

RESEARCH ARTICLE

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Eye position and target amplitude effects on human visual saccadic latencies

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Abstract Gaze shifts vary in the extent of eye and head contribution; a large amplitude and/or an eccentric ocular orbital starting position alter the participation of head movement in the shift. The interval between eye onset and head onset determines compensatory counterrolling before and after the shift and the extent of vestibular ocular reflex reduction during the shift. The latency of eye saccades in the head-fixed condition was measured with respect to target amplitude and orbital position in order to establish base-line operations of these two variables as they apply to the head-free condition. Eye movements were measured during single-step saccades in nine young adult humans. The target step, hereafter called a jump, started from three possible fixation lights; e.g., rightward saccades started from the midline (0°) or from –20 or –40° left of the midline, with a maximum amplitude of 80°. The latency of saccades starting from the primary position *increased* with jump amplitude (amplitude-latency relation). When the eye started eccentrically, the latency was *decreased* (orbital position-latency relation), with the largest jump amplitudes most affected. These changes can be related to active eye-head coordination. Thus, with a leftward maximal orbital eccentricity, compensatory eye rotation would be impossible with a rightward head movement; however, incorporating the orbital position-latency relation, the forward ocular saccade is expedited by 90 ms. Conversely, with a primary starting position, the ocular component of an 80° gaze saccade could be slowed 125 ms by incorporating the amplitude-latency relation, thus facilitating a head contribution to the gaze shift. The orbital position and amplitude-latency relations were prominent in those

subjects with habitually large head contributions to the gaze shift and minimal in individuals with typically small head contributions.

Key words Eye-head coordination · Reaction time · Gaze · Ocular · Human

Introduction

As a freely moving individual explores an environment, saccadic gaze shifts may be made by coordinated eye-head movements. When these saccadic movements are analyzed in the laboratory with the head fixed in position, the head is typically aligned with the trunk and the eyes typically begin each saccade from a constant position, usually straight-ahead. However, in the free-ranging individual many gaze shifts, especially exploratory shifts, are initiated with the head eccentric on the trunk and the eyes eccentric in the orbit. This is because head movement amplitude is generally hypometric relative to the gaze (Fuller 1992a), and therefore the eye must be eccentric from the ocular primary position.

It has been suggested that the starting position of the eye in the orbit affects visually evoked saccadic latencies; this will be referred to as the *orbital position-latency relation* (Fuller 1994). This suggestion was based on the relative onset of eye and head movements in the behaving cat (Fuller et al. 1983): for example, if the eye is deviated leftward in the orbit, then in a rightward, contraversive gaze shift the eye leads the head; but in a leftward, ipsiversive gaze shift the head leads the eye, with the eye counterrotating until the ocular (or gaze) saccade starts. Similarly, eye movement latency to cat superior colliculus stimulation is affected by ocular-orbital position at the time of stimulation (McIlwain 1986; see Fuller 1992a for review). The orbital starting position in primates also affects the latency of visually evoked natural saccadic eye

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movements in primates (Becker and Jurgens 1992; Tusa and Becker 1989).

The latency of visually evoked ocular saccades additionally depends upon stimulus amplitude (angular distance between fixation and saccade target positions): larger amplitudes have longer latencies (Baizer and Bender 1989; Barnes 1979; Becker 1989; Biguer et al. 1984; Zahn et al. 1978; Zambarbieri et al. 1982); this will be referred to as the *amplitude-latency relation*. While there is contrary evidence that latency is unaffected by amplitude (Baloh and Honrubia 1976; Frost and Poppel 1976; Hallett and Lightstone 1976; Zangemeister and Stark 1981; see Fuller 1992a for review), in some of these studies a systematic experimental procedure may have neutralized the amplitude-latency effect (see Discussion). It has been proposed that the amplitude-latency relation is due to a central sensorimotor transformation delay, not a delay imposed by retinal eccentricity or other purely visual processes (Zambarbieri et al. 1982). This communication therefore considers two elements included in transformation delays, the stimulus amplitude and the orbital starting position. The objective is to determine how much and why ocular saccadic latencies vary according to these two variables and to relate them to eye-head coordination.

In active eye-head coordinated movements, the latency of eye movements relative to head movements affects the time during which the vestibulo-ocular reflex (VOR) may be functional before the gaze shift begins. If the ocular saccade is delayed, the head movement may precede the gaze shift and the ocular counterrotation before the ocular saccade begins might reflect a functional VOR (Becker and Jurgens 1992; Fuller et al. 1983; Guitton and Volle 1987; Ron and Berthoz 1992). Conversely, and at the other extreme, expediting the ocular saccade onset might actually result in completion of the gaze shift before the head movement: now a fully functional VOR is required at the end of the gaze shift, while the head is oriented toward the target. Intermediate between these two extremes, the VOR can be altered such that the head can contribute to (reduced VOR), or even drive alone (cancelled VOR), the gaze shift. Thus, in addition to reflecting differing sensorimotor transformations, the amplitude-latency and orbital position-latency relations together might have the teleological role of altering the eye-head onset interval based on the sufficiency of "orbital reserve" at the beginning, and/or at the end of the saccade. Orbital reserve is the extent of eye movement possible either by counterrotation at the beginning of a head movement, or by perrotation at the end of the gaze shift. The two extremes can be redefined: plenty of initial orbital reserve and a large saccade should result in the head preceding the eye, whereas insufficient orbital reserve and a small saccade should result in maximum expedition of saccade onset. Since the present subjects have already been characterized by their head move-

ment propensity (Fuller 1992b), these considerations of ocular and head saccadic characteristics will be resumed in the Discussion.

