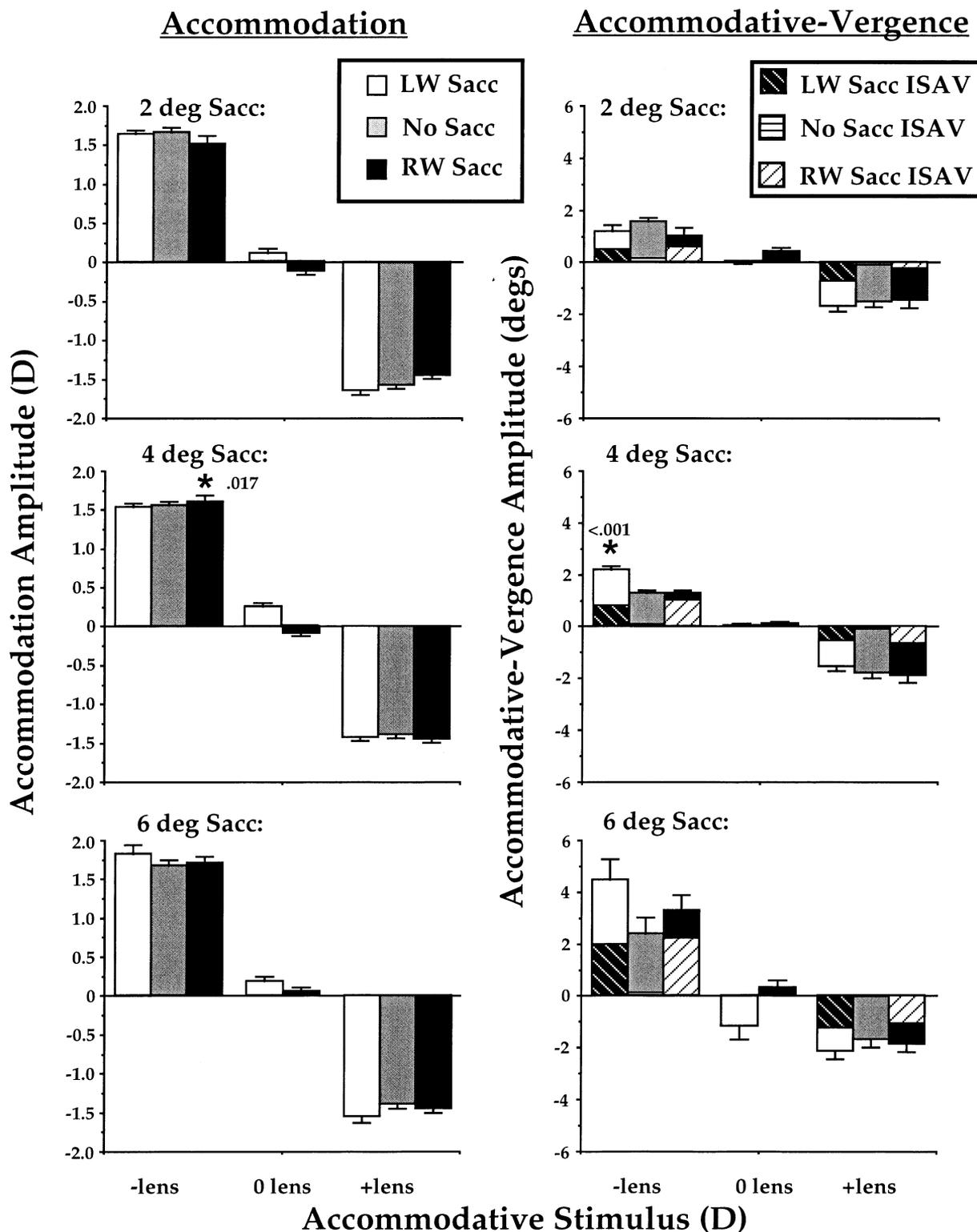


Fig. 6. Mean amplitudes of accommodation (left graphs) and accommodative-vergence (right graphs) for 2, 4 and 6° saccades for EG and LL. Leftward saccades (LW), left/white bars; rightward saccades (RW), right/black bars; no-saccade condition, middle/gray bars. Error bars indicate +1 S.E.M. The total accommodative-vergence response is indicated by the height of the bars, and the hatched patterns in the figure depict the intra-saccadic accommodative-vergence (ISAV). Note that in some no-saccade conditions, the ISAV amplitude is so low that it is not apparent in the histogram. Asterisks and *P* values indicate significant differences between the saccade and no-saccade total amplitudes at the 0.05 level.

4.2. Apparatus

See Section 2.

4.3. Procedure

The same procedure described in experiment 1 was employed. However, only the 4° saccade stimulus, and a smaller range of accommodative stimuli (−1.5, −1.0, −0.75, 0, 0.75, 1.0 and 1.5 D) were used. As in experiment 1, the 0 D stimulus to accommodation was included as a control to determine if changes in accommodation resulted from vergence accommodation that could be coupled with the divergence spike which normally occurs when conjugate saccades are stimulated (Erkelens et al., 1989; Maxwell & King, 1992). We used an ANOVA to examine whether accommodative stimulus amplitude affected the degree of saccadic facilitation of latency, velocity and amplitude of either accommodation and/or accommodative vergence. The analyses of subjects EG and LL were conducted separately for the leftward and rightward saccade conditions and for the positive and negative accommodative stimuli. Any significant interaction ($P < 0.05$) would indicate that the degree of saccadic facilitation was influenced by accommodative stimulus amplitude.

4.4. Results

There was no evidence of any consistent interaction between accommodative stimulus amplitude and saccade facilitation of accommodation and accommodative vergence. However, there were a few conditions in which idiosyncratic interactions occurred. As in experiment 1, accommodation latencies for both subjects were shorter when associated with a saccade. However, there was no systematic effect of accommodative stimulus amplitude on saccade interactions with accommodation or accommodative vergence latencies. An exception for subject EG was a reduction of accommodative latency during leftward saccades that increased with decreasing positive ($P = 0.008$) and negative ($P = 0.04$) accommodative stimulus amplitudes. Accommodative stimulus amplitude had no effect on saccade interactions with his accommodative-vergence latencies.

Velocity of accommodation and accommodative vergence were facilitated by saccades, independently of accommodative stimulus amplitude. An exception for subject EG was an elevation of accommodation vergence velocity during leftward saccades that increased with increasing negative accommodative stimulus amplitude ($P = 0.01$). An exception for subject LL was an elevation of accommodative-vergence velocity during rightward saccades that increased with increasing negative accommodative stimulus amplitude ($P = 0.04$).

