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THE AMPLITUDE AND ANGLE OF SACCADES TO DOUBLE-STEP TARGET DISPLACEMENTS*

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Abstract—Two experiments examined the magnitude and direction of the initial saccade to a target that underwent two displacements within 200 msec. When the amplitude of the two target displacements was held constant at 10 deg but the angle of the displacements differed by 45 deg, a small but significant number of intermediate-angle saccades occurred. These intermediate-angle saccades were directed to locations between the two targets, thereby generating an angle transition function, and their amplitude was 10–20% less than the amplitude on single-step displacements. These intermediate-angle saccades were not simply the result of programming an oblique saccade because amplitude transition functions virtually identical to those reported by Becker and Jürgens [*Vision Res.* **19**, 967–983 (1979)] for horizontal saccades were obtained for double-step target displacements limited to oblique saccades. Finally, when both target amplitude and target angle were varied in double-step displacements, it became clear that the timing of the amplitude transition function and the angle transition function was not coincident. Across conditions, the angle transition function occurred at a consistent time prior to the initial saccade, whereas the amplitude transition function occurred at a variable time prior to the initial saccade. Because these amplitude and angle transition functions appeared to be dissociated, a modified model of the saccadic programming system for double-step displacements was proposed.

Saccadic eye movements   Double-step saccades   Horizontal, vertical, and oblique saccades

INTRODUCTION

The programming of saccadic eye movements has classically been viewed as ballistic (Westheimer, 1954). That is, once the neural command for a saccade of a specific amplitude and direction has been programmed, that neural command cannot be altered or cancelled during the remainder of the latency period prior to the onset of eye rotation. A number of studies have challenged this view of the saccadic system by briefly displacing a target to one position and then to a second position, and evaluating the ability of the saccadic control system to modify or cancel the initial command to move the fovea to the first target position (e.g. Wheeless *et al.*, 1966; Komoda *et al.*, 1973). Lisberger *et al.* (1975) noted that much of the variation in the literature on these double-step target displacements could be explained by taking into account each subject's mean reaction time to initiate a saccade to a single target displacement. In general, the probability of making two saccades (i.e. responding to both the first and second target displacements) increases as Step-1 duration increases. However, if a subject has a particularly long reaction time for initiating the first saccade, even long Step-1 durations will lead to single saccade responses. Thus, Lisberger *et al.* (1975) normalised each subject's data by subtracting Step-1 duration from mean reaction time. There was remarkable consistency, across both subjects and studies, in the resultant normalized function relating the probability of a double saccade to the time available for modifying or cancelling the first saccade (reaction time minus Step-1 duration).

Becker and Jürgens (1979) advanced Lisberger *et al.*'s (1975) contribution by normalizing an individual subject's data on each trial rather than to the mean reaction time across trials. The critical feature of their model is that the time available for altering the saccadic program to the first target displacement begins with the onset of the *second* target displacement and ends with the onset of the initial

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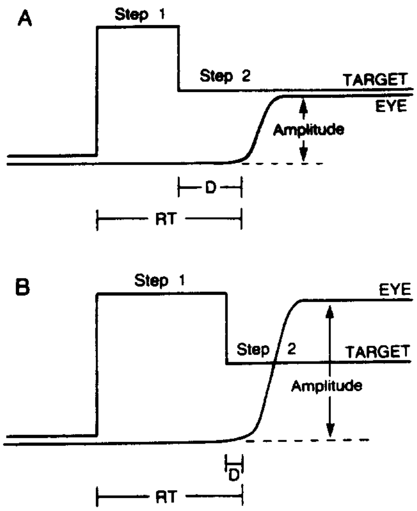

Fig. 1. Schematic of the timing relations between a double-step target displacement and the amplitude of the initial saccadic eye movement. The parameter D indicates the interval between the second target displacement and the onset of the initial saccade. RT = saccadic reaction time. (A) Final-amplitude response with a long value of D. (B) Initial-amplitude response with a short value of D. Note the identical RT's in (A) and (B).

saccade. This temporal reprogramming interval was labelled D. For double-step displacements in which the target moved to one side of the original fixation point and then back to the other side of the original fixation point (*pulse overshoot*), the initial saccade was either to the first target position (for short values of D) or to the second target position (for long values of D). In contrast, for double-step displacements in which the target moved to two positions on the same side of the original fixation point (either two steps in the same direction [*staircase*] or one larger step followed by a partial return toward the original fixation point [*pulse undershoot*]), the amplitude of the initial saccade varied continuously between the first target position and the second target position. Long D values [Fig. 1(A)] allow sufficient time to reprogram the initial saccade, resulting in a final amplitude response. For short D values [Fig. 1(B)], reprogramming cannot occur and an initial amplitude response is executed. For intermediate D values, the amplitude of the initial saccade falls midway between the first and second target displacements. This continuous variation in the amplitude of the initial saccade as a function of D generates an amplitude transition function (AmpTF).* The presence of an AmpTF implied to Becker and Jürgens that some form of parallel processing occurs during a significant portion (e.g. 100 msec) of the saccadic latency period, that the computation of target position involves an averaging process, and that the decision process (to saccade right vs left) is discontinuous whereas the amplitude estimation process (the angular extent of the saccade) is continuous.

Feustel *et al.* (1982), Groll and Ross (1982) and Findlay and Harris (1984) replicated and extended the findings of Becker and Jürgens (1979) for double-step target displacements along the horizontal axis of the stimulus field. The major contribution of these studies was the use of reduced amplitudes of target displacements (2–9 deg instead of 15–60 deg). Displacement amplitude was reduced to ensure that AmpTFs were present for the smaller saccades (< 15 deg) typically employed under normal viewing conditions (Bahill *et al.*, 1975). All of the essential features of Becker and Jürgens' data for large double-step displacements were replicated with small target displacements. Moreover, quantitative estimates of the timing (duration and midpoint) of the AmpTF were in close agreement with the estimates provided by Becker and Jürgens. The present report examines the applicability of Becker and Jürgens' (1979) model of transition functions for the amplitude and angle of saccades to double-step target displacements involving both horizontal and vertical components.

EXPERIMENT 1

Becker and Jürgens' (1979) model emphasized the uniqueness of the *pulse overshoot* condition, which involves a modification of the decision to make a saccade in a given direction (i.e. right vs left) from the original fixation point. Because the second target step redirects the goal of the initial saccade to the opposite side of the visual field, the saccade to the second target position involves a mutually exclusive set of oculomotor commands to the extraocular muscles compared to the saccade to the first target position. In contrast, for the *staircase* and *pulse undershoot*

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*Although Becker and Jürgens used the abbreviation ATF for amplitude transition function, such an abbreviation could be confused with the *angle* transition functions presented in later sections of the present report. Thus, we will use the abbreviation AmpTF for amplitude transition function and AngTF for angle transition function.

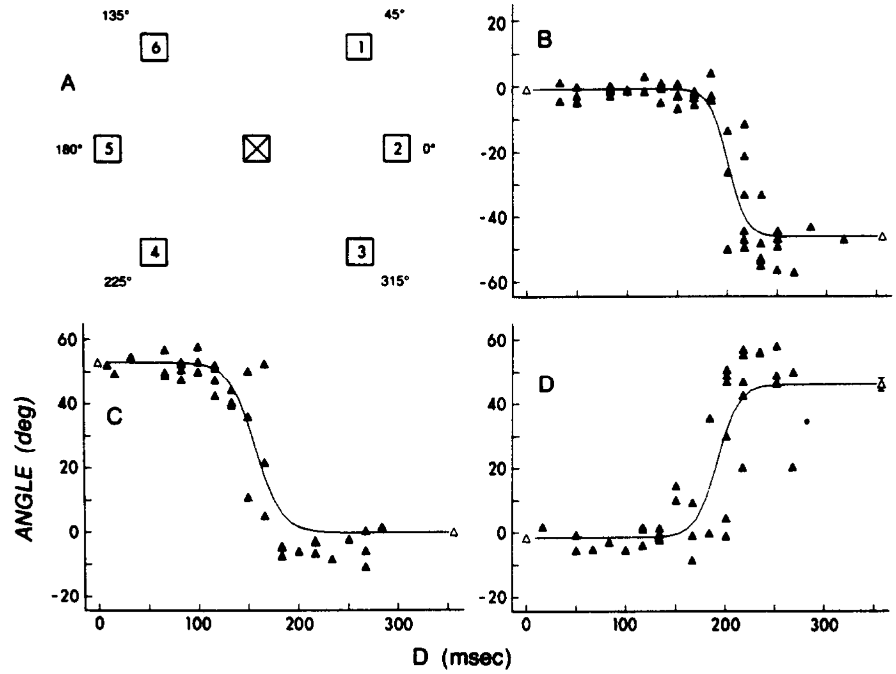

Fig. 2. (A) Diagram of the target locations in Experiment 1. All target steps were 10 deg in amplitude from the central fixation point, X, along the two horizontal and four oblique axes. The eight double-step conditions are X,1,2; X,2,1; X,2,3; X,3,2; X,4,5; X,5,4; X,5,6; and X,6,5. (B–D) Representative angle transition functions (AngTFs) for a double-step condition in Experiment 1 from each of the three subjects. A logistic function was fitted to each set of saccade angles. (B) Subject R.N.A.'s double-step target condition was X,5,4. (C) Subject J.C.L.'s double-step target condition was X,6,5. (D) Subject E.P.O.'s double-step target condition was X,2,1. Open triangles at the beginning and end of each logistic function are means for the single-step calibration trials for each condition. Standard errors for the single-step trials were smaller than the plotted symbols, except for one point in (D).

conditions the direction, but not the amplitude, of the saccades elicited by the first and second target steps is identical relative to the initial point of fixation. It is unclear whether the discontinuity in the AmpTF for the *pulse overshoot* condition is specific to a change in the horizontal target hemifield or whether it is present in any double-step condition involving the activation of a different configuration of extraocular muscles. One test of this question involves double-step displacements within a given hemifield that are not limited to the horizontal axis.