Materials and methods

Eye movements were recorded in young adults (age 22–35 years, mean $26 \pm SD 4$ years) with silver-silver chloride electro-oculographic electrodes. Five female and four male emmetropic (two with corrective contact lenses) subjects with no history of gaze disorders were given a description of the experiment and signed informed consent forms; all protocols were approved by the university internal review board. The subjects' heads were rigidly fixed by a helmet and an acrylic occlusal bite plate made from casts of each subject's maxillary dentition. They sat facing a perimeter arc located 114 cm from the axis of normal head rotation (i.e., about 106 cm from the center of the eye). The subjects were identified by number (1–9), based on their head saccadic gain (head movement amplitude/jump amplitude), with subject 1 having the highest gain (Fuller 1992b).

Procedure

Nine sets of lights spaced 10° apart extended from -40 to $+40^\circ$ (right is positive throughout the text and illustrations). The saccadic task was a single-step jump paradigm. There were three starting or fixation positions (Fig. 1), at 0° , -20° , or -40° , labeled a, b, c, respectively.

In the present experiments a block of saccade trials consisted of right and left fixation-target steps. In Fig. 1 there are 15 right jumps, and four left jumps, which were always presented intermixed with the right jumps in random order. The four left saccades per block were only included as distractors (not as part of the data base), to keep the task as unpredictable as possible without adding excessively to the length of the experimental sessions (1–1.5 h). Finally, each block always began with a predictable left jump from 0 to -30° or -40° , the amplitude was variable between, but consistent within, sessions. The first jump alerted the subject to the beginning of a new block; unlike all of the following 19 jumps, this jump was predictable in timing, direction, amplitude, and sequence. The standard 15 rightward jumps are arranged in Table 1. "Iso-orbital jumps" refers to all jumps starting from the same orbital position, and "iso-amplitude jumps" refers to all jumps with the same amplitude regardless of starting orbital position. Examples of these two conditions are outlined with rectangles in Table 1.

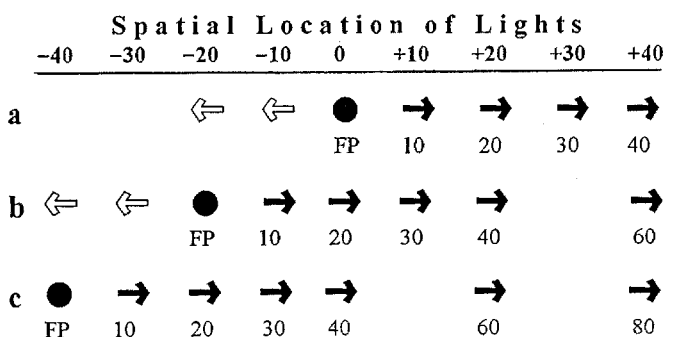


Fig. 1 Designation of saccades by spatial position. All saccades are illustrated, with right saccades represented by *filled arrows*, left by *open arrows*. The starting position (FP, or fixation point) is indicated by a *filled circle* and the amplitude of each jump is indicated *below each arrow*. The *top row of numbers* is the spatial (earth-fixed) position of each light. *Left column* indicates three series (a, b, c) of saccades and represents the three starting positions

Table 1 Designation of saccades by amplitudes. A total of 15 rightward saccades can be grouped according to two criteria: (1) orbital starting position: three series of jumps (*a*, *b*, *c*) start at three positions (0° , -20° , -40°). Jumps vary in amplitude from 10 to 80° . Each series (*a*, *b*, *c*) is iso-orbital, indicated by the *horizontal rectangle* for the *b* series, starting at spatial location -20° . All numbers within table (-40 through $+40$) are spatial, earth-fixed, locations. (2) Amplitude: saccades are also grouped across the three series (iso-amplitude, delineated for 40° jumps by the *vertical rectangle*), having in common the same amplitude of the jump, but varying in start position

Series	Fixation position (deg)	Amplitude of target step (deg)					
		10	20	30	40	60	80
a	0	+10	+20	+30	+40		
b	-20	-10	0	+10	+20	+40	
c	-40	-30	-20	-10	0	+20	+40

The initiation of the jumps was randomly timed (fixation intervals 1.0–2.2 s), and the subjects were instructed to look at the target light as quickly as possible, which remained illuminated for 1.4–1.7 s after the jump. The subjects were instructed to look at all lights as accurately as possible for as long as they remained illuminated. Accuracy (within $1-2^\circ$) of saccades, including starting position and correctives, was confirmed in every saccade measured. Spacing between each trial was around 3 s. The head-fixed blocks reported here were interleaved with head-free blocks (see Fuller 1992b for details). Each session consisted of 15–25 blocks separated by 1–2 min, and each subject completed three to six sessions separated by 2 or more days.

Light stimuli

Each of nine target positions contained three sets of lights: a tungsten (white) light (General Electric ML 327, 0.34 MSCP at 28 V) was flanked by a red light-emitting diode (LED; Archer, 276-026, 650 nm, T-1) 0.6° to one side and by a green LED (Jimpack XC556G, 565 nm, T-1 3/4) 0.6° to the other side of the white light. The red LED was 0.1° in diameter, while the tungsten and green LED lights were reduced to 0.1° by a pinhole aperture.

Each of the light intensities was tested in the adapted subject (room luminance 2.2 cd/m^2) with 1 log unit layers of neutral density gelatin filters placed over each light; all lights were of equal

intensity, visible with 4 but not 5 log units reduction of intensity. Although the data for tungsten lights (after correcting for rise-time) was essentially identical to the LED data, data for only LED trials will be considered.