Neither subject had any systematic increases in sac-

cadic facilitation of the amplitude of accommodation, accommodative-vergence or intra-saccadic accommodative-vergence as a function of accommodative stimulus amplitude. An exception for subject EG was an elevation of accommodative response amplitude during leftward saccades that increased with increasing positive accommodative stimulus amplitude ($P < 0.001$) and an elevation of accommodative vergence amplitude during leftward saccades that increased with increasing negative stimulus amplitude ($P = 0.003$). As in experiment 1, accommodation and accommodative-vergence did not change systematically during saccades when there was no change in the accommodative stimulus.

5. Experiment 3

This experiment presented saccadic and accommodative stimuli with various stimulus onset asynchronies to determine the optimal timing to yield facilitation of latency and velocity of accommodation.

5.1. Apparatus

See Section 2.

5.2. Subjects

All three subjects from experiment 1 (LL, EG and MC) participated in experiment 3.

5.3. Procedure

Each trial began with a warning tone. The subject was instructed to fixate steadily on one of the two peripheral targets (shown in Fig. 1) before initiating the trial. S/he was told that over the course of the trial, a second tone might occur. If the tone occurred, the subject was to saccade as quickly as possible to the other peripheral target. If no tone was heard, (no saccade condition) the subject maintained fixation on the original target while accommodating in response to blur. At the same time, the subject was instructed to keep the target as clearly focused as possible (or to clear the target as quickly as possible if it became defocused). Following several practice trials, this procedure was readily accomplished by all three subjects.

Four levels of accommodation (−2.0, −1.5, 1.5, 2.0 D) relative to the −3.33 D stimulated by the 30 cm viewing distance were presented in each experimental session. Saccade cueing tones occurred between −700 and 500 ms relative to the change of the accommodative stimulus. Both these variables were randomly interleaved. A 4° saccade stimulus was used for all trials in this experiment. Subjects made leftward saccades on

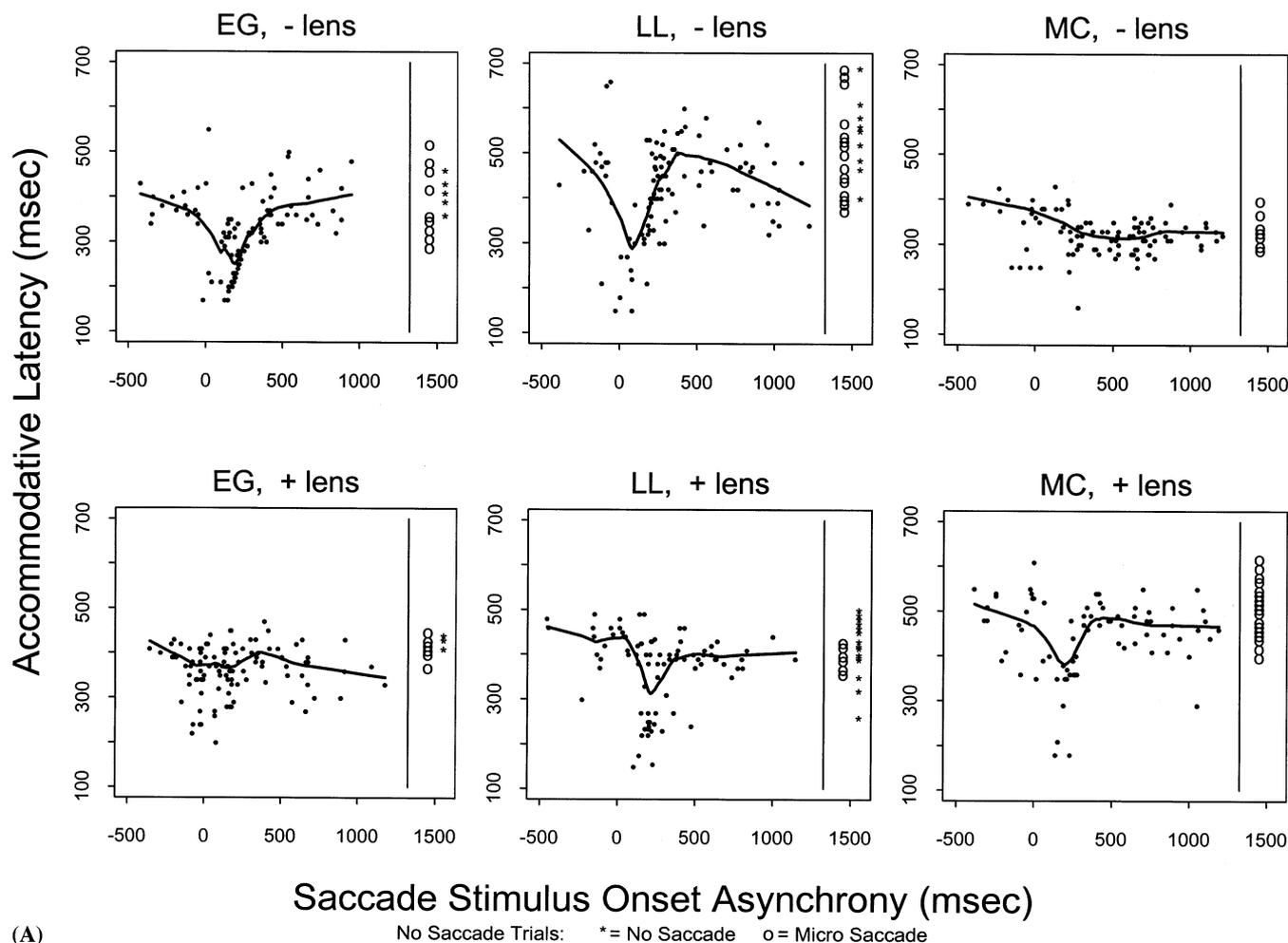


Fig. 7. (A) Accommodation latency for the three subjects as a function of temporal onset asynchrony between the saccadic response and the stimulus for accommodation (SSOA) (top row, trials requiring an increase in accommodation; bottom row, trials requiring a decrease (relaxation) of accommodation). The data were fit with a lowess function that illustrates the variation of accommodation latency as a function of saccade onset asynchrony with respect to the accommodative stimulus. Also shown at the right are accommodative latencies when no saccade was stimulated (no saccade trials). Open symbols represent no saccade trials in which inadvertent microsaccades occurred and asterisks are for trials in which no saccade occurred. (B) A robust regression was fit to data in the recovery zone in (A) from the minimum latency, near time zero, to the baseline accommodative latency. The regressions were used to examine whether responses in this recovery zone could be described by either of the two models whose predictions are shown by the diagonal dashed lines. Computation of the minimum latency required that we distinguish between facilitated and non-facilitated responses in the transition zone. Responses in the initial transition zone that were greater than baseline latencies were obviously not captured and were removed (shown by open circles). The number of data points (n) and the number of removed points are shown for each plot.

half the trials and rightward saccades on the remaining trials, and alternated saccade direction following every ten trials. Sixty trials were run in each session. Subjects took part in 4–5 experimental sessions separated by at least 3 days.