The purpose of the present experiment was to determine if there are gradual transition functions for double-step displacements involving both horizontal and oblique components. All of the displacements were 10 deg from a central fixation point, but the angular direction of each step was either along the horizontal axis (0 or 180 deg) or along one of the oblique axes within each quadrant [45, 135, 225, or 315 deg; Fig. 2(A)]. Thus, each double-step condition contained a horizontal and an oblique displacement. These trials were similar in design to the "adjacent presentation" trials employed by Hou and Fender (1979) and Findlay and Harris (1984). Because all steps were of equivalent amplitude from the original fixation point, the resultant transition function involved the *angle* of the initial saccade, or an AngTF, in contrast to the AmpTF in earlier studies.

Methods

Subjects. Three observers served as subjects: author R.N.A., an experienced observer in eye movement experiments; E.P.O., an inexperienced observer who was aware of the overall design of the experiment; and J.C.L., an inexperienced observer who was unaware of the design of the experiment. R.N.A. was a corrected myope and both E.P.O. and J.C.L. were emmetropes. Because of the randomization scheme across trials (see Procedure below), subjects could not predict the direction of target displacement or Step-1 duration on any given trial.

Apparatus. The target, a black square (11 × 11 min) on a red background (2 cd/m^2), was displayed on a Sanyo video monitor. Viewing distance was 75 cm, yielding a screen size of 25.2 × 19.4 deg. The target was positioned on the video screen under software control from a PDP-11/34 computer. All room illumination was eliminated or masked so that only the target and background were visible to the subject. When the target was displaced on the video screen there was no perceptible phosphor decay. During testing the subject's head was restrained by a forehead and chin rest.

An automated corneal reflection eye monitoring system (Applied Science Laboratories Model 1994) was used to provide voltages, corresponding to horizontal and vertical eye position, that were sampled by the A/D converter of the computer at a rate of 60 Hz. System linearity is excellent within ±20 deg of screen center and resolution is approximately 30 min arc (Young and Sheena, 1975). The gains of the horizontal and vertical outputs of the system for equivalent saccade amplitudes were equated by adjustments to the analysis circuitry prior to digitization by the computer.

Procedure. All subjects were tested for 10 sessions under monocular viewing conditions using an opaque patch. Each session included a total of 44 trials: 12 single-step displacements [2 each at the 6 locations shown in Fig. 2(A)] and 32 double-step displacements (4 each of the 8 horizontal-oblique pairs). The amplitude of all displacements was 10 deg from screen center. Step-1 durations of 50, 100, 150, and 200 msec were presented for each of the 8 double-step combinations, yielding a total of 32 double-step trials per session. One subject (R.N.A.) was tested on an additional 5 sessions with the same trials and displacements, but with Step-1 durations of 67, 83, 117 and 133 msec.

Each trial began with the target at screen center. An experimenter gave a verbal "ready" signal and, after a variable 1–4 sec delay, initiated a trial. The computer program randomly selected one of the 44 possible conditions and stepped the target to one or two locations on the video screen. On single-step trials the target remained at the displaced location for 2 sec before returning to screen center. At the end of all double-step trials the target remained at the second displaced location for 2 sec before returning to screen center.

All data were scored by an automated software algorithm that computed both the amplitude and angle of the initial saccade. The onset of the saccade was defined by an observer who viewed the raw eye movement samples on a point-plot oscilloscope (DEC VR-14) and positioned a cursor at the last sample prior to saccade onset. The termination point of the saccade was defined by a local velocity minimum. The Pythagorean difference between the x–y pairs for saccade onset and termination provided an unscaled measure of saccade amplitude. Eye position data from fixations prior to saccade onset and from fixations after the double-step displacement provided calibration of the unscaled saccade amplitude on each trial. The resultant saccade amplitudes were converted to visual degrees.

Results and Discussion

Figure 2(B), (C) and (D) illustrate the distribution of initial saccade angles as a function of D for a representative double-step condition from each of the three subjects, and a least squares fit of a logistic function* to each set of data. The purpose of this logistic fit was to provide a more objective characterization of the AngTF than the traditional fits by eye. The endpoints of each logistic function were determined by the mean saccade angle on single-step trials. The two free parameters were the midpoint (mean) between an initial-angle and a final-angle response and the slope of the transition (SD) from an initial-angle to a final-angle response. Notice that in all three examples the AngTF has a steep slope, corresponding to a duration along the D-axis of approximately 30–50 msec. In fact, there are few data points that fall midway between an initial-angle and a final-angle response. Thus, one could question for these data whether the AngTF is continuous, or whether the transition from an initial-angle to a final-angle response is discontinuous as in Becker and Jürgens' (1979) *pulse-overshoot* condition.

To determine whether the AngTF was continuous, individual trials on which the initial saccade was approximately midway between an initial-angle and a final-angle response were examined in detail. Figure 3 shows three such eye movement records, one from each panel in

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*The formula for the cumulative logistic function is $f(x) = 1/[1 + \exp(-x)]$ or $f(x) = 1 - \{1 + \exp[(x - a)/k]\}$, where a equals the mean of the distribution and $k(\pi)/\sqrt{3}$ equals the standard deviation. Additional details can be found in Hastings and Peacock (1974).

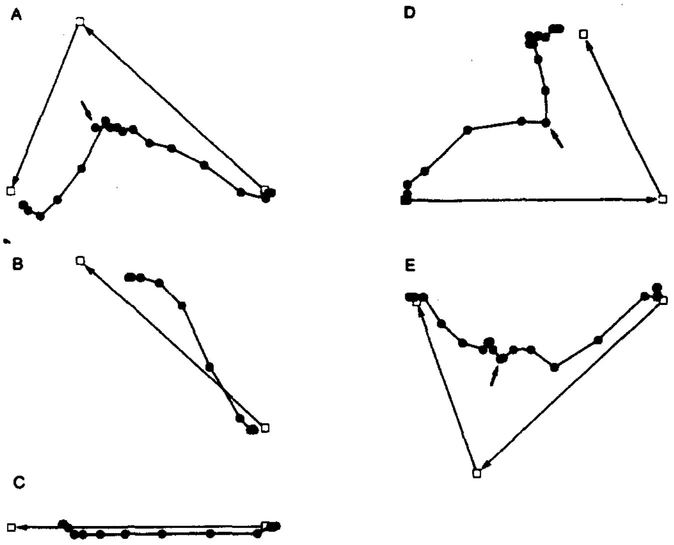

Fig. 3. Sample *x,y* eye movement plots of intermediate-angle responses from each of the three subjects in Experiment 1. The open squares represent the target locations and the long arrows indicate the direction of target displacement. The solid dots represent individual samples of eye position. Panels A, B, and C are from subject J.C.L. (A) Intermediate-angle response to target displaced obliquely then horizontally. The short arrow indicates the end of the first saccade. (B) Same subject's initial saccade to a single-step oblique displacement. (C) Same subject's initial saccade to a single-step horizontal displacement. (D) Subject E.P.O.'s intermediate-angle response to a target displaced horizontally then obliquely. (E) Subject R.N.A.'s intermediate-angle response to a target displaced obliquely then horizontally.

Fig. 2, as well as single-step trials for one subject. It is readily apparent that each example represents an actual case of an intermediate-angle response. Similar "mid-flight" corrective saccades have also been reported in the monkey by van Gisbergen *et al.* (1982). Thus, at least within a limited range of the timing dimension *D*, there are instances of saccades directed toward a location halfway between the angle of the two target steps.