Data analysis

Saccadic latencies were measured from the calibrated oculogram signal after it was (analog) differentiated. Signals were recorded on an FM tape recorder; the frequency response of the oculogram was limited to 100 Hz. The data for each block were sampled by computer at 1 kHz, slowed by one-tenth, and reproduced on a pen recorder for measurement of latencies from the differentiated (velocity) signals. The latency was measured as the interval between target light activation (time of semiconductor switch closure) and the time when eye velocity exceeded $5-15^\circ/\text{s}$. A presaccadic spike artifact was occasionally seen in some subjects and could be due to eyelid movement accompanying horizontal saccades or to extraocular muscle electromyogram crosstalk (Thickbroom and Mastaglia 1985) or both (Becker 1989). When this artifact was present, the latency was measured from the approximated rise-time of the saccade; in this laboratory, the artifact typically began 3–8 ms before the eye began to move and was easily distinguished. Significance of differences was determined by Tukey HSD multiple comparisons; the matrix of pairwise comparison probabilities is presented at the end of the Results section.

Results

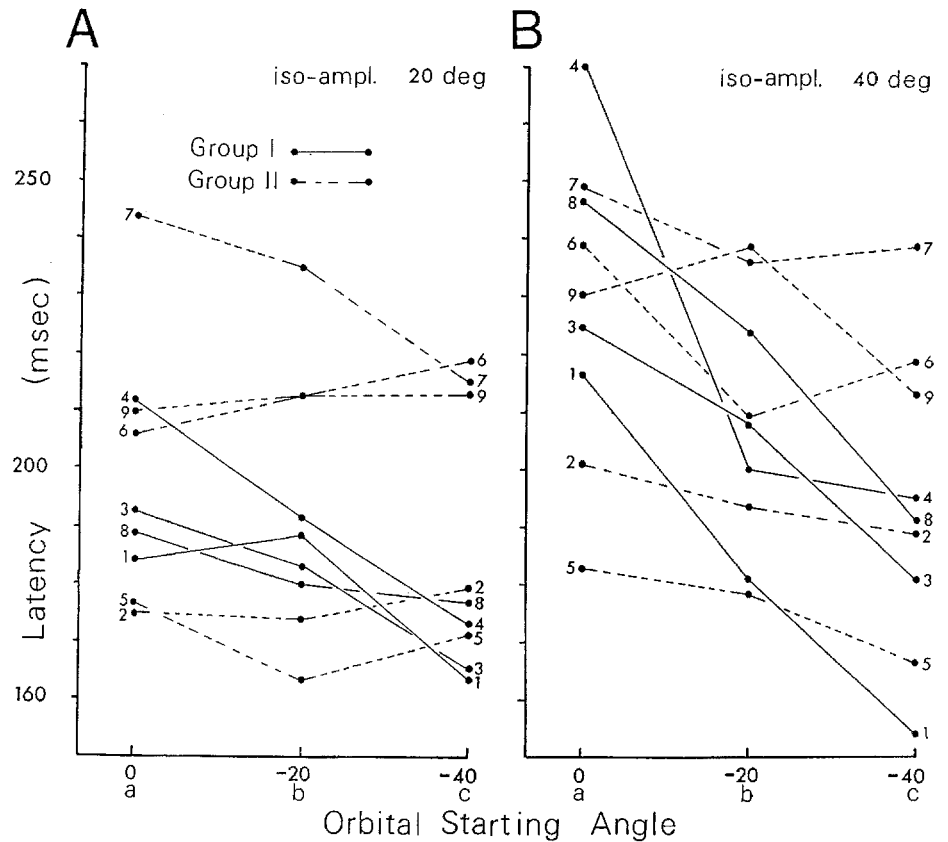
The nine subjects differed in dependence of saccadic latency on both orbital starting position of the saccades and the amplitude of the saccade. Table 2 and Fig. 2 show individual data sets of the latency of saccades of the same amplitude as a function of orbital starting position. In Fig. 2A the variation in latency of 20° isoamplitude saccades is shown for each subject; the slopes and correlation coefficients are shown in Table 2. Similarly in Fig. 2B and Table 2, the same data are presented for 40° amplitudes. Finally, Table 2 shows individual subject data for iso-orbital plots (Fig. 4), with the 0° starting position as the example. By rank ordering the slopes in each of the three sets of columns

Table 2 Regression analysis of saccadic latency plots for each subject. Three sets of saccade tasks are shown for the nine subjects, segregated into two groups. The three saccade tasks consist of two iso-amplitude and one iso-orbital series (see Table 1). Each of the three sets of columns contains the slopes (*B*) and correlation

coefficients (*r*) for each individual's latencies, as plotted in Fig. 2A (20° iso-amplitude), 2B (40° iso-amplitude) and Fig. 4 (iso-orbital a). Representative latency SDs are shown for each jump ($n = 9-25$), listed for each subject in the iso-orbital a series for 10° (*SD 10*) and 40° (*SD 40*)

Group	Subject	Iso-ampl. 20° (ms/deg)		Iso-ampl. 40° (ms/deg)		Iso-orbit. a (ms/deg)		SD10 (ms)	SD40 (ms)
		<i>B</i>	<i>r</i>	<i>B</i>	<i>r</i>	<i>B</i>	<i>r</i>		
I	1	-0.50	-0.55	-1.58	-0.87	1.45	0.75	18	15
	3	-0.70	-0.83	-1.10	-0.80	1.82	0.85	10	14
	4	-0.98	-0.86	-1.88	-0.83	1.98	0.81	14	16
	8	-0.30	-0.40	-1.38	-0.78	1.91	0.78	13	18
II	2	+ 0.10	+ 0.21	-0.30	-0.32	1.07	0.65	11	21
	5	-0.10	-0.14	-0.40	-0.53	0.42	0.34	13	13
	6	+ 0.30	+ 0.23	-0.50	-0.33	1.32	0.63	8	23
	7	-0.73	-0.61	-0.28	-0.15	0.90	0.35	12	41
	9	+ 0.08	+ 0.10	-0.43	-0.25	1.00	0.42	20	32