5.4. Results

Fig. 7A presents accommodation latency for the three subjects as a function of temporal onset asynchrony between the saccadic response and the stimulus for accommodation (saccade stimulus onset asynchrony SSOA). Time zero on the horizontal axis indicates the

onset of the accommodative stimulus. Negative points along the horizontal axis indicate times when saccades preceded the accommodative stimulus, and positive points indicate times when saccades followed the accommodative stimulus. In trials where an inadvertent saccade occurred prior to the intended saccade, the data are plotted at the onset asynchrony between the intended saccade and the accommodative stimulus. Responses to all accommodative stimulus amplitudes are combined since the prior experiment illustrated that this parameter did not affect latency or velocity of saccadic facilitation. A scatter-plot smoother, based on repeated robust locally linear regressions (lowess) (Cleveland,

1979), was applied to the data to illustrate the variation of accommodation latency with saccade onset asynchrony with respect to the accommodative stimulus. Also shown at the right are accommodative latencies when no saccade was stimulated (no saccade trials). Open circles represent no saccade trials in which inadvertent microsaccades occurred and asterisks represent trials in which no saccade occurred.

All subjects exhibited the same overall pattern of results. The mean latency for the no saccade trials (shown on the right) was equal to or slightly higher than the mean latency for saccade trials in which the saccade occurred before the accommodative stimulus was presented (negative SSOA's) or after the accommodative response occurred (i.e. at positive SSOA's greater than the baseline latency of the no-saccade condition). However, there was an intermediate zone in which saccades appear to 'capture' the accommodative response and markedly reduce its latency. This capture zone ranges from time zero, where the accommodative

stimulus occurred, to the time when the baseline accommodative response occurred (nominally at 400 ms). Accommodation latency decreased abruptly beginning at time zero to a minimum value ranging from 5 to 200 ms after the accommodative stimulus. The region containing the minimum appears to be a transition zone from non-facilitated to facilitated accommodation. It contains responses with both facilitated and non-facilitated latencies. The transition zone is defined from time zero to the lowest point of the lowest curve. In one plot (EG, + lens) the latency was reduced for saccades occurring just prior to the accommodative stimulus (negative time values) however these trials contained secondary inadvertent saccades that occurred after the accommodative stimulus was presented. In all but one case (MC, - lens), latency gradually increased as SSOA increased from the minimum point up to the baseline latency of accommodation, as estimated from the no saccade condition. The exceptional case (MC) had reduced latencies at all onset asynchronies, pre-

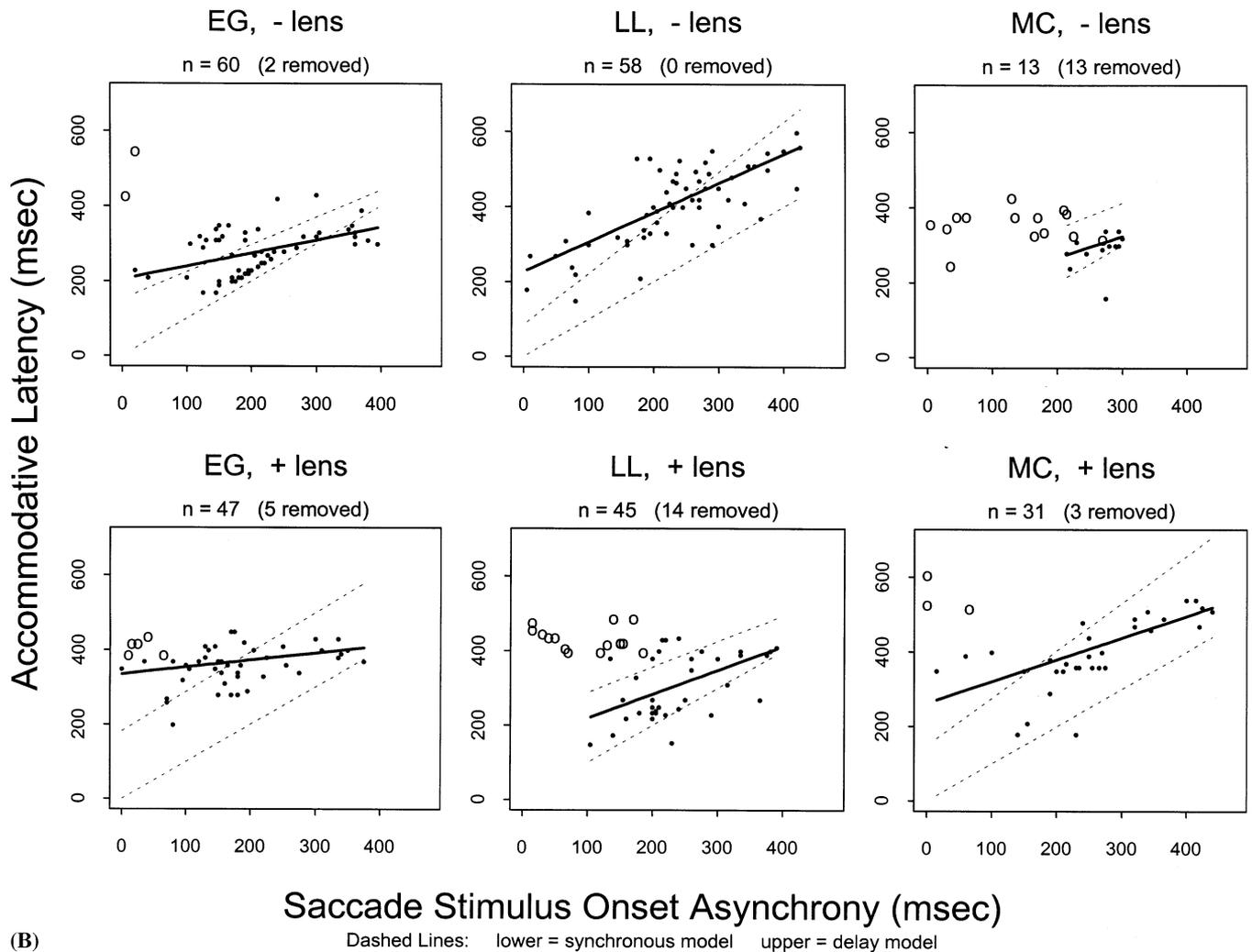


Fig. 7. (Continued)

sumably due to the uncontrolled presence of his inadvertent microsaccades.