To provide a more quantitative summary of the characteristics of the continuous AngTFs obtained from each subject, we used the best-fitting logistic function to define three regions along the *D*-axis: initial-angle responses, transition responses, and final-angle responses. Transition responses were defined as saccade angles within 1 SD of the mean of the best-fitting logistic function (Fig. 4). Initial-angle responses were defined as saccade angles with *D* values less

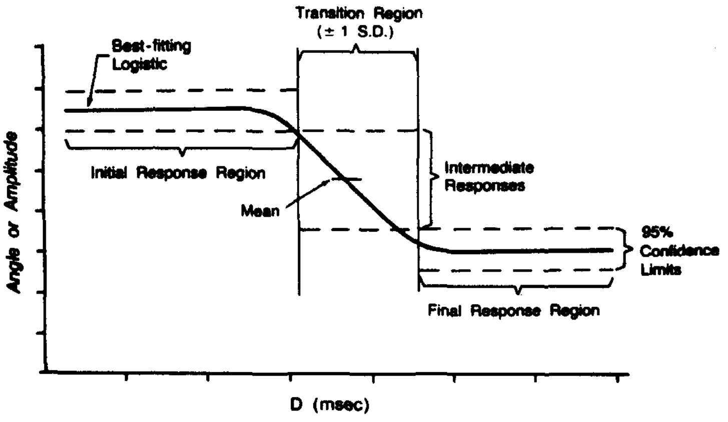

Fig. 4. Schematic illustration of a best-fitting logistic function and the definition of the initial and final response regions, the transition region, and intermediate-angle responses. SD = standard deviation. *Y*-axis was either angle or amplitude depending on experimental condition. See text for details.

Table 1. Mean saccade angle to single-step and to double-step target displacements within the initial-angle, final-angle, transition, and intermediate-angle response regions of the *D* axis for Experiment 1

Subject	Target Step-1	Target Step-2	Initial angle (deg)	Final angle (deg)	Transition region (msec)	*N*	Intermediate	
							angle (deg)	%
R.N.A.	0	45	0.7	45.3	151–173	3	29.1	67
	45	0	44.2	0.0	186–222	2	28.3	50
	180	135	179.7	128.2	153–169	5	156.8	80
	135	180	133.2	181.3	182–196	9	170.3	44
	180	225	182.1	225.2	221–255	3	200.0	67
	225	180	225.9	181.6	152–192	20	205.6	65
	0	315	0.6	323.7	184–216	9	347.8	56
	315	0	319.7	−0.8	162–208	11	351.0	64
	0		−0.3					
	45		45.3					
	135		131.9					
	180		181.2					
	225		226.4					
	315		317.3					
J.C.L.	0	45	−7.4	31.8	138–258	20	15.0	60
	45	0	40.7	−8.3	133–181	7	26.3	43
	180	135	179.4	129.2	122–286	17	161.0	41
	135	180	130.7	184.2	144–202	6	161.8	67
	180	225	182.4	227.2	157–259	0	—	—
	225	180	231.1	182.4	148–232	11	212.6	27
	0	315	−5.2	310.1	190–200	16	337.3	69
	315	0	308.4	−7.8	135–209	17	323.8	41
	0		−8.1					
	45		42.8					
	135		127.5					
	180		180.4					
	225		231.9					
	315		307.5					
E.P.O.	0	45	0.1	46.1	156–230	8	23.2	37
	45	0	45.7	−2.8	220–230	2	17.6	100
	180	135	182.2	137.4	172–210	7	165.5	29
	135	180	135.9	167.9	213–219	0	—	—
	180	225	181.0	—	214–322	5	194.3	80
	225	180	219.8	177.8	184–232	4	193.2	50
	0	315	−4.7	312.2	241–331	12	343.5	25
	315	0	320.8	−2.1	166–194	7	348.1	29
	0		−1.6					
	45		45.6					
	135		133.9					
	180		179.8					
	225		225.3					
	315		313.7					

than 1 SD below the mean. Final-angle responses were defined as saccade angles with *D* values greater than 1 SD from the mean. Ninety-five percent confidence limits were calculated separately for initial-angle and final-angle responses. Transition responses that fell between these two confidence limits were defined as instances of intermediate-angle responses.

Table 1 provides a summary of the initial saccade angles from each of the three regions along the *D*-axis. Note that, as expected, single-step responses and initial-angle responses corresponded very closely to the first target location whereas final-angle responses corresponded very closely to the second target location. Across all eight double-step conditions, the transition region was centered at 189, 187, and 221 msec for the three subjects, with transition durations of 30, 82, and 50 msec, respectively. Intermediate-angle responses were infrequent (column labeled N in Table 1), but across all eight double-step conditions they accounted for 61, 50, and 40% of the three subjects' saccades within the transition region. Moreover, these intermediate-angle responses were consistently directed to a location nearly midway between the two target locations. Thus, because the incidence of intermediate-angle responses was significantly greater than zero ($P < 0.05$ for all three subjects), these data provide evidence that the AngTF was, in fact, continuous.

There were no systematic within-subject

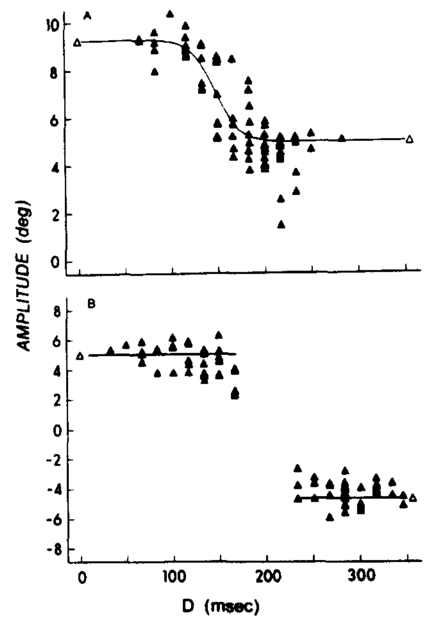

Fig. 5. (A) Amplitude transition function (AmpTF) for *pulse undershoot* condition. Best-fitting logistic function is shown, with open triangles representing the mean amplitudes on single-step trials. (B) AmpTF for the *pulse overshoot* condition. Straight line segments are extensions of the means on the single-step conditions, represented by the open triangles.

differences among saccade amplitudes for single-step, initial-angle, or final-angle responses. However, saccade amplitudes from the transition regions were smaller than the mean amplitude of single-step saccades by 1.37, 1.07, and 0.25 deg for the three subjects. Moreover, the amplitudes of intermediate-angle saccades (a subset of transition responses) were significantly smaller than single-step amplitudes by 1.58, 1.66, and 0.75 deg ($P < 0.05$ for all three subjects). Thus, despite the fact that both target steps had an amplitude of 10 deg, intermediate-angle responses had amplitudes that were approximately 10–20% smaller than single-step responses.

It is unclear whether the difference between the duration of the AngTF in Experiment 1 and the duration of the AmpTF reported in studies that limited target displacements to the horizontal axis could be attributed to the use of target displacements involving two angular components, to the use of the logistic function to estimate the AngTF, or whether the programming of saccades along the oblique axis *per se* differs from the programming of saccades along the horizontal axis. Therefore, a follow-up study was conducted. Subject R.N.A. was presented with target displacements limited to one of the two oblique axes. Double-steps within a given quadrant (*pulse undershoot* and *staircase*), double-steps that crossed the midline into the opposite quadrant (*pulse overshoot*), and single-step displacements were presented. If the resultant AmpTFs were identical to those obtained by Becker and Jürgens (1979), then the AngTGs obtained in Experiment 1 for conditions involving two equal-amplitude steps could not be attributed to some inherent difference between the programming of oblique rather than horizontal saccades.

Figure 5(A) illustrates the distribution of initial saccade amplitudes as a function of D for a typical *pulse undershoot* condition along with its best-fitting logistic function. Note that the AmpTF is clearly continuous. The midpoints of the logistic fits occurred at D values of 195 and 202 msec for the upward and downward *staircase* conditions and at 147 and 167 msec for the upward and downward *pulse undershoot* conditions. The transition regions had mean durations of 76 and 67 msec for the *staircase* conditions and 47 and 45 msec for the *pulse undershoot* conditions. Thus, the shorter duration of the transition region in the present experiment compared to the estimate provided by Becker and Jürgens (1979) appears to be the result of the criterion associated with the use of logistic fits. The majority of saccades within the transition regions (42, 72, 82, and 61%) had amplitudes that fell between the 95% confidence limits surrounding initial-amplitude and final-amplitude responses. Moreover, the mean amplitudes of these intermediate saccades were 6.7 and 6.8 deg for the *staircase* conditions and 6.8 and 6.4 deg for the *pulse undershoot* conditions.

