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ABSTRACT

The examination of saccadic eye movements--rapid shifts in gaze from one visual area of interest to another--is useful in studying pilot's visual learning in flight simulator training. Saccadic eye movements are the basic oculomotor response associated with the acquisition of visual information and provide an objective measure of higher perceptual processes. In this investigation, three adult subjects fixated a single point of light, which was then extinguished and replaced either by one target which appeared at plus or minus 5, 10, or 15 degrees, or by two targets which appeared symmetrically at those same eccentricities. All subjects showed a directional preference (averaging about 80%) in the two-target condition, and it was found that this preference could be eliminated by delaying by about 40 milliseconds the onset of the target presented in the preferred direction. This indicated that a 40-millisecond "window" of time was allocated for deciding response direction. It was also found that the saccadic latency of responses in the nonpreferred direction was affected more by a second target presented in the preferred direction than vice versa. This asymmetry in the system which controls saccadic eye movements has not previously been described. (JGL)

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AIR FORCE HUMAN RESOURCES LABORATORY

ASYMMETRIES IN THE CONTROL OF SACCADIC EYE MOVEMENTS TO BIFURCATING TARGETS

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The task of responding to one of two simultaneously presented targets often reveals unexpected yet profound preferences in the direction of saccadic eye movements. In the present investigation, a simple experimental paradigm was used in which a single point of light bifurcates symmetrically to the left and right of the fixation point. Under these conditions, most subjects show an eye movement response preference to either the left or right. The present data show that this preference can be eliminated by delaying the onset of the target, presented in the preferred direction, by about 40 milliseconds. This indicates that in the sequence of events occurring prior to the execution of a saccade, a "window" of time of this duration is allocated for decisions concerning direction of response even when targets are presented to both visual hemifields. It was also found that the bifurcating targets interact to significantly increase response latencies in both the preferred and nonpreferred directions. Further, the interaction is asymmetrical, in that a target presented in the preferred direction has a greater effect than a target in the nonpreferred direction on responses in the counter direction. The results suggest an asymmetry in hemispheric interaction that has not previously been demonstrated in the visual-oculomotor system.

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SUMMARY

The effective use of wide-field-of-view flight simulators requires that pilots process all of the visual information available in the simulator environment. Saccadic eye movements are the basic oculomotor response associated with the acquisition of visual information. Further, they provide an objective measure of higher perceptual processes. In the present investigation, a simple experimental paradigm was used in which subjects fixated a single point of light, which was then extinguished and replaced either by one target which appeared at ±5, ±10, or ±15 degrees or by two targets which appeared symmetrically at those same eccentricities. All subjects showed a directional preference (averaging about 80%) in the two-target condition, and it was found that this preference could be eliminated by delaying by about 40 msec the onset of the target presented in the preferred direction. This indicates that in the sequence of events that precedes a saccade, a 40-msec "window" of time is allocated for deciding response direction. It was also found that the saccadic latency of responses in the nonpreferred direction was affected more by a second target presented in the preferred direction than vice versa. Thus, the second target has a different effect on response latency depending on whether it is presented to the left or right of the fixation point. This asymmetry in the system which controls saccadic eye movements has not previously been described.

PREFACE

The research reported here was performed in support of the Aircrew Training Thrust at the Operations Training Division of the Air Force Human Resources Laboratory, Williams Air Force Base, Arizona. The purpose of the research is to elucidate the basic mechanisms underlying visually guided behavior in flight simulators, and specifically, those using helmet-mounted displays.

This research was performed at the Man-Vehicle Laboratory of the Massachusetts Institute of Technology and was supported by Air Force Contract F33615-84-C-0066 (UDRI).

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I. INTRODUCTION

A saccadic eye movement is the rapid shift in gaze from one visual area of interest to another. Saccades are perhaps the most common type of eye movement and represent the primary oculomotor mechanism by which images of objects of interest are brought into coincidence with the fovea. Most studies of the saccadic system have employed stimuli composed of single points (see Zeevi, Wetzel, & Young, 1983; Zuber, 1981). These studies have revealed important information about oculomotor control but provide little insight into visual information processing and the interactions that may occur among visual stimuli. Studies with complex images (e.g., Noton & Stark, 1971) on the other hand have the disadvantage that the stimuli cannot be completely specified and the conclusions that can be drawn from responses to them are limited. Complex eye movement responses can be elicited by relatively simple stimuli. In fact, a stimulus composed of as few as two light sources is sufficient to explore many of the organizational principles of the eye movement control system and, as the present data will suggest, even higher-order visual information processing.