The data in the capture zone are analyzed and compared to two models in greater detail in Fig. 7B. The capture zone, defined from time zero to the time each subject's baseline accommodative response occurred, consists of an initial transition zone from non-facilitated to facilitated accommodation followed by a recovery zone in which latencies return to baseline levels. In order to examine whether the recovery from reduced (i.e. facilitated) latencies could be described by either of the two models, whose predictions are shown by the diagonal dashed lines, the obviously non-captured responses in the transition zone (open circles) were removed. A locally weighted regression model (lowess) (Cleveland & Devlin, 1988) was fit to the data in the capture zone. The end of the transition zone and beginning of the recovery zone was defined as the SSOA at which the smallest predicted latency occurred (the minimum). Any responses in this transition zone falling above the baseline latency were obviously not captured by saccades and were removed. Since non-captured responses are difficult to identify in the recovery zone as SSOA increases and the captured responses approach baseline levels, rather than attempting to remove them, the data were fit with a robust regression (solid line) (Hampel, Ronchetti, Rousseeuw & Stahel, 1986) that is relatively insensitive to outliers. One additional point was removed from MC – lens due to its extreme leverage.

The synchronous model (lower dashed line) predicts that saccades and accommodation responded simultaneously. The delay model (upper dashed line) predicts that the accommodative response followed the saccadic response by the combined neuromuscular delay of the ciliary body and plant delay for accommodation. Neuromuscular-accommodative plant delay was estimated by regressing temporal asynchrony between accommodation and accommodative-vergence (dependent variable) on saccade stimulus onset asynchrony (SSOA) (x axis in Fig. 7A and B) (independent variable). As described above, accommodative vergence precedes accommodation by the neuromuscular response time for accommodation (Wilson, 1973). The asynchrony was added to the accommodative latency predicted by the synchronous model. Accommodative plant delay was estimated as a function of SSOA in the event that higher response velocities of accommodation associated with saccades might affect neuromuscular and plant delays. A prediction of this delay model is that accommodative latency will be longer than the baseline value when a saccade occurs at the time when an unaccommodated accommodative response would normally occur (i.e. at a saccade stimulus onset asynchrony equal to the unaccommodated baseline latency for accommodation). Interest-

Table 3

Slopes predicted by the delay model and the slope estimated by the robust regression are shown for each subject in the plus and minus lens conditions^a

Subject	Condition	Delay slope	Robust regression estimated slope
EG	– Lens	0.73	0.35
EG	+ Lens	1.06	0.19
LL	– Lens	1.35	0.78
LL	+ Lens	0.69	0.64
MC	– Lens	0.69	0.56
MC	+ Lens	1.27	0.58

^a In all cases, the slope of the regression was less than that predicted by either of the delay model.

ingly, each subject exhibited elevated latencies at the end of the capture zone for one direction of accommodation as indicated by peak of three lowess plots in Fig. 7A.

Inspection of Fig. 7B reveals that nearly all the remaining data in the recovery zone fall above the line predicted by the synchronous model, indicating that the accommodative response follows the saccadic response by some delay factor. Table 3 shows that in all cases, our robust regression estimates of recovery slopes were significantly greater than zero, however they were slightly less than those predicted by our delay model. The recovery slope, estimated by the regression lines, is reduced in part by the combination of responses with reduced and unaffected accommodative latencies. Interestingly, the slopes of the plus and minus lens conditions are similar for individual subjects, indicating that the direction of accommodation did not influence the magnitude of saccadic facilitation of accommodative latency.

The stimulus conditions in which latency for accommodation is reduced when associated with saccades is summarized in a schematic shown in Fig. 8. When the saccade occurs during the baseline accommodative latency period, the accommodative response is captured by the saccade. Accommodative latency is reduced to within a delay of the saccadic response that is approximated by the neuromuscular delay of the ciliary body and plant delay of accommodation.

Figure 9 plots peak accommodative velocity as a function of onset asynchrony between saccade response and accommodation response for the three subjects (Fig. 9A–C). Negative values of saccade response onset asynchrony (SROA) indicate when the saccade preceded the accommodative response and positive values indicate when the saccade followed the accommodative response. This analysis was intended to evaluate the range of temporal proximity of saccades and accommodative response that resulted in velocity facilitation. The horizontal lines indicate the mean velocity for accommodation during the no saccade condition, and

the gray area indicates ± 2 S.D. We plotted the response rather than the stimulus onset asynchronies to determine if velocity enhancement occurred for accommodative responses that had been ‘captured’ by saccades.

Subject EG (Fig. 9A) had increased peak velocities for both directions of accommodation. His velocity was elevated over a broad range of onset asynchronies from -400 to 500 ms for plus lens responses (circle symbols). Velocity was enhanced from -100 to 250 ms for minus lens responses with the highest velocities from -100 to 150 ms (square symbols). LL (Fig. 9B) had small increases in peak velocity for both directions of accommodation. Velocity was elevated over a range of onset asynchronies from -350 to 750 ms for plus lens responses. It was enhanced from -300 to 900 ms for minus lens responses with the highest velocities in the range from -300 to 300 ms. MC (Fig. 9C) exhibited similar velocity responses for all stimulus conditions and response onset asynchronies. His highest velocities for minus lens stimuli were over a range from -400 to 500 ms and between -200 and 700 ms for plus lens stimuli. As discussed above in Fig. 7, it appears that for MC, the detected inadvertent saccades in the no saccade condition were associated with the same high velocity responses as observed with voluntary saccades in the saccade condition. The high velocity at larger response onset asynchronies above 300 ms could have result from undetected microsaccades in the saccade condition that occurred before the main saccade was stimulated. It is also possible that velocity of accommodation was not facilitated by voluntary saccades above the velocity with inadvertent microsaccades because of a velocity saturation limit of the plant mechanism.

The range of response onset asynchronies over which peak velocities were reached (-300 to 300 ms) shown

in Fig. 9 include accommodative responses with both reduced (captured) and normal (baseline) latencies. It is possible that high velocity responses in this region may have only occurred with reduced latency accommodative responses. To investigate this possibility we replotted the data in the peak velocity range as a function of latency of the accommodative response (Fig. 10). The data correspond to points lying between -300 and $+300$ ms on the abscissa of Fig. 9 (between the two vertical lines). Square symbols are points that fell in the gray zone in Fig. 9 (normal velocity responses) and circle symbols are points lying outside the gray zone in Fig. 9 (high velocity responses). Inspection of the figures for the three subjects clearly illustrates that both reduced and normal (baseline) latencies were associated with high-facilitated and low-baseline velocities of accommodation. It is possible that enhanced velocity for longer baseline latencies could have resulted from delayed saccades occurring at the baseline response time for accommodation or from inadvertent microsaccades. However this possibility does not explain all of the results. Many short response onset asynchronies for EG and LL were associated with normal velocity responses. The independence of accommodation latency and response velocity suggests that separate processes may underlie reduced latencies and velocity enhancement.