Figure 5(B) illustrates the distribution of saccade amplitudes as a function of D for the *pulse overshoot* condition. There is no evidence of a continuous AmpTF for these data. The two straight lines plotted in each panel represent the mean amplitude of saccades on single-step trials and the discontinuity between initial- and final-amplitude responses was characterized by the absence of data points. A similar gap was noted in the data of Becker and Jürgens (1979), Feustel *et al.* (1982), Groll and Ross (1982), and Findlay and Harris (1984) for horizontal saccades in the *pulse overshoot* condition. Such a gap implies that the decision to make a saccade in a direction opposite to the first target step interrupts the process of computing the amplitude of the saccade for approximately 50–

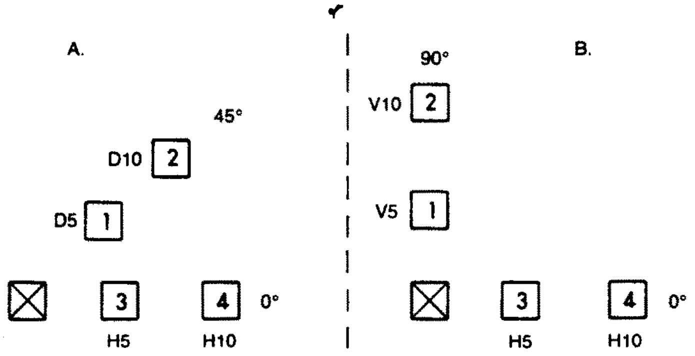

Fig. 6. Diagram of the target locations in Experiment 2. Target steps were 5 or 10 deg from the central fixation point, X, in either the (A) Diagonal or the (B) Vertical configuration. The double-step conditions are X,1,4; X,4,1; X,3,2; X,2,3; X,1,3; X,3,1; X,2,4; and X,4,2. See text for details.

70 msec. In contrast, the continuous AmpTFs for the *staircase* and *pulse undershoot* conditions imply that the process of computing the amplitude of the saccade occurs uninterrupted over this 50–70 msec interval (the duration of the transition region).

A final question with regard to oblique saccades to double-step displacements is whether the *angle* of the initial saccade always lies along the oblique axis. Although the AmpTF for the *pulse overshoot* condition was discontinuous, it is possible that a subset of initial-amplitude and final-amplitude responses had angles that bisected the angle of the first and second target locations (e.g. 135 deg for *pulse overshoots* along the 45–225 deg axis). Only a single instance of an intermediate-angle response occurred in the two *pulse overshoot* conditions. Thus, the decision mechanism that shifts the amplitude of the saccade also appears to shift the angle of the saccade, implying a close linkage between the computation of target amplitude and target angle. However, the results from Experiment 1 demonstrated that saccade angle can be modulated continuously even when saccade amplitude is held constant, although intermediate-angle responses tended to be of somewhat smaller amplitude than either initial-angle or final-angle responses. In addition, for the *staircase* and *pulse undershoot* conditions in the follow-up to Experiment 1, the mean angle of intermediate-amplitude responses (51.1 deg) did not differ from the mean angle of single-step responses (51.4 deg) along the oblique axes. Thus, it remains unclear whether there is an interaction between the computation of target angle and target amplitude. To examine directly the possible linkage between the computation of target amplitude and target angle, these two aspects of double-step displacements were combined in Experiment 2.

EXPERIMENT 2

Experiment 2 combined modulations in target angle with modulations in target amplitude by presenting *staircase* and *pulse undershoot* conditions in which the *angle* of the first and second target steps differed by either 45 or 90 deg and the *amplitude* of the two target steps differed by 5 deg. As shown in Fig. 6, all target steps were restricted to the first quadrant of the stimulus field, but the changes in both angle and amplitude within a trial allowed for the determination of the interaction between target angle and target amplitude. In addition to *staircase* and *pulse undershoot* conditions, both 5 and 10 deg *equal amplitude* steps, with target angles differing by 45 or 90 deg, were presented to replicate and extend the results from Experiment 1.

Methods

Subjects. Author R.N.A. served as the subject in this experiment while wearing appropriate correction for his myopia.

Apparatus. The apparatus was identical to that used in Experiment 1.

Procedure. The subject was tested under monocular viewing conditions (right eye patched) for 20 sessions in each of the two configurations (Diagonal and Vertical) shown in Fig. 6. Half of these sessions were conducted using the standard Step-1 durations of 50, 100, 150 and 200 msec, while the other half used the Step-1 durations introduced in Experiment 1 (67, 83, 117 and 133 msec). Each session included a total of 40 trials: 8 single-step displace-

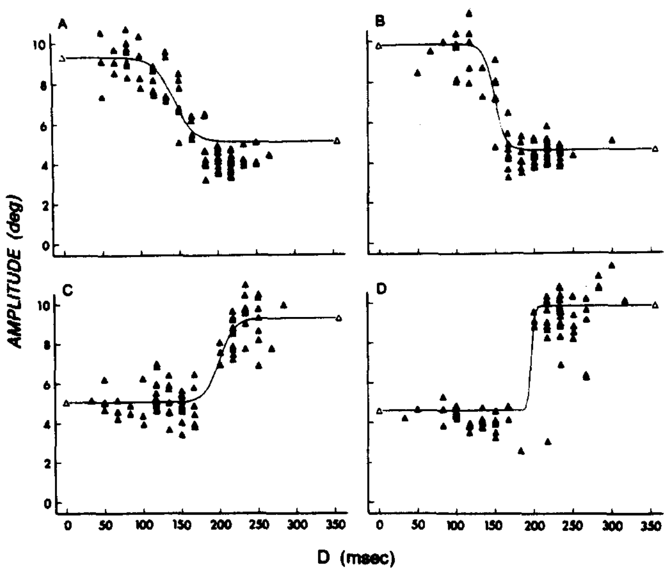

Fig. 7. Representative amplitude transition functions (AmpTFs) for the *pulse undershoot* (A, B) and *staircase* (C, D) conditions in Experiment 2. Diagonal test configurations are shown in (A) and (C); Vertical test configurations are shown in (B) and (D).

ments (2 each at the 4 target locations shown in Fig. 6) and 32 double-step displacements. The magnitudes of the target steps were 5 and 10 deg. The double-step displacements consisted of all possible combinations of *staircase*, *pulse undershoot*, and *equal-amplitude* conditions. Trial presentation and data analysis were conducted as in Experiment 1.

Results and Discussion

Amplitudes. Figure 7 illustrates the distribution of initial saccade amplitudes as a function of *D* for representative *pulse undershoot* and *staircase* conditions from the Diagonal and Vertical target-step configurations. Best-fitting logistic functions, with endpoints determined by the mean saccade amplitudes on single-step trials, are also shown in Fig. 7. AmpTFs in the *pulse undershoot* conditions were clearly continuous for both the Diagonal and Vertical target-step configurations. As shown in Table 2, the transition regions, defined as the logistic mean ± 1 SD, had durations of 48, 56, 50, and 26 msec for the four *pulse undershoot* conditions

Table 2. Mean saccade amplitudes to single-step and to double-step target displacements within the initial-amplitude, final-amplitude, transition, and intermediate amplitude response regions along the *D* axis for Experiment 2

	Step-1	Step-2	Initial amplitude	Final amplitude	Transition region (msec)	*N*	Intermediate amplitude	%
Diag.	D10	H5	8.95	4.46	119–167	13	7.02	77
	H10	D5	8.70	5.22	101–157	24	6.87	71
	D5	H10	5.09	8.96	182–216	3	7.54	100
	H5	D10	5.08	9.00	161–183	8	7.32	38
	D5		5.06					
	H5		5.16					
	D10		9.35					
	H10		9.27					
Vert.	V10	H5	9.49	4.76	129–179	17	7.60	82
	H10	V5	9.41	4.46	136–162	7	7.05	86
	V5	H10	4.17	9.30	192–200	0	—	—
	H5	V10	4.81	9.12	180–184	1	8.21	100
	V5		4.60					
	H5		5.13					
	V10		9.45					
	H10		9.83					

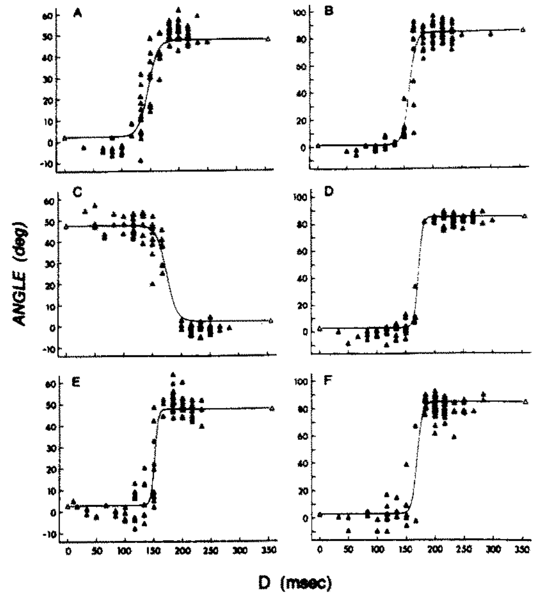

Fig. 8. Representative angle transition functions (AngTFs) for the *pulse undershoot* (A, B), *staircase* (C, D) and *equal amplitude* (E, F) conditions in Experiment 2. Diagonal test configurations are shown in (A), (C) and (E); Vertical test configurations are shown in (B), (D) and (F).