Fig. 2A, B Mean saccadic latencies of each subject for different orbital starting angles (orbital position-latency relation). Nine subjects were divided into two groups (I, solid lines; II, broken lines). The mean of 9–25 jumps originating from one of three orbital starting positions (abscissa) is represented by a single point for each subject, with the subject's number (1–9) at each end of the curve. Saccadic latencies to jumps of 20° (A) or 40° (B) amplitude (iso-ampl.) are plotted. Horizontal axis shows orbital starting positions: 0° a; -20° (left of midline), b; and -40° c



shown in Table 2 (e.g., in the Iso-ampl. 40° column, subject 4 has -1.88, the most negative slope, whereas subject 7 has -0.28, the least negative slope) and combining these rank orders for the complete data set, the results from each subject are summarily and relatively shown in Table 3 (note in the column labeled 40° subject 4 has a rank of 1 and subject 7 has a rank of 9 corresponding to the above examples of -1.88 and -0.28, respectively). Condensing the eight plots in Table 3 (mean) shows the subjects can be divided into two significantly different groups and there are only a very few instances of cross-over (dGrp) in ranked grouping.

Pooling the data separately for the two groups (Fig. 3) emphasizes the trends in the slopes. In group I there is always a decrease in latency with an increase in eccentric position. The effect increases as amplitude of the jump increases. The same trend is not apparent in group II.

In Fig. 4 and Table 2 the dependence of latency on amplitude of the jump is shown for each subject for saccades initiated from 0°. In this case all slopes are positive, as reported by others (e.g., Fig. 4 of Zambardi et al. 1982), with the difference between group I and II consistent: in Table 3, columns a, b, and c, the means of the two groups were highly

Table 3 Rank order of slopes of curves of each subject as shown in Table 2 and Figs. 2 and 4. For iso-amplitude the rank of 1 is the most negative slope, whereas for iso-orbital the rank of 1 is the most positive slope. The mean of all eight rankings for each subject are shown; the difference between the means of the two groups is highly significant (Student's *t*-test, $P < 0.001$). In 72 cases (nine subjects \times eight columns) there only 4 instances of subjects having individual ranks placing them in the opposite group (dGrp)

Group	Subject	Iso-amplitude (deg)					Iso-orbit (deg)			Mean	dGrp
		10	20 ^a	30	40 ^a	60	a ^a	b	c		
I	1	2	4	2	2	4	4	6	2	3.3	1
	3	3	3	3	4	3	3	1	1	2.6	0
	4	1	1	1	1	2	1	5	4	2.0	1
	8	4	5	4	3	5	2	3	3	3.6	2
II	2	9	8	8	8	8	6	7	9	7.9	0
	5	5	6	6	7	7	9	9	5	6.8	0
	6	7	9	7	5	9	5	8	6	6.3	0
	7	6	2	5	9	1	8	2	8	5.1	3
	9	8	7	9	6	6	7	4	7	6.8	1

^a Complete data in Table 2

Fig. 3A, B Mean latencies for saccades of same amplitude, varying in orbital starting angle. Each curve is for the same amplitude (iso-amplitude), but varies in orbital starting position (as in Fig. 2). Data for group I (A) and group II (B). The jump amplitude (iso-ampl., in degrees) is indicated to the right of each curve (triangle a, circle b, square c)