6. Summary of results

The current study elucidates the role of accommodation and accommodative-vergence in saccade facilitated vergence. The results illustrate saccadic facilitation of latency and velocity of accommodation and accommodative-vergence. The main findings of this study are:

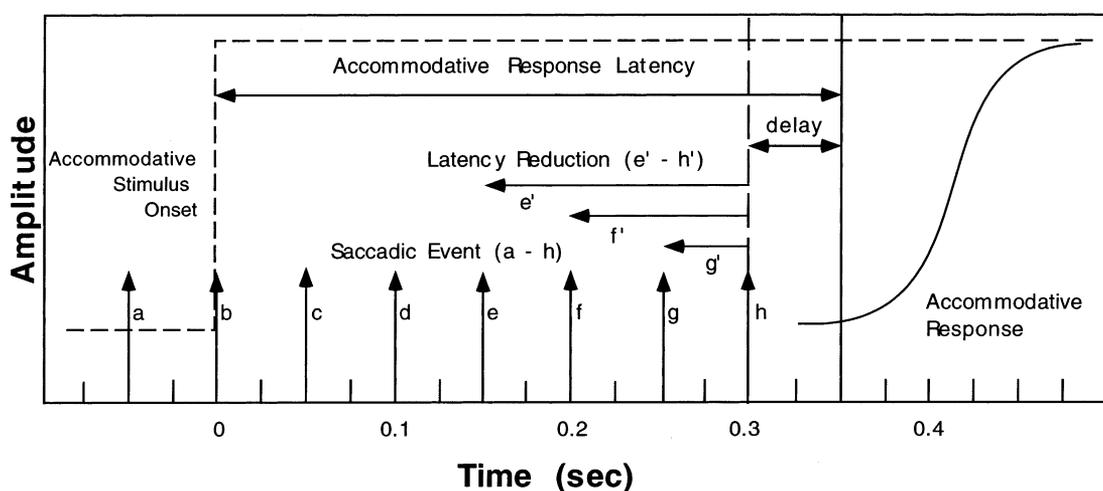


Fig. 8. The illustration summarizes the stimulus conditions in which latency for accommodation is reduced when associated with saccades. When the saccade occurs during the nominal 400 ms latency period following the ACStim, the accommodative response is captured by the saccade so that its latency is reduced to a delay that is approximated by the neuromuscular delay of the ciliary body and plant delay of accommodation.

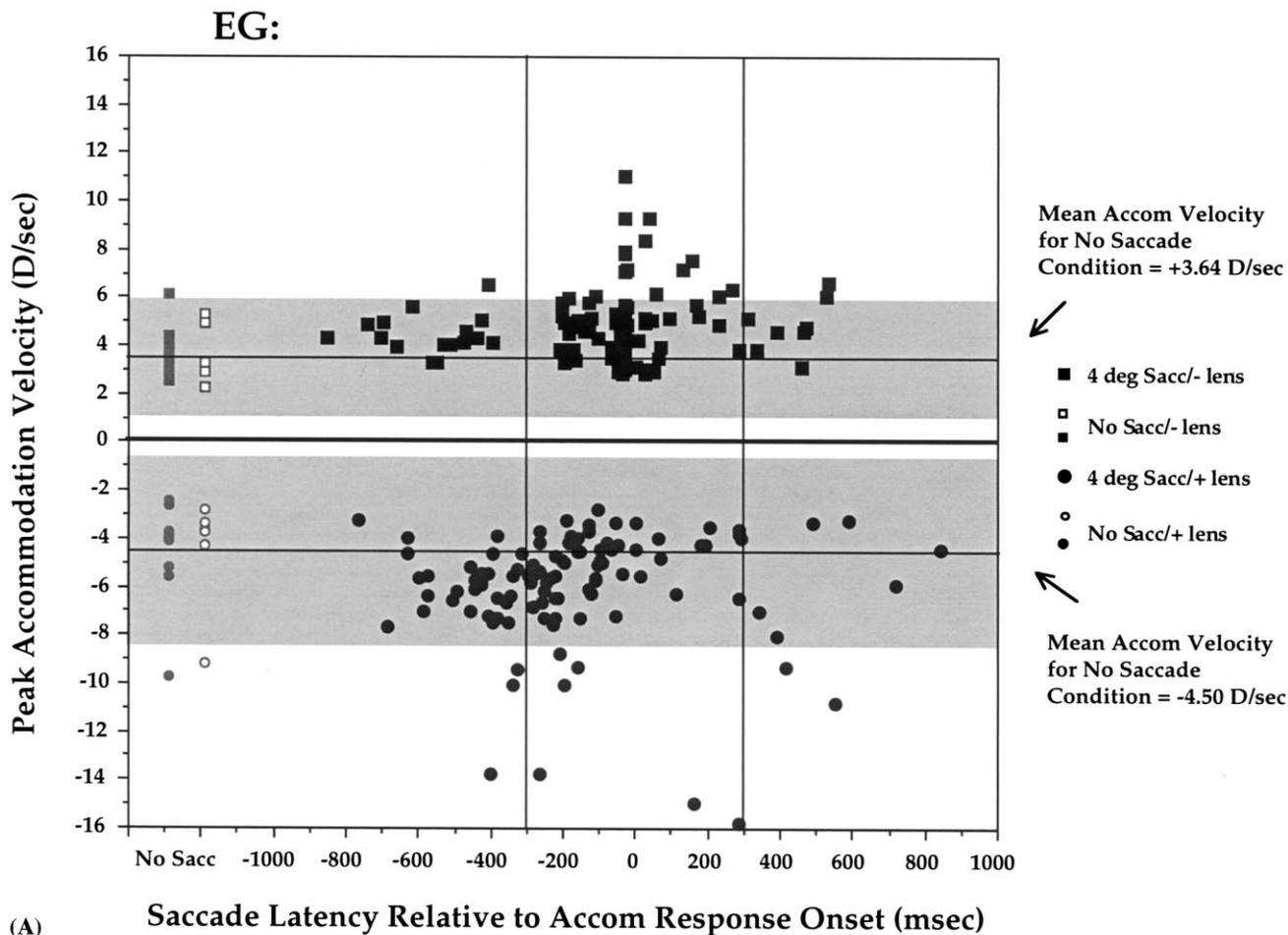


Fig. 9. Accommodative velocity as a function of onset asynchrony between saccades and accommodative responses (SROA) for three subject: EG (A), LL (B), and MC (C). Squares/positive values, trials requiring an increase in accommodation; circles/negative values, trials requiring a decrease in accommodation. Horizontal lines indicate the mean accommodative velocity for no-saccade condition surrounded by a gray zone equal to ± 2 standard deviations of the no saccade condition. Vertical lines to indicate the SROAs used for Fig. 10. Trials requiring no saccade are plotted to the far left in the figure. Trials requiring no saccade, where no saccade occurred are plotted as open symbols, trials requiring no saccade where a small saccade occurred are plotted as filled symbols.