(D10-H5, H10-D5, V10-H5, and H10-V5). Moreover, intermediate-amplitude responses, defined as saccades that fell between the 95% confidence limits surrounding initial-amplitude and final-amplitude responses, accounted for 77% of the trials within these four transition regions. As expected, the mean intermediate-amplitude response (7.14 deg) fell approximately midway between the mean initial-amplitude (9.12 deg) and the mean final-amplitude (4.71 deg) responses.

In contrast to the continuous AmpTFs in the *pulse undershoot* conditions, evidence for continuous AmpTFs in the *staircase* conditions was less consistent. As shown in Fig. 7 and summarized in Table 2, very few saccades fell within the transition regions of the best-fitting logistic functions, although 58% of these saccades qualified as intermediate-amplitude responses. Infrequent intermediate-amplitude responses in the *staircase* conditions compared to the *pulse undershoot* conditions resulted in part from shorter transition durations, particularly in the Vertical configuration (V5-H10 = 8 msec; H5-V10 = 4 msec).

A final aspect of the AmpTFs is the relative timing of the transition regions in the *pulse undershoot* and *staircase* conditions. All four *pulse undershoot* functions had midpoints that occurred earlier along the D-axis (129, 143, 149 and 154) than the midpoints of any of the four *staircase* functions (172, 182, 196 and 199). A similar asymmetry (147 and 167 msec vs 195 and 202 msec) was found for the *pulse undershoot* and *staircase* conditions in the oblique target displacement data from the followup to Experiment 1. Thus, it appears that decreases in saccade amplitude (as in the *pulse undershoot* condition) can be programmed and executed more rapidly (i.e. shorter D values) than increases in saccade amplitude, and this asymmetry was present for double-steps along a single axis or along two axes differing by as much as 90 deg. Despite the sharp AmpTFs in some of the *staircase* conditions, there was no evidence of the 50–70 msec gap in the AmpTF seen in the *pulse overshoot* condition of the oblique target displacement data from the follow-up to Experiment 1 [see Fig. 5(B)].

Angles. Figure 8 illustrates the distribution of initial saccade angles as a function of D for representative *pulse undershoot*, *staircase*, and *equal amplitude* conditions from the Diagonal and Vertical target-step configurations. Best-fitting logistic functions, with endpoints determined by the mean saccade angle on single-step trials, are also shown in Fig. 8. AngTFs in the *pulse undershoot* conditions were clearly continuous for both the Diagonal and Vertical target-step configurations. As shown in Table 3, intermediate-angle responses, defined as saccades that fell between the 95% confidence limits surrounding initial-angle and final-angle responses, accounted for 82% of the trials within the four *pulse undershoot* conditions (D10-H5, H10-D5, V10-H5, H10-V5). As expected, the mean intermediate-angle responses fell approximately midway between the angles on Horizontal (H) and Diagonal (D) target steps (H = 1.0 deg; D = 47.1 deg; intermediate = 25.4 deg) and midway between the angles on Horizontal and Vertical (V) target steps (H = 1.3 deg; V = 83.1 deg; intermediate = 44.3 deg).

There was less consistent evidence for continuous AngTFs in the *staircase* conditions than in the *pulse undershoot* conditions, particularly for the Vertical target-step configuration. Very few saccades fell within the transition regions of the best-fitting logistic functions, although 65% of these qualified as intermediate-angle responses [Fig. 8(C, D) and Table 3].

The *equal amplitude* conditions replicated and extended the findings from Experiment 1. As shown in Fig. 8(E) and (F) and summarized in

Table 3. Mean saccade angles to single-step target displacements within the initial-angle, final-angle, transition, and intermediate angle response regions along the *D* axis for Experiment 2

	Step-1	Step-2	Initial angle	Final angle	Transition region (msec)	*N*	Intermediate angle	%
Diag.	D10	H5	44.0	0.5	154–188	13	25.7	77
	H10	D5	−1.1	50.3	131–161	21	18.3	90
	D5	H10	46.4	−0.8	159–189	6	34.3	83
	H5	D10	4.1	46.2	150–174	13	25.9	46
	D5	H5	45.1	0.5	144–180	7	36.6	100
	H5	D5	2.5	49.7	146–156	9	19.8	78
	D10	H10	46.6	0.2	146–198	17	32.2	94
	H10	D10	1.6	47.3	144–160	8	16.2	87
	D5		47.6					
	H5		2.9					
	D10		46.3					
	H10		2.3					
Vert.	V10	H5	85.6	−2.0	166–172	5	66.0	80
	H10	V5	0.7	83.1	148–170	16	28.8	75
	V5	H10	83.2	2.6	181–191	1	63.6	100
	H5	V10	0.3	83.0	166–178	3	17.3	100
	V5	H5	81.1	0.5	170–182	0	—	—
	H5	V5	3.7	80.8	161–177	2	66.8	50
	V10	H10	85.4	2.6	164–192	9	52.5	67
	H10	V10	3.9	84.4	162–186	14	54.4	64
	V5		84.4					
	H5		3.0					
	V10		85.2					
	H10		1.6					

Table 3, the AngTFs were clearly continuous for the Diagonal target-step configuration, but they were inconsistent for the Vertical target-step configuration, particularly for the 5 deg amplitudes. Intermediate-angle responses occurred on 90% of the transition trials in the Diagonal target-step configuration and on 65% of the transition trials in the Vertical configuration. In addition, the duration of the transition region was significantly shorter in the Vertical (16 msec) than in the Diagonal configuration (29 msec; $t = 2.60$, d.f. $= 7$, $P < 0.05$).

Finally, the midpoints of the best-fitting logistic functions for the AngTFs in the two *pulse undershoot* conditions (146, 159, 169 and 171 msec), and the two *staircase* conditions (162, 172, 174 and 186 msec) from both the Diagonal and Vertical configurations did not differ. This contrasts with the asymmetry between the timing of AmpTFs for those same *pulse undershoot* and *staircase* conditions. Thus, the modulation of saccade angle appears to occur at a more consistent time prior to the initial saccade than the modulation of saccade amplitude.

Amplitude-angle interactions. There remains a question about the linkage between the computation of saccade amplitude and saccade angle on double-step displacements. In Experiment 1, double-step displacements of *equal amplitude* that differed in angle by 45 deg resulted in intermediate-angle responses whose mean amplitude was 10–20% less than the mean amplitude on single-step trials [see Fig. 9(A)]. This finding was replicated in Experiment 2 for both the Diagonal and the Vertical target-step configurations with 10 deg displacements (D10-H10, H10-D10, V10-H10, H10-V10). The mean amplitude of intermediate-angle responses in these conditions was significantly smaller than the mean single-step amplitudes [see Fig. 9(B, C)]. A similar reduction in the amplitude of intermediate-angle responses for the *equal amplitude* conditions with 5 deg displacements was present in the Diagonal target-step configuration, but there were too few data points to draw any conclusions concerning the Vertical target-step configuration. In general, then, *equal amplitude* double-step displacements differing in angle by 45 or 90 deg result in a 10–20% reduction in amplitude when the angle of the initial saccade falls between the first and second target locations.