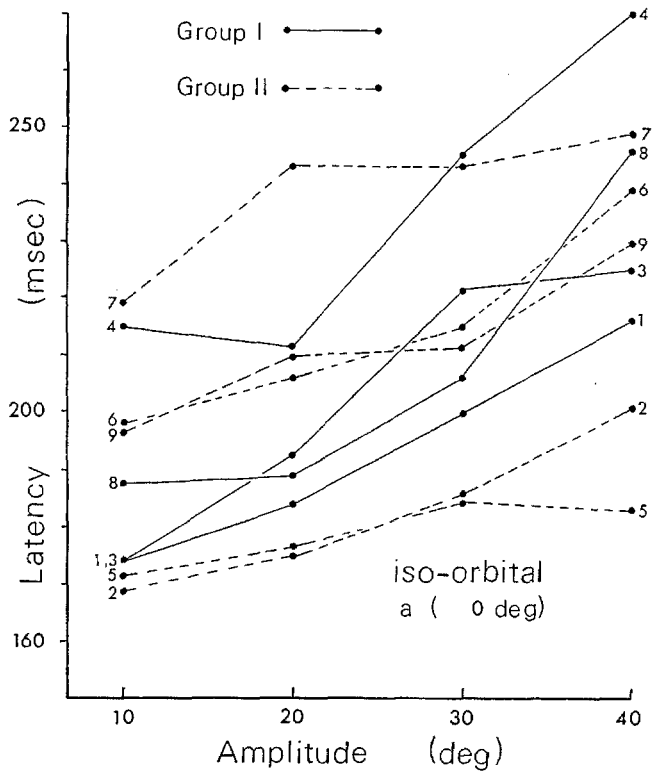
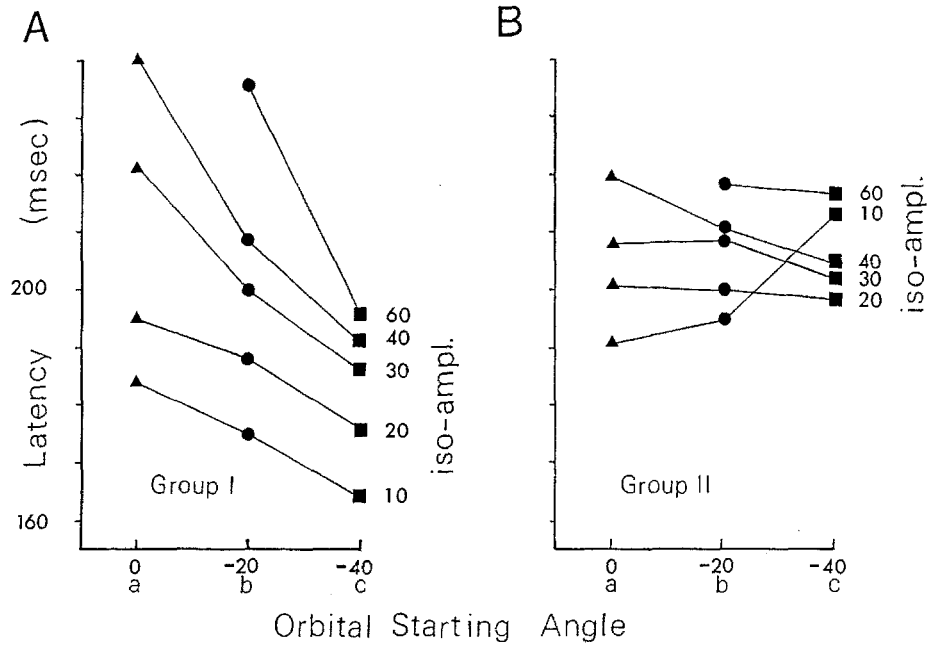


Fig. 4 Mean saccadic latencies of each subject for different jump amplitudes (amplitude-latency relation). Subjects were divided into two groups (I and II, as in Fig. 2). The mean of 9–25 jumps starting at 0° (iso-orbital a series) and ending at 10, 20, 30, and 40° from the midline is represented by a single point for each subject, with the subject's number (1–9) at each end of each curve

significantly different (Student's *t*-test, $P < 0.001$). The variance in latency generally increases with amplitude; the representative standard deviations (Table 2) for 10°

and 40° show this trend in seven of nine subjects (see also Fig. 6).

Combination of orbital- and amplitude-latency relations

Figure 5 shows the dependence of saccadic latency on the amplitude of the jump for three different orbital starting positions. As can be seen from the regression lines, the effect of orbital angle is to rescale the latency (downward) for a given amplitude, since the three intercepts are within 1 ms. (Note, the 0° intercept on Fig. 5 is moved to the right of the vertical axis for clarity.) For example, the mean latency of a 40° saccade initiated from the primary position (0° start, 241 ms) is 50 ms longer than a 40° saccade starting from -40° (191 ms); similarly, the mean difference between two saccades of 60° amplitude initiated from -20° and -40° is 38 ms.

Table 4 shows that pair-wise comparisons of each adjacent data point are significant along the 0° iso-orbital axis, whereas, on the -20° and -40° axes close to the intercept, only alternate paired points are significantly different. Similarly, for iso-amplitude comparisons, near the intercept (10°, 20°) every other point is significantly different ($P < 0.05$), whereas for larger amplitudes (30° or more) all three points are significantly different.

The inset in Fig. 5 shows the curves for group II (the data points are already plotted in Fig. 3). The main and noteworthy difference is the intercept for the -40° curve. This is due to the latency of the series c 10° saccade (-40 to -30° jump; Fig. 3), which is exceptionally long (218 ms, versus 164 ms for group I). In three of the five subjects the mean series c 10 latencies were

Fig. 5 Latencies of saccades varying in jump amplitude for three orbital starting positions. A family of curves labeled *a*, *b*, and *c* represent plots of saccadic latencies originating from a given orbital starting position or iso-orbital positions of 0° (*triangles*), 20° to the left (−20°, *circles*), or −40° (*squares*). Regression lines have the following respective values for intercept, slope, and correlation coefficient: curve *a*, 161, 1.96, and 0.70; curve *b*, 163, 1.17, and 0.66; curve *c*, 162, 0.67, and 0.59. See Table 2 for representative data for each subject. The *inset* at the lower right shows curves for group II, the individual points for which can be found in Fig 3