1. Latencies for accommodation and accommodative-vergence were shorter for the saccade than the no-saccade conditions in one or both directions of accommodation. When latencies were reduced by saccades, the onsets of accommodative-vergence and saccades were synchronous and preceded the onset of accommodation by an average of 125 ms. This delay of the accommodative response from accommodative-vergence has been attributed to the neuromuscular delay of the ciliary body and plant delay for accommodation (Wilson, 1973). However, differences in histogram distributions of latency for accommodation and accommodative-vergence are inconsistent with a pure delay element, and as concluded by Wilson (1973) they suggest that independent neural signals contribute to the control of accommodation and accommodative-vergence responses.

2. The two subjects who could control saccade timing and amplitude had enhanced velocities for accommodation and accommodative-vergence under the saccade condition. Compared to other subjects, the subject (MC) who made inadvertent micro saccades had elevated velocities for the majority of accommodative response to the plus lens stimulus, including the saccade and no saccade conditions. The lack of his saccade facilitation could be due to undetected inadvertent saccades or perhaps to a velocity saturation limit of the plant mechanism. Reduced latencies for accommodation were not always accompanied by enhanced velocities for accommodation. This observation suggests that separate mechanisms underlie the latency reduction and velocity facilitation of accommodation by saccade.
3. The reduction of latency of accommodation and accommodative-vergence increased with saccade amplitude but not accommodative stimulus ampli-

- tude. Velocity of accommodative-vergence increased with saccade amplitude for all subjects. The amplitude of total accommodative-vergence increased with saccade amplitude. The majority of this increase occurred during the intra-saccadic component of accommodative-vergence. This agrees with prior studies (Enright, 1984; Maxwell & King, 1992; Collewijn et al., 1995) that demonstrated a facilitation of vergence velocity that increased with saccade size.
4. The increase in the open-loop accommodative-vergence amplitude was not accompanied by an increase in the closed-loop amplitude of the accommodative response. This constitutes an increase in the gain of accommodative-vergence that is described as the ratio of accommodative driven convergence per diopter of accommodation (AC/A ratio). Previously Schor and Kotulak (1986) noted a similar nonlinear increase in the AC/A ratio with accommodative response velocity and it is likely that small enhancements of accommodative

velocity by saccades produce the same nonlinear interaction with accommodative-vergence.

5. Changes in accommodative response did not occur when saccades were stimulated without a change in accommodative stimulus. This suggests that changes in accommodation that occurred when the stimulus to accommodation was changed were not the result of an indirect interaction between transient vergence spikes that are normally associated with saccades (Erkelens et al., 1989; Maxwell & King, 1992) and the cross-coupling of vergence and accommodation (convergence accommodation) (Schor & Kotulak, 1986).
6. When saccades occurred during the baseline latency period for accommodation, response latency of accommodation was often reduced so that the accommodative response followed the saccadic response approximately by an estimated neuromuscular delay of the ciliary body and plant delay of accommodation.

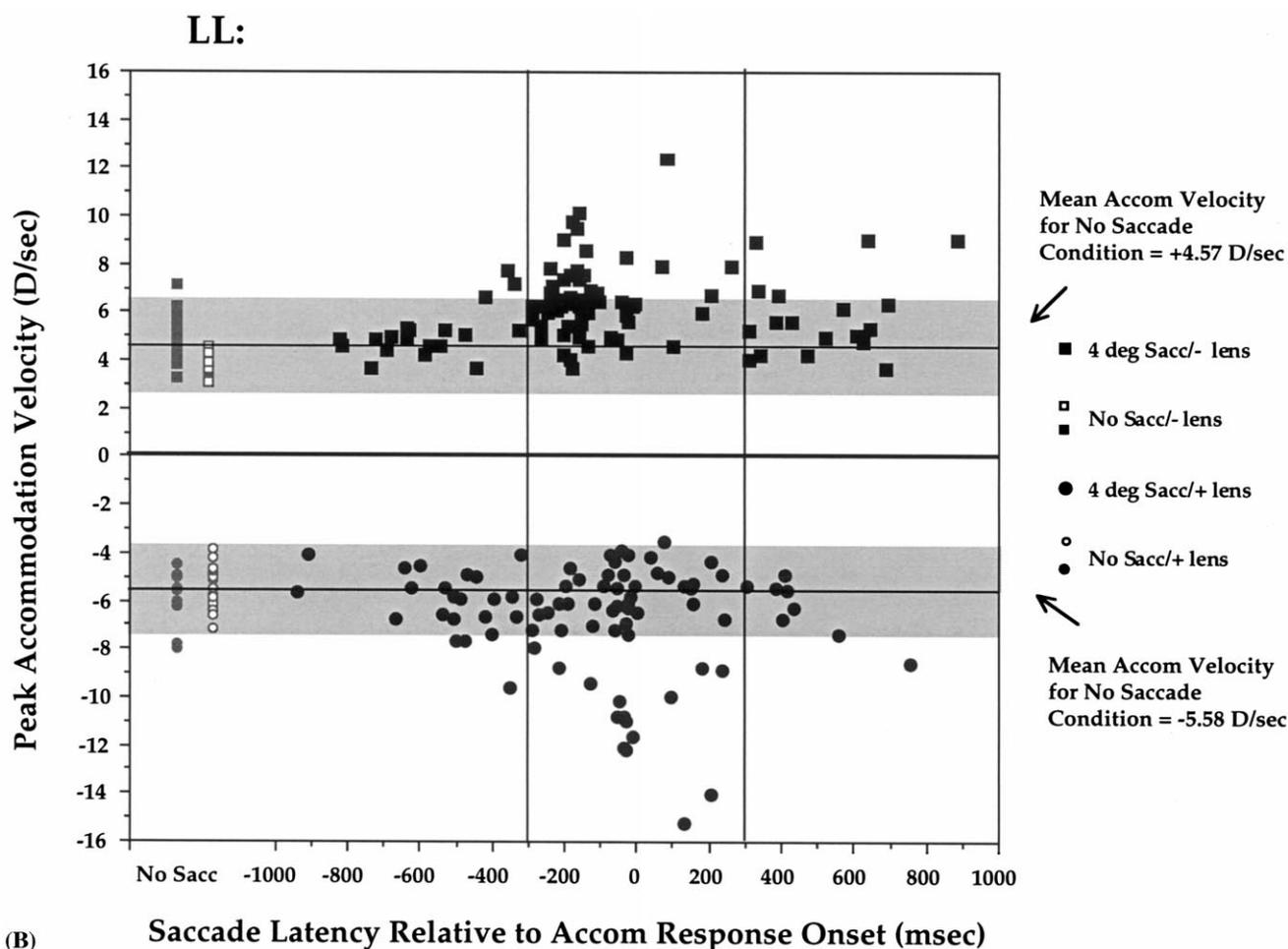


Fig. 9. (Continued)