The human visual system is typically conceptualized as a parallel processing system. This is evidenced, for instance, by the well-known systems which subserve chromaticity and luminance discrimination, as well as the spatiotemporal aspects of the stimulus. It has recently been recognized, however, that serial processing of visual information is also important as apparent, for example, from the sequence of saccades generated during exploration of the visual environment (Noton & Stark, 1971; Yarbus, 1967). To explore this serial mode requires stimuli comprised of a minimum of two components.

In progressing along the visual pathway from retina to cortex, visual signals are segregated such that information from the right visual field, as imaged on both retinas, is projected onto the left cortical hemisphere and vice versa (see Figure 1). How does such a system which does not map the entire visual field in either hemisphere respond when the stimulus is distributed in both the left and right visual fields? For example, if the stimulus is presented symmetrically about the fixation point, one hemisphere might dominate, and the resulting eye movement will reflect a preference in the corresponding direction. If this is the case, how then does the information sent to the other hemisphere affect the response? If a preference exists to targets bifurcating symmetrically in time, then it may be eliminated, for instance, by delaying the onset of the target in the preferred direction. If the preference can be manipulated in this way, it implies a combination of serial and parallel processing at some level. Further, the delay that eliminates the preference reflects the "window" in time over which a decision is made concerning the direction of response.

Interactions between the cortical hemispheres can be studied by considering the effects, on responses to stimuli projected in the preferred visual hemifield, of stimuli presented in the nonpreferred hemifield and vice versa. Further, as depicted in Figure 1 by the arrows of various sizes, the interhemispheric interactions may be asymmetrical. In the present investigation, we have augmented the findings of Zeevi et al.