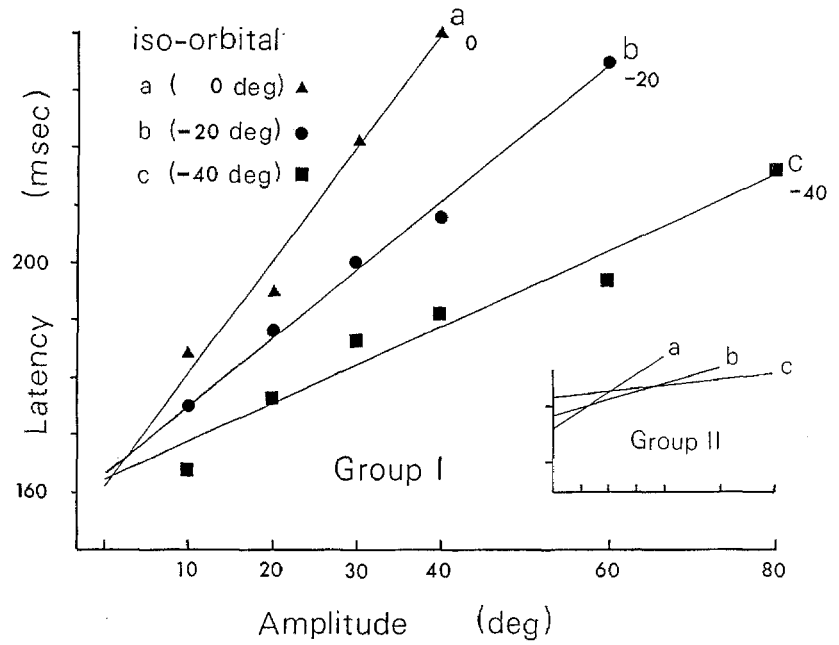


Table 4 Pair-wise statistical comparisons. Tukey HSD multiple comparison of each of the plotted data point means shown in Fig. 5 (group I). Three iso-orbital series, starting from 0° (*a*), −20° (*b*), and −40° (*c*). Pair-wise comparison is similarly labeled to the left of each row by start position (*a*, *b*, *c*) and amplitude (10°, 20°, etc.) for each jump

a (0°)		b (−20°)					c (−40°)							
10	20	30	40	10	20	30	40	60	10	20	30	40	60	80
a10	*2	*5	*5	*1	*1	*2	*2	*5	*2	*1	*1	*1	*2	*5
	a20	*3	*5	*2	*1	*1	*2	*4	*5	*4	*1	*1	*1	*4
		a30	*2	*5	*5	*3	*2	*1	*5	*5	*4	*4	*3	*1
			a40	*5	*5	*4	*2	*1	*5	*5	*5	*5	*5	*2
				b10	*1	*3	*4	*5	*1	*1	*1	*1	*2	*4
					b20	*3	*2	*5	*2	*1	*1	*1	*1	*5
						b30	*1	*5	*5	*2	*1	*1	*1	*2
							b40	*5	*5	*4	*3	*2	*1	*1
								b60	*5	*5	*5	*5	*5	*2
									c10	*1	*4	*5	*4	*5
										c20	*2	*2	*2	*5
											c30	*1	*1	*5
												c40	*1	*3
													c60	*4

*1 $P > 0.05$; *2 $P < 0.05$; *3 $P < 0.01$; *4 $P < 0.005$; *5 $P < 0.001$

10–60 ms longer than the series *c* 20° saccade (−40 to −20° jump). The variance of latencies in these subjects was not different for this jump than for the same amplitude jump in the other two series. Figure 6 shows the data for a single subject. As stated regarding Table 2, and as seen by others (e.g., Zambardi et al. 1982), variance increases as latency increases.

Discussion

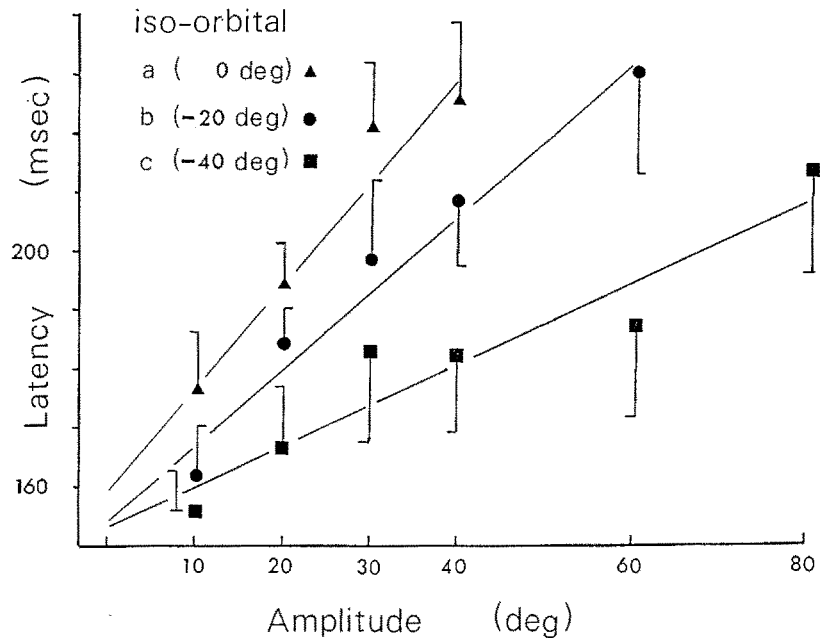
There were two observations: first, as the eccentricity of the orbital starting position was increased (contraversively or opposite the impending gaze shift), the saccadic latency was shortened (orbital position-latency relation). Second, as the amplitude of a target jump was increased, latency was lengthened (ampli-

tude-latency relation). The amplitude-latency relation was reduced in slope such that the difference between saccadic latencies was reduced if the saccades start from −20° or −40° in the orbit. This confirms predictions made earlier (Fuller 1992a), based on the onset latencies of eye and head movements during visually elicited gaze shifts. The present findings will be examined in light of previous studies, and in regard to implications for eye-head coordination.