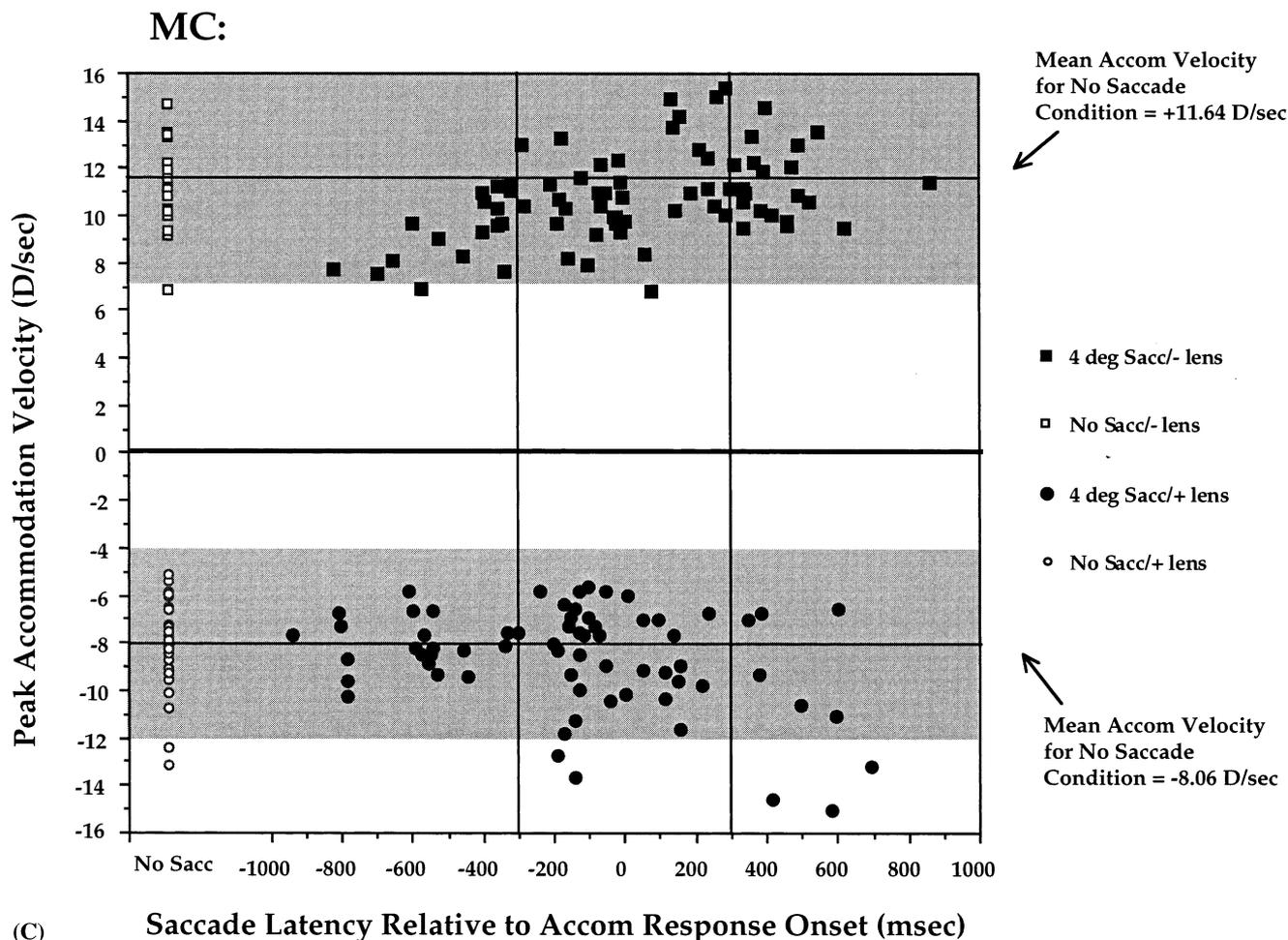


Fig. 9. (Continued)

7. General discussion

Sites that are traditionally related to versional eye movements that project to internuclear neurons subserving vergence movements (May, Baker, Vidal, Spencer & Baker, 1987) could orchestrate temporal interactions between saccades and accommodation. One site is the superior colliculus whose intermediate layer represents a motor map for gaze shifting saccades (Robinson & Jarvis, 1974; Sparks & Mays, 1983). Recent studies in the cat report that the cells scattered throughout the intermediate layer of the colliculus also project to accommodation and convergence-related area in the pretectum (Henkel & Edwards, 1978; Sato & Ohtsuka, 1996; Nagasaka & Ohtsuka, 1998) and electrical stimulation of the superior colliculus results in increases in ocular accommodation (Sawa & Ohtsuka, 1994). Relaxation of accommodation associated with saccades also results from electrical stimulation of the rostral and caudal regions of superior colliculus in rhesus monkeys (Billitz & Mays, 1997). Neurons in the intermediate layer of superior colliculus project to re-

gions near the oculomotor nucleus (Edwards & Henkel, 1978; Grantyn & Grantyn, 1982). Vestibular nuclei also project to this region (Graybiel, 1977; Lang, Buttner-Ennever & Buttner, 1979) and these afferents could also be involved in the temporal interaction between accommodation and saccades.

The amplitude of saccade-related accommodation could be facilitated by an interaction between omnipause neurons (OPNs) and near-response cells in the mesencephalic reticular formation (MRF) (Mays, 1984; Judge & Cumming, 1986). Near response cells are composed of both bursters and tonic cells whose activities are correlated with velocity and position of binocular vergence, respectively (Mays, 1984; Mays, Porter, Gamlin & Tello, 1986). These cells are believed to provide velocity and position signals to the medial rectus motoneurons in the control of vergence as well as commands to the Edinger–Westphal nucleus to stimulate accommodation (Gamlin, Zhang, Clendaniel & Mays, 1994). The near response cells are composed of a heterogeneous population made up of cells that respond to accommodative stimuli, or vergence stimuli or a combination of accommodation and vergence