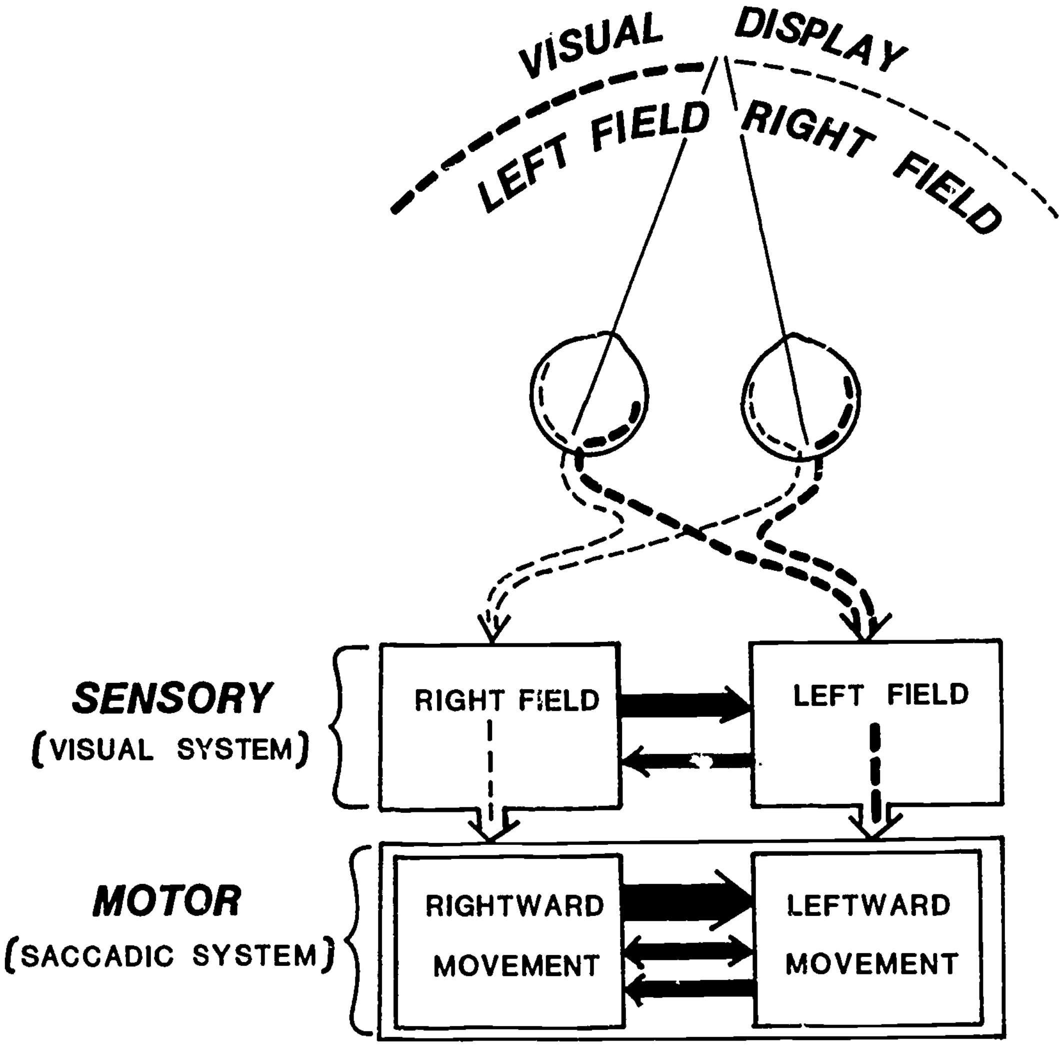

Figure 1. A Diagram Illustrating the Segregation of Visual Information Along the Visual Pathway. Note that the right visual hemifield projects to the left hemisphere of the brain and vice versa. Asymmetries in the lateral interactions between the hemispheres are depicted by arrows of various sizes.

(1983) by separately analyzing the latencies of saccadic eye movements made in the preferred and nonpreferred visual directions. In addition, we have explored in more detail the response of the eye movement system to visual targets presented non-simultaneously in the left and right visual fields.

II. METHOD

Subjects

Three subjects between the ages of 21 and 33 participated in the present experiments. Two of the subjects (BL and GG) were emmetropic, and the vision of the third was corrected to normal by contact lenses. All three subjects exhibited normal eye movements, as evidenced by their saccadic latencies and trajectories. Two of the subjects (BL and MB) had extensive experience in eye movement research but were naive as to the purpose of the effort. Also, they had previously participated in a similar eye movement study (Zeevi et al.,1983). The third subject (GG) was one of the authors, who had extensive visual research experience but not in the area of eye movements.

Apparatus

A schematic diagram of the experimental setup is shown as Figure 2. The display consisted of 21 computer-controlled, green, light-emitting diodes or LEDs (Fairchild FTV-310). The diodes were flush-mounted every 5 degrees along the meridian of a flat-black, 100-degree, semicircular arc with a radius of 1 meter. To reduce the visual angle of each target, a 1mm-diameter field stop was placed over each LED. The visual angle of each target when viewed from a distance of 1 meter was 3.7 minutes of arc. The spatial and temporal characteristics of the LED stimulus patterns were controlled by a special-purpose controller which interfaced with a DEC PDP-11/34 computer.

The stimulus patterns consisted of either a single target, in which the fixation point was extinguished and another target at either 5, 10, or 15 degrees to the left or right was simultaneously presented, or a double target, in which the fixation point was extinguished and two targets were presented symmetrically again at either 5, 10, or 15 degrees to the left and right of the fixation point. The two-target condition gave the visual impression of a single target bifurcating into two targets. In addition, for the two-target condition, the presentation of either the rightward or leftward target could be delayed by 5, 10, 20, or 60 msec.

Horizontal eye position was measured by using a standard infrared (IR) limbus-tracking technique. The eye position monitor consisted of a DC-powered IR emitter (Texas Instruments TIL33) and a pair of IR phototransistors (Texas Instruments LS-400) separated by 20mm and mounted on each side of the IR emitter. The emitter/detector assembly was aimed from below the eye and at the left and right sides of the limbus. As the eye changed its horizontal position, signals from the phototransistors were differentially amplified, thus producing an analog voltage proportional to eye position. With this system, eye position could be accurately measured to better than 0.25 degree over a range of ± 15 degrees. The analog output