Amplitude and orbital starting position

The lengthening of latency with larger amplitudes (amplitude-latency relation) observed here confirms and extends the data of several previous reports (Baizer

Fig. 6 Data from subject 3. Same display as Fig. 5; variances (vertical lines) displayed are 1.0 SD; each data point is the mean derived from the same 12 blocks (i.e., $n = 12$ for all points, and each of the 12 blocks contained all 15 jumps)



and Bender 1989; Barnes 1979; Becker 1989; Biguer et al. 1984; Zahn et al. 1978; Zambbarbieri et al. 1982), in which the slope ranged from 0.6 to 2.0 ms/deg (Becker 1989; Fuller 1992a), values that compare favorably with the present individual range (0.42–1.98, Table 2). The orbital position-latency relation may explain why other laboratories (Baloh and Honrubia 1976; Frost and Poppel 1976) may have failed to see an effect of amplitude on saccadic latency. In the latter studies the amplitude effects may have been diluted or even canceled. If the starting position is progressively shifted opposite the direction of the saccade to increase amplitude (e.g., in a restricted visual field), latency would be shortened due to the orbital position-latency relation. Lengthening of latency due to increased amplitude would be neutralized, since the latency would be progressively shortened by progressively increasing orbital eccentricity of the starting position. In another case a free head may account for the same result (Zangemeister and Stark 1981): since the head is typically hypometric (re gaze), the eccentric fixation points will be associated with contraversive orbital starting positions, producing proportionately shorter latencies, again diluting the amplitude-latency relation. For example, if a -50° fixation point produces a -30° head position, the eye will start the saccade at -20° in the orbit, shortening the latency. This does not mean that the relation will not be seen in head-free studies, since the amount of orbital eccentricity depends on the head movement propensity of the subjects; if the subject pool is composed of head movers (Fuller 1992b), there will be little orbital eccentricity at the beginning of each saccade, and therefore the amplitude-latency relation can be more clear (e.g., Barnes 1979). Finally, in other cases the differences in

saccade amplitude may have simply been too small to see the relation (Hallet and Lightstone 1976).

In all iso-amplitude plots, the same part of the retina is stimulated for each point on the curve (Figs. 2, 3). This eliminates purely sensory contribution (e.g., distance from the fovea) to the latency changes seen, the conclusion of Zambbarbieri et al. (1982), who compared button-press latencies to saccade latencies. Their conclusion was that the longer ocular latencies (with larger amplitudes) were due to longer central processing time for larger eye movements, since button-press latencies were unaffected by jump amplitude. [It is noted that in the present report, as in others, amplitude refers to target jump amplitude, not saccadic amplitude. As is well known (Becker 1989), primary saccades greater than $20\text{--}30^\circ$ are typically hypometric. It was concluded by Zambbarbieri et al. (1982) that the amplitude of the primary saccade was not the determinant of the amplitude-latency slope, as confirmed in the present study.]

The observation that saccadic latency is shortened by a contraversive shift in the starting position nicely complements observations in head-free cats (Fuller et al. 1983) or humans (Lauritis and Robinson 1986): if the eye is already deviated contraversively, it begins the gaze shift before the head moves. If the eye is initially deviated ipsiversively, a brief counterrotary eye movement accompanies the earlier head movement before the forward or ipsiversive ocular saccade initiates the gaze step. Incorporating the present data, the farther the eye is contraversively, the sooner it will move. In eye-head coordinated gaze shifts, this has the effect of ensuring that no counterrotary eye movements will be attempted if there is minimal contraversive orbital reserve. Such counterrotary eye movements would draw the eye toward the limits of the orbit,

resulting in retinal image motion. To prevent this, the short-latency forward eye movement is well underway before the head begins to move.

Technical considerations

The design of these experiments was governed by maximal separation of starting positions; the -40° starting point poses the following limitation. One could propose that the dependency of latency on orbital starting position reflects a decreased probability for leftward steps: the -40° left starting point cannot be coupled with a left saccade owing to limitation of the oculomotor range. However, the results of the 0° and -20° series cannot be explained this way, since both series contained unpredictable right-left choices; both series each had two left saccades (with amplitudes of 10° and 20°) randomly interspersed with the right saccades. These left saccades were intended to ensure that differences in latencies between the a and b series were not due to predictability. It seems unlikely that the -40° series, which could allow prediction, would follow the continuum seen in the a and b series (Fig. 5) for equal amplitudes. In fact, predictability would cause a relatively uniform downward step in latencies, not a shift in slope with the same intercept. It is noted that, when these nine naive subjects were routinely questioned at the end of their participation, they were unanimously unaware that there were no left saccades originating from -40° , but only that there seemed to be more right than left saccades. These considerations reduce the possibility that the orbital effects were due to changes in directional predictability in the -40° series. A solution to the problem of predictability might be to use 5° increments of amplitude (instead of the present 10° increments). With four right and four left targets in each series (for a total excursion of $\pm 20^\circ$) and with fixation points at $0, -5, -10, -15,$ and -20° , five iso-orbital curves would be generated, and every saccade would have an equal probability of a right or left direction. This scheme could also be used for ipsiversive orbital eccentricities, with starting positions of $+5^\circ, +10^\circ$ etc. This experiment is more appealing using monkeys, in which the variance in latency is sufficiently small so that the smaller latency differences would be significant (Tusa and Becker 1989). In the present experiments, even the 10° increments were frequently not significantly different close to the axis (Table 4), reflecting the relatively large variance typical of humans.

Limits of central processing time

It would appear that in the present conditions the limit of the central nervous cycle-time has been reached. First, a range of 180–220 ms is typical for simple, sin-

gle-step (i.e., excluding gaps producing express saccades), saccadic latencies seen in a normal human population (Becker 1989). Indeed, in the present population, the 0° series mean latencies for 10° saccades was 170–220 ms. However, the -40° series had a mean of 164 ms (range of 140–180 for group I) for 10° saccades. These latencies are clearly below the normal limit; the reduction is progressively greater for larger amplitudes (Fig. 5). Second, the slope of the amplitude-latency relationship is very shallow in the -40° series. This expediency of saccade generation reduces the slowing effect of increased amplitude trajectories. This expediency shortened the latency by 50 ms for a 40° saccade and theoretically could shorten the latency by 90 ms for an 80° saccade (extrapolating the 0° series to 80° ; see next paragraph).