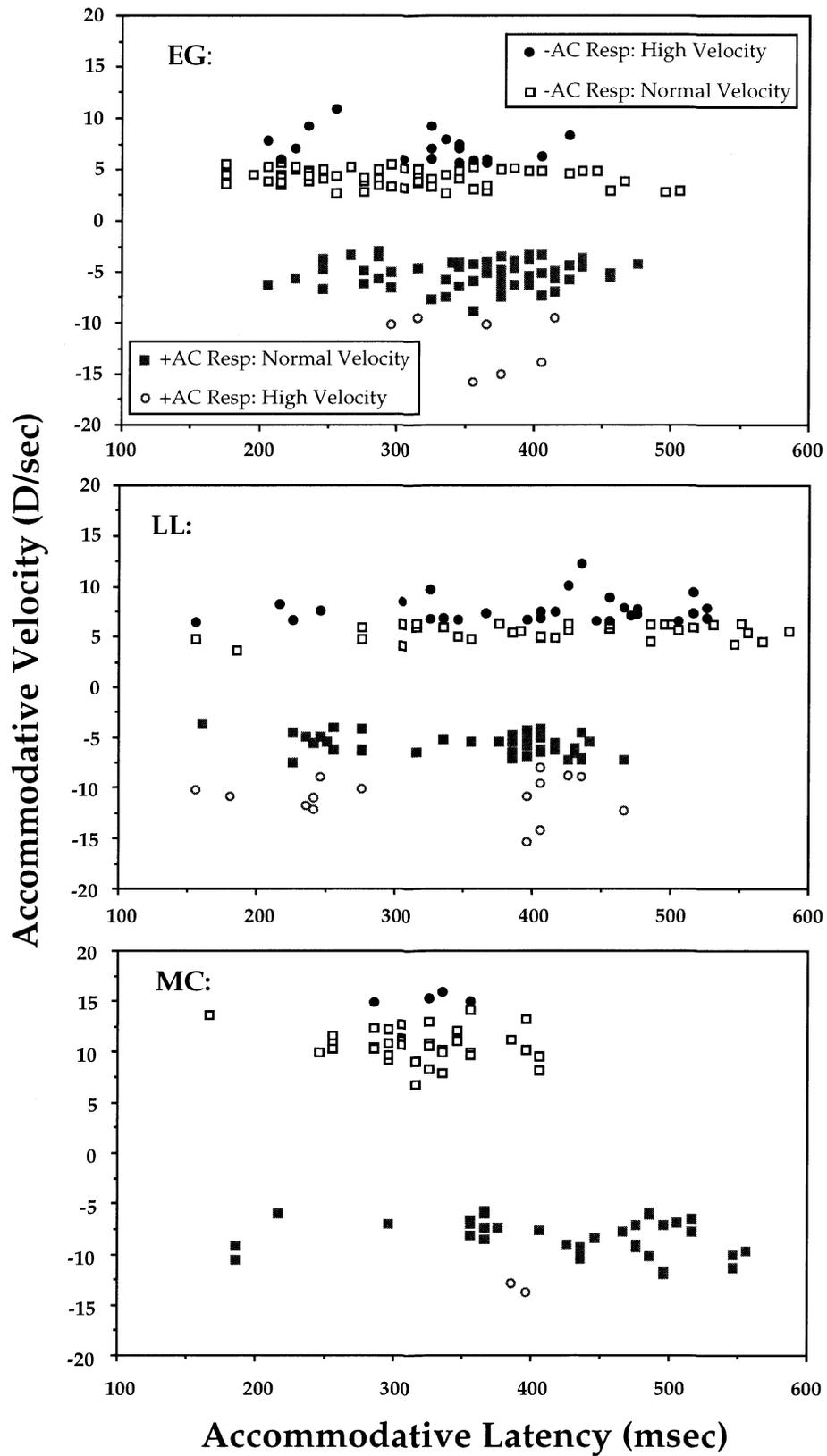


Fig. 10. Accommodative velocity as a function of accommodative latency for SROAs between -300 and $+300$ ms for three subjects. Circles, accommodative response with velocities that were beyond 2 standard deviations of the no saccade condition. Squares, accommodative response with velocities that fell within 2 standard deviations of the no saccade condition.

stimuli (Judge & Cumming, 1986; Zhang et al., 1992). Most cells respond to both blur and disparity stimuli but they differ in the relative influence or weight of these inputs. The ratio of average relative weighting coefficients of convergence and accommodation stimuli accounts for the behavioral measures of the AC/A ratio (Zhang et al., 1992). Because near response cells carry control signals for both accommodation and convergence, saccadic enhanced burst activity at this site would be expected to facilitate both near motor responses.

Gaze shifts in 3-D space require changes in ocular direction and alignment distance which are accomplished by saccades, vergence and accommodation of the eyes. Saccades facilitate the velocity of both vergence and accommodation. Current models of saccade-vergence interactions suggest that omnipause neurons (OPNs) in the midbrain gate the activity of both saccade bursters and vergence bursters (Zee, Fitzgibbon & Optican, 1992). Zee et al. (1992) proposed that accelerated vergence caused by saccadic facilitation results from release of inhibition of vergence bursters by reduced firing of the OPNs which share their inhibition with saccadic and near response bursters. This facilitation is correlated with an augmentation of firing rate of a sub-set of convergence burst neurons of the near response cells (Mays & Gamlin, 1995a,b).

This latter model has been developed further by Mays and Gamlin (1995a,b) to include the potential for saccadic facilitation of accommodation. Because near response cells provide innervation for both accommodation and vergence, release of inhibition from OPNs would augment activity of both accommodation and vergence when associated with saccades. This augmentation would not only enhance velocity of the near response, but it would also gate or synchronize innervation for vergence, accommodation and saccades. The saccade amplitudes in the current study (2–6°) are similar to the smallest amplitude used by Collewijn et al. (1997) (5–30°) who showed increased amplitudes of 0.5–0.75° for transient vergence spikes associated with these small saccades. Here we show a saccadic facilitation of accommodation with the same size stimulus as well as with microsaccades in one subject. The question is whether these small saccades have sufficient duration to effectively reduce the inhibition by OPN of near response bursters? Even more challenging would be the facilitation of near response cells by OPNs related to microsaccades. Saccade durations for amplitudes of 0.5–56° range approximately from 25 to 70 ms (Bahill et al., 1975). It remains to be seen if these durations are sufficient to produce a change in burster activity that could cause the behavioral changes we have observed.

The model could account for greater variability of latencies for accommodation than for accommodative-vergence as seen in their latency histograms (Fig. 4A and B) if during monocular stimulation of accommodation, OPNs are turned off to augment bursters that mainly activate vergence as well as bursters that activate both accommodation and convergence. Similarly, the model could account for the increased AC/A ratio during saccadic facilitation of monocularly stimulated accommodation if OPNs augmented vergence bursters that had a higher velocity tuning than the mean of the population of near response cells. The current investigation provides behavioral support for this hypothesis by demonstrating saccadic facilitation of separate motor events (accommodation and convergence) controlled by independent plant mechanisms.

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