A simple vector-average model predicts that all saccades falling at angles between Step-1 and Step-2 will have an amplitude equal to the mean of the amplitudes on single-step trials. This prediction is illustrated in Fig. 9 by the solid curved line connecting the single-step vectors. The actual saccade amplitudes on intermediate-

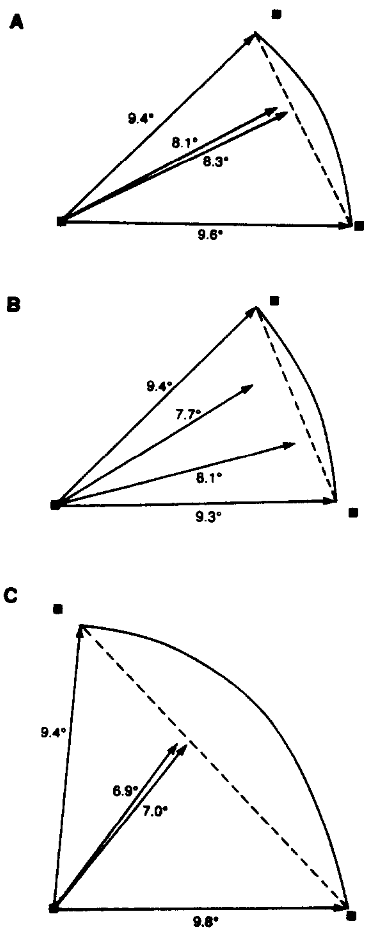

Fig. 9. Summary data of single-step and intermediate-angle responses for *equal amplitude* conditions in Experiments 1 (A) and 2 (B, C). Solid squares indicate target locations at the beginning and end of single-step trials. Numbers indicate mean amplitude of initial saccades. Solid arc is prediction of simple vector-average model. Dashed line is prediction of modified vector-average model.

angle responses were consistently less than this vector-average. For example, a simple vector-average for an intermediate-angle response on an *equal amplitude* trial that falls exactly midway between Step-1 and Step-2 can be expressed as

$$H = \cos\{[(\text{Ang1}) + (\text{Ang2})]/2\} \times \text{Amp}$$

$$V = \sin\{[(\text{Ang1}) + (\text{Ang2})]/2\} \times \text{Amp}$$

where H is the horizontal saccade amplitude, V is the vertical saccade amplitude, Ang1 and Ang2 are the angles of Step-1 and Step-2, and Amp is the mean amplitude on single-step trials. If the angles of Steps 1 and 2 were 0 and 45 deg and their single-step amplitudes were both 10 deg, then

$$H = \cos\{(22.5\ \text{deg})\} \times 10 = 9.24\ \text{deg}$$

$$V = \sin\{(22.5\ \text{deg})\} \times 10 = 3.83\ \text{deg}.$$

In contrast to this simple vector-average model, it appears that the cosine and sine of *each* component vector is averaged rather than taking the cosine and sine of the *average* vector

$$H = \{[\cos(0\ \text{deg}) + \cos(45\ \text{deg})]/2\} \times \text{Amp}$$

$$V = \{[\sin(0\ \text{deg}) + \sin(45\ \text{deg})]/2\} \times \text{Amp}$$

This modified vector-average yields the following predictions for the *equal amplitude* example describes above

$$H = [(1 + 0.707)/2] \times 10 = 8.53\ \text{deg}$$

$$V = [(0 + 0.707)/2] \times 10 = 3.53\ \text{deg}.$$

These horizontal and vertical coordinates correspond to a saccade amplitude that is 9.24 deg rather than the 10 deg predicted by the simple vector-average model. Thus, the prediction of the modified vector-average model is a straight line connecting the two single-step amplitudes, whereas the prediction of the simple vector-average model is an arc connecting these single-step amplitudes. As can be seen in Fig. 9, the data obtained on *equal amplitude* trials in which the initial saccade was an intermediate-angle response fell closer to the predictions of the modified vector-average model.

Predictions of the modified vector-average model also fit the data from *staircase* and *pulse undershoot* trials in Experiment 2. As shown in Fig. 10, intermediate-angle responses on trials in which Step-1 and Step-2 differed in amplitude by 5 deg and in angle by either 45 or 90 deg were consistently closer to the predictions of the modified vector-average model than to the predictions of the simple vector-average model.

A final aspect of amplitude-angle interactions in the data from Experiment 2 concerns the relative timing of AmpTFs and AngTFs. In the *pulse undershoot* conditions, the mean amplitude of intermediate-angle responses (6.19 deg) was only slightly greater than the mean amplitude of *final*-angle responses (4.72 deg). In contrast, for the *staircase* conditions, the mean amplitude of intermediate-angle responses (5.16 deg) did not differ significantly from the mean amplitude of *initial*-angle responses (4.79 deg). The reason for this asymmetry between the amplitude of intermediate-angle responses in the *pulse undershoot* and *staircase* conditions is illustrated in Fig. 11. The average best-fitting logistic func-

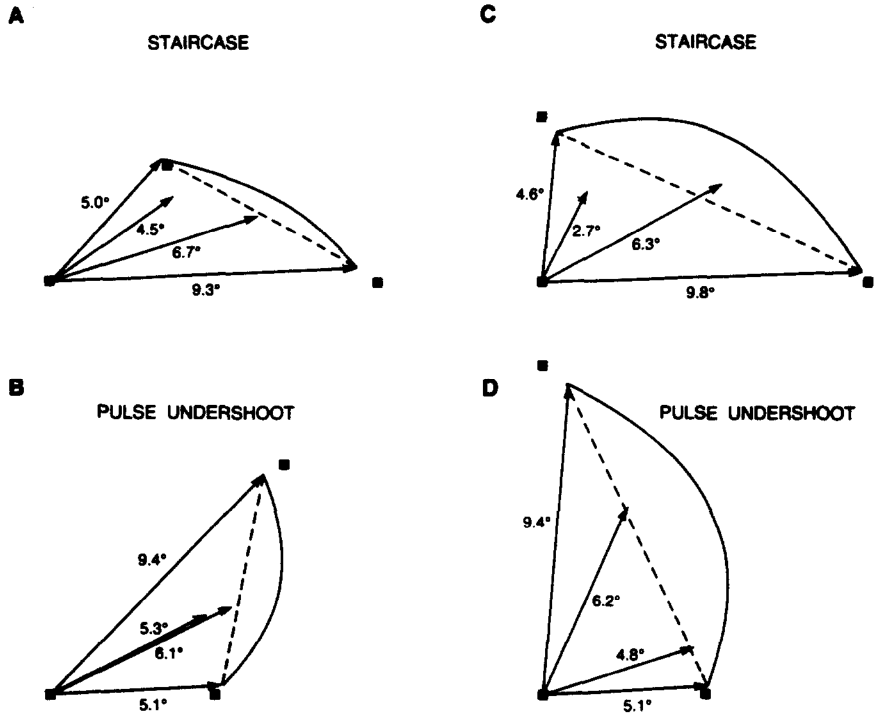

Fig. 10. Summary data of single-step and intermediate-angle responses for *staircase* (A, C) and *pulse undershoot* (B, D) conditions in Diagonal (A, B) and Vertical (C, D) configurations from Experiment 2.

tions for the AmpTFs and the AngTFs in the *pulse undershoot* and *staircase* conditions were normalized and plotted together to facilitate comparison. As shown earlier in Tables 2 and 3, the midpoint of the AmpTFs for the *pulse undershoot* conditions occurred earlier along the D-axis than the midpoints for the *staircase* conditions. However, the midpoints of the AngTFs did not differ between conditions. Figure 11 shows that the midpoint of the AngTF occurred at the end of the transition region for the *pulse undershoot* AmpTF and at the beginning of the transition region for the *staircase* AmpTF. Recall from Fig. 1 that D-values are referenced to the reaction time of the initial saccade. Thus, an AmpTF or an AngTF with long D values indicates that a change in amplitude or angle occurred *early* in the latency period, whereas short D values indicate a late-occurring change. Thus, for the majority of *pulse undershoot* trials, modulations in saccade amplitude were completed after the transition from an initial-angle to a final-angle response. In contrast, for the majority of *staircase* trials, modulations in saccade amplitude occurred just prior to the transition from an initial-angle to a final-angle response.

GENERAL DISCUSSION

The experiments described in the present report have replicated and extended Becker and Jürgens' (1979) model for the programming of saccadic eye movements. First, when the amplitude of two target displacements was held constant but the angle of the displacements differed by 45 deg, a small but significant number of intermediate-*angle* responses occurred and formed a continuous AngTF. The midpoint of this AngTF corresponded to a D-value of approximately 175 msec and the duration of the transition from an initial-angle to a final-angle response was 30–80 msec. Thus, the AngTF shares many of the qualitative characteristics of the AmpTF described by Becker and Jürgens for double-steps confined to the horizontal axis. These results also provide a quantitative extension of preliminary evidence for an AngTF by Findlay and Harris (1984).