If the iso-orbital 0° start series is extrapolated to 80° amplitude, a latency of 310 ms can be compared with the measured c series 80° amplitude latency of 220 ms (Fig. 5); thus, this theoretically maximum shortening of latency accounts for a 90-ms decrease in processing time to evoke the same amplitude saccade. Similarly, comparing two saccades starting from 0° , but differing in amplitude (10° vs 80°): the larger saccade can be delayed by 125 ms (185 vs 310 ms, respectively). Finally, note that saccades starting from -40° remain linearly related to amplitude-latency, covering nearly the whole ocular motor range without apparent saturation.

Eye-head coordination

The amplitude and orbital relations together teleologically simplify eye-head coordination. In the normal head-free condition if little of the oculomotor range remains for counterrotary movement, the ocular saccadic onset ought to be expedited, owing to the orbital position-latency relation. Thus the saccade would typically be well underway, or even completed, before the head begins to move (Fuller et al. 1983; Laurutis and Robinson 1986). Conversely, the amplitude-latency relation delays the eye saccade relative to the head onset: a large-amplitude saccade is delayed if little or no ipsiversive orbital reserve will remain at the end of the shift. This delay allows head movement to either be well underway before the ipsiversive orbital reserve is expended or precede the eye, expanding the ipsiversive orbital reserve. Intermediate between these two extremes is the more common character of large gaze shifts: the eye saccade is truncated while the head saccade contributes to driving the gaze shift, with a complicated interaction between saccade central internal representation of gaze movement and/or peripheral external sensory correlates of the movement (Barnes 1979; Fuller et al. 1983; Guitton and Volle 1984; Laurutis and Robinson 1986). In this intermediate case, both latency relations will summate, contributing to the optimal onset of the ocular saccade.

Any foregoing or following statements regarding eye-head interactions are made with the tacit and simplistic stipulation that absolute head latencies (interval between jump stimulus and head response) are not covariantly altered with eye latencies in head-free gaze shifts. In a review of some dozen studies (Fuller 1992a) both trends – increase or decrease in head latencies with jump amplitude – were reported in the earlier literature. In the present subjects no change in head latency was found related to jump amplitude (in preparation); this finding has been reported briefly by others (Becker and Jurgens 1992). Thus, the contribution or confounding effect that varying head movement latencies may have on eye-head onset intervals is tentatively regarded as moot, but must await further investigations for confirmation.

The distinction in the present study of groups I and II is of interest in relation to head movement, since the nine subjects have been studied in a head-movement paradigm (Fuller 1992b). While there are undoubtedly many determinants of a subject's sensitivity to orbital and amplitude effects on latency, one simple effect is whether the subject is likely to include head movements as part of their normal gaze-shifting repertoire. In an earlier report (Fuller 1992b), subjects 1–4 were head movers, and this group constitutes three of the four members of group I. Naturally, individuals prone to move their heads will have greater and more frequent need to monitor orbital reserve before and during gaze shifts more assiduously than nonmovers (Fig. 3), for whom head movements are more rare, smaller, and less likely to contribute to the gaze shift (see last paragraph of the Introduction). Likewise, head-movers ought to have a stronger amplitude-latency relation, as was seen in group I, to slow the onset of large-amplitude ocular saccades (Fig. 5). This latter point may be supported by the study of Barnes (1979), which was analyzed along with other studies (Fuller 1992a, Figs. 3A, D, 4B); his amplitude-latency data had the steepest curve and his head-movement amplitude gains were among the highest, with a gain near 1.0. In other words, subjects with high head-movement gain would benefit from a steep amplitude-latency curve, progressively delaying ocular saccades of larger amplitude.

There are logical functional reasons why the orbital position and spatial context of targets must be appraised before a head-free gaze shift is executed. First, the gain and time of gain decrease in the VOR have been shown to vary (Fuller et al. 1983; Pellison et al. 1988); thus, determining when and how much to compensatorily rotate the eyes is partly adjusted by when the ocular saccade starts. Second, the absolute latency of head and eye movements, which are highly variable (Guitton and Volle 1987; Ron and Berthoz 1991; Fuller 1992a), may actually be part of the same strategy to couple the shortest latency of gaze shift (independent of head velocity) onset with the longest

possible retinal stability before and after the shift; this requires ample orbital reserve at either extreme of the shift. Third, the process of large gaze shifts is greatly simplified, since there is an automatic vernier shifting of eye onset relative to head onset dependent on existing and impending orbital reserve eccentricities. The consequences of altered spatial constructs with active head movements and of how the subject incorporates them into the generation of extracorporeal coordinates may underlie the differences between groups I and II (Fuller 1992b). Since the two groups were generally characterized as head movers (group I) and nonmovers (group II), the methods of external constant coordinate construction may be related to, contribute substantially to, or even cause, the subjects' sensitivity to orbital and amplitude effects on latency.

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Note added in proof. The recent data of Zambarbieri et al. (1995) are in agreement with the present series a and b data: they found reduced visual saccadic latencies and slopes for 20° eccentric starting positions similar to that seen in the present Fig. 5. Furthermore, referring to the technical considerations (Discussion) raised in the present paper, Zambarbieri et al. used 5° increments, thus allowing a greater randomization of right and left mixture of jumps. The similarity of results in the two studies further confirms the present proposition that the shortened latencies in the series b and c curves were not due to increased predictability of jump direction.