Second, all of the qualitative characteristics of the AmpTF along the horizontal axis were replicated for double-steps confined to one of the two oblique axes. That is, modulations of target amplitude within a hemifield (*pulse undershoot* and *staircase* conditions) yielded con-

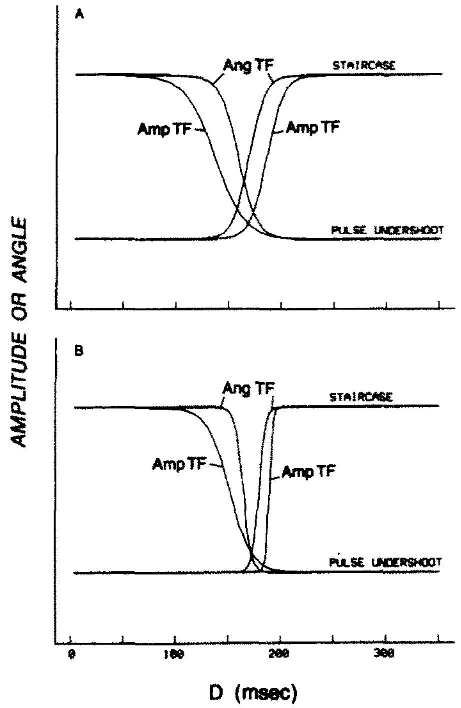

Fig. 11. Normalized best-fitting logistic functions for both the AmpTFs and the AngTFs in the *pulse undershoot* and *staircase* conditions of Experiment 2. (A) Diagonal test configurations; (B) Vertical test configurations.

tinuous AmpTFs, whereas target amplitudes that crossed hemifields (*pulse overshoot* condition) yielded a discontinuous AmpTF. Moreover, this discontinuous AmpTF was characterized by a gap of approximately 50–70 msec along the D-axis, suggesting that the process of cancelling and reprogramming a saccade to the opposite hemifield interrupted the process of averaging information about target position. A similar gap was present in the *pulse overshoot* data of Feustel *et al.* (1982), Groll and Ross (1982), and Findlay and Harris (1984) in which target displacements were confined to the horizontal axis. The gap was less consistently present in the *pulse overshoot* data from Becker and Jürgens (1979), perhaps because they used much larger target displacements (15–60 deg vs 3–10 deg).

Third, there was a clear asymmetry in the timing of the AmpTF for the *pulse undershoot* and the *staircase* conditions. In both the oblique displacement data from the follow-up to Experiment 1 and the data from Experiment 2, the midpoint of the AmpTF in the *pulse undershoot* condition occurred closer to the initiation of the first saccade than in the *staircase* condition (150 vs 195 msec). Because the duration of the AmpTF did not appear to vary between these two conditions, this timing asymmetry implies that *decreases* in saccade amplitude can occur later in the reprogramming of the initial saccade than *increases* in saccade amplitude. A comparable asymmetry between the timing of the AmpTFs in the *pulse undershoot* and *staircase* conditions was evident in the data presented by Becker and Jürgens (1979), Feustel *et al.* (1982), Groll and Ross (1982), and Findlay and Harris (1984). However, in the present report these timing relations were more objectively specified by using a least squares fit to the data rather than a fit by eye.

Finally, the combination of changes in target angle and changes in target amplitude investigated in Experiment 2 revealed two new findings. First, even when the two target steps differed in angle by 45 or 90 deg, the AmpTFs were continuous for both the *pulse undershoot* and the *staircase* conditions. Thus, the reprogramming required to alter the direction of a saccade by as much as 90 deg does not result in the *dis*continuous AmpTF present when saccade direction is altered by 180 deg (the *pulse overshoot* condition). Second, the relative timing of AmpTFs and AngTFs was consistently different. For the *pulse undershoot* condition, the AmpTF began at approximately 170 msec prior to the initial saccade and ended at approximately 120 msec prior to the initial saccade, whereas the AngTF was centered at approximately 160 msec prior to the initial saccade. Thus, intermediate-*angle* responses in the *pulse undershoot* condition were typically *final-amplitude* responses. In contrast, for the *staircase* condition, the AmpTF began at approximately 210 msec prior to the initial saccade and ended at approximately 160 msec prior to the initial saccade, whereas the AngTF was centered at approximately 160 msec. Thus, intermediate-*angle* responses in the *staircase* condition were typically *initial-amplitude* responses.

This asymmetry in the timing of the AmpTF between the *pulse undershoot* and the *staircase* conditions, in combination with the *invariance* in the timing of the AngTF, suggests that saccade amplitude and saccade angle are programmed independently. Komoda *et al.* (1973) and Hou and Fender (1979) reached a similar conclusion despite considerable differences in the spatial configuration of their double-step displacements and the details of their analyses. Becker and Jürgens (1979) also concluded that the computation of saccade angle and saccade amplitude involved separate mechanisms, but they proposed a fixed hierarchy for the timing of these two computations: "computation of the amplitude is carried out after the direction decision has been completed" (p. 976). The results from Experiment 2 (see Fig. 11) provide compelling evidence that the angle computation does not always *precede* the amplitude computation when the direction of the second target step is 45 or 90 deg discrépant from the direction of the first target step.

A model of saccadic programming

Based on the results from the present set of experiments, we now propose an updated model of saccadic programming that builds on the model outlined by Becker and Jürgens (1979). They proposed a two-channel decision mechanism that receives an error signal corresponding to the angular distance between the fovea and the first target step. If the error signal exceeds a displacement threshold, it activates one of two decision channels. Because the target steps were limited to the horizontal axis, the two channels of the decision mechanism correspond to rightward and leftward directions. Once activated, the decision channel operates on the error signal for a variable delay (the "decision time") before the decision regarding the direction of the saccade is finalized. If the error signal changes during this variable decision time, one of two processes occurs. If the new error signal matches the direction of the initial direction channel, the decision process continues uninterrupted. However, if the new error signal corresponds to the opposite direction, the initial decision process is aborted and the decision process begins anew in the second decision channel. For the five subjects tested by Becker and Jürgens, the range of decision times was estimated to be 76–129 msec (mean = 102 msec).

Obviously, the two-channel decision mechanism proposed by Becker and Jürgens (1979) was constrained by the use of only horizontal target steps. A complete model must incorporate a multi-channel decision mechanism, with the number of channels determined by the minimum direction difference that can be executed by the saccadic system (e.g. if ±2 deg, then 90 channels). Such a multi-channel decision mechanism calls into question the scheme by which a change in the error signal halts the decision process in the initial decision channel. Our results demonstrate that a 45 or 90 deg change in the angle error signal, with or without amplitude changes, is *not* sufficient to abort the original decision process. Rather, directional error-signal changes as great as 90 deg are apparently *averaged* within a limited duration of the initial saccadic latency period. Thus, Becker and Jürgens' proposal that "(the) decision to elicit a saccade is therefore identical with the decision about the direction of the saccade" (p. 975) may only apply to target excursions limited to a single stimulus axis.

The second part of Becker and Jürgens' (1979) model takes the output of the decision mechanism and computes the amplitude of the saccade by averaging target information over a limited duration (estimated to be approximately 120 msec). If the variable duration decision mechanism occurs rapidly, then the amplitude computation can compensate for the second target step and a final-amplitude response is executed. If the variable duration decision mechanism occurs slowly, then the amplitude computation cannot compensate for the second target step and an initial-amplitude response is executed. If the decision mechanism occurs after an intermediate duration, then the amplitude computation averages the two target steps and an intermediate-amplitude response is executed.

Some aspects of the results from Experiment 2 are consistent with the computation of saccade amplitude outlined in Becker and Jürgens' (1979) model. For example, the duration of the averaging window did not appear to vary systematically with stimulus condition (*pulse undershoot* vs *staircase*). However, these transition durations tended to be shorter when the angle between the two target steps differed by 90 deg than when they differed by 45 or 0 deg. This suggests that the direction decision mechanism interacts with the amplitude computation process, but does not appear to correspond to the hierarchical scheme outlined by Becker and Jürgens. They proposed that the directional decision process is completed *before* the amplitude averaging process is initiated because "before the amplitude can be calculated it must be known whether the 'right' or 'left' saccadic system shall perform it" (p. 976). Not only do our results from Experiment 2 on the relative timing of the AmpTF and the AngTF contradict this hierarchy (see Fig. 11), but Becker and Jürgens' own results are inconsistent with their proposal. As discussed earlier, Becker and Jürgens reported that the AmpTF for the *staircase* condition occurred at longer D values

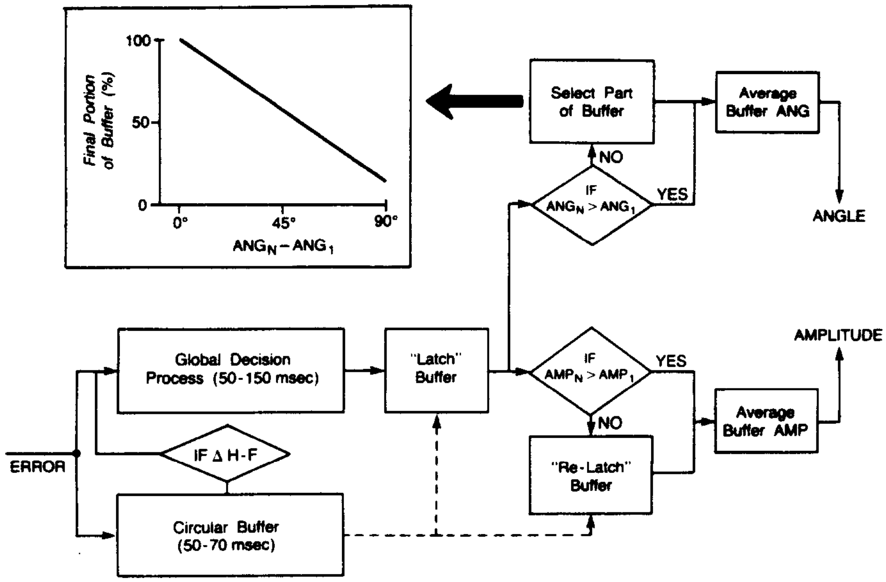

Fig. 12. A revised model for the saccadic programming system. H-F: hemi-field. See text for details.

relative to the AmpTF for the *pulse undershoot* condition (mean onset times were 203 and 81 msec, respectively). Again, recall that longer *D* values imply an *earlier* occurring event in the saccadic latency period. Because there was no difference in the *duration* of the AmpTF, Becker and Jürgens correctly pointed out "that the modification time for shortening the response amplitude is much smaller than that needed for lengthening" (p. 978). They argued that this timing asymmetry, which was also evident in the results of the present set of experiments, could not have arisen via feedback during the saccade itself, and therefore must "arise prior to the neural pulse generator" (p. 978). However, unless one were to assume that the directional decision process had an additional constant delay in the *pulse undershoot* condition, it is not clear why the onset of the AmpTF was 100 msec or more earlier in the *staircase* condition than in the *pulse undershoot* condition.

Figure 12 illustrates a revised model of saccadic programming that is consistent with our data as well as the data reported in other double-step experiments. This model employs a computer analogy in an attempt to outline the logical mechanisms underlying saccadic programming and is *not* intended as a description of the neural mechanisms controlling saccades, but rather as a heuristic for the processes that must operate in some form during the saccadic latency period. As in the Becker and Jürgens (1979) model, an error signal, which must exceed a displacement threshold (or saccadic deadzone), enters a variable duration decision mechanism. However, in contrast to Becker and Jürgens, we propose that this decision mechanism is not organized into discrete directional channels. Rather, the decision mechanism is simply a stochastic delay associated with the process of deploying attention to an extrafoveal target and activating the subsequent saccadic computation mechanisms. During this global decision interval, a target-location buffer is being continuously filled with the horizontal and vertical coordinates (or vector) of the peripheral target. Thus, as soon as the target is displaced to a new location (Step-1), the target-location buffer is continuously updated with information about the horizontal and vertical coordinates of the target. We assume that this buffer has a finite length (approximately 50–70 msec) because of the maximum observed duration of the AmpTF. Thus, the buffer is actually analogous to a *circular* buffer in which new samples replace the oldest samples to maintain a constant buffer length.

The filling of the circular buffer occurs in parallel with the global decision process. In addition, a comparator checks the current target location to flag any samples that fall in the opposite hemifield. If this flag is triggered by a sample fed to the circular buffer, then the decision process is aborted and restarted. This feature of the model is identical to that of Becker and Jürgens (1979), except that no blocking of opposite direction channels is required. Once the decision process has been aborted and restarted, it will proceed to completion more rapidly because the attentional components of the decision process have already been activated. We hypothesize that a re-started decision process adds approximately 50–70 msec to the overall decision process. This additional time corresponds to the gap seen in the AmpTFs for the *pulse overshoot* condition [see Fig. 5(B)]. Moreover, this lengthened decision process delays the entire saccadic programming process, as reflected in the longer reaction times to the initial saccade in the *pulse overshoot* condition compared to all other conditions (*staircase*, *pulse undershoot*, and *equal amplitude*).

After the global decision process has been completed, the saccade *must* occur. Separate amplitude and angle computations are made from the current contents of the circular buffer. In essence, the information in this circular buffer is "latched" so that operations can be performed on these data while the buffer continues to be updated with target information. Parallel computations for saccade amplitude and saccade angle are then made. We will consider the angle computations first because they are somewhat more complex.

The two critical features of the angle computation are (a) that it occurs at the same time after the first target step regardless of stimulus condition (this is *not* true of the amplitude computation; see below), and (b) that the duration of the AngTF varies with the angular discrepancy between the target locations on Step-1 and Step-2. We propose that a weighted average of the angle information contained in the "latched" circular buffer is used to provide the angle signal for the initial saccade. As shown in the inset to Fig. 12, if the angle of the target samples at the beginning and at the end of the circular buffer are very similar (e.g. ±15 deg), then all samples in the circular buffer are weighted equally. However, as these first and last samples become more discrepant, less and less of the *initial* portion of this circular buffer information is used to compute the angle of the initial saccade. For example, when Step-1 is 0 deg and Step-2 is 90 deg [as in Experiment 2; see Figs 6(B) and 8(B)], the duration of the AngTF is very brief (e.g. 10 msec). In contrast, when Step-1 and Step-2 differ by 45 deg [see Figs 6(A) and 8(A)], the duration of the AngTF is significantly longer (e.g. 30 msec).

In parallel with the angle computations, the "latched" circular buffer information is evaluated to compute the initial saccade amplitude. The computations again involve a comparison of the first and last samples in the circular buffer. If the last sample is greater than or equal to the first sample (± a "noise" factor), then the entire buffer is averaged and this average is used as the amplitude signal for the initial saccade. However, if the last sample is significantly *less* than the first sample, then the circular buffer is "re-latched". The purpose of this additional latching operation is to guard against overshoots. That is, because the saccadic system is apparently biased to prevent overshoots (Henson, 1978), any second target step that moves the target further from the fovea than the first target step will lead to an overshoot if the system simply averages the first and second target locations. Moreover, because the saccadic system can apparently *decrease* the gain of the saccade more easily than it can increase saccadic gain (Miller *et al.*, 1981), there is sufficient time prior to the onset of the initial saccade to recompute the target's location from the information in the circular buffer. Finally, there is some indication that saccade amplitude is affected by the *angular* difference between the two target steps (AmpTF durations were shorter in the Vertical configuration of Experiment 2). However, because these shorter AmpTFs were only present in the *staircase* condition, we have not incorporated a weighting function into the amplitude computation of our model.

These computation processes account for the temporal relationship between the AngTF and the AmpTF in the various stimulus conditions. For example, as shown in Fig. 13, the AngTF occurs at approximately 90–130 msec after Step-1 in both the *staircase* and *pulse undershoot* conditions in Experiment 2 for the Diagonal configuration. However, the AmpTF occurs at approximately 75–105 msec after Step-1 in the *staircase* condition and at approximately 100–160 msec after Step-1 in the *pulse undershoot* condition. Thus, the *angle* computation appears to occur at a relatively invariant time after Step-1, whereas the *amplitude* computation occurs at a variable time after Step-1, with a bias for overshoots to be reduced in frequency by delaying the sampling of amplitude information (shorter *D* values) in the *pulse undershoot* condition.

In summary, we have provided an expanded model of saccadic programming to double-step target displacements that builds on the model

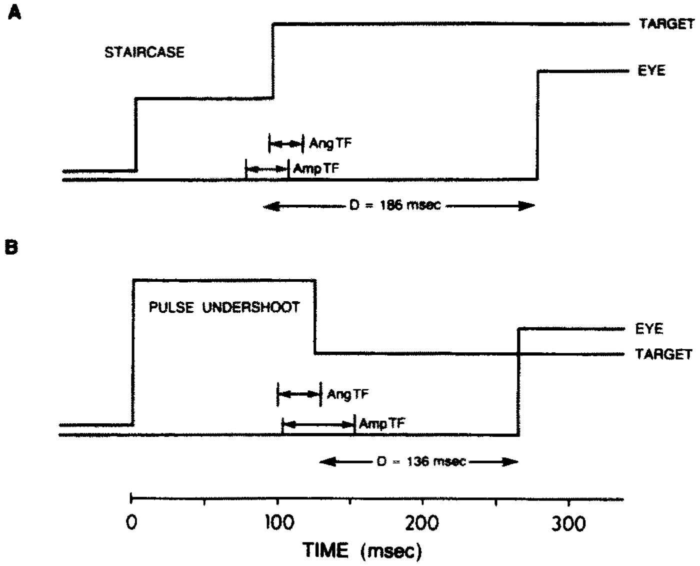

Fig. 13. Temporal relationship between the AngTF and the AmpTF in the *staircase* and *pulse undershoot* conditions from Experiment 2. See text for details.

outlined by Becker and Jürgens (1979). Our expanded model accounts for both the angle and the amplitude of the initial saccade to double-step displacements. It incorporates parallel computations of saccade amplitude and saccade angle as outlined in Fig. 12 and a modified vector-average of saccade amplitude (see Figs 9 and 10). Although our model provides a complete descriptive account of the programming of double-step saccades, its primary aim is to act as a heuristic for further empirical studies of saccadic eye movements and neural models of their underlying control system.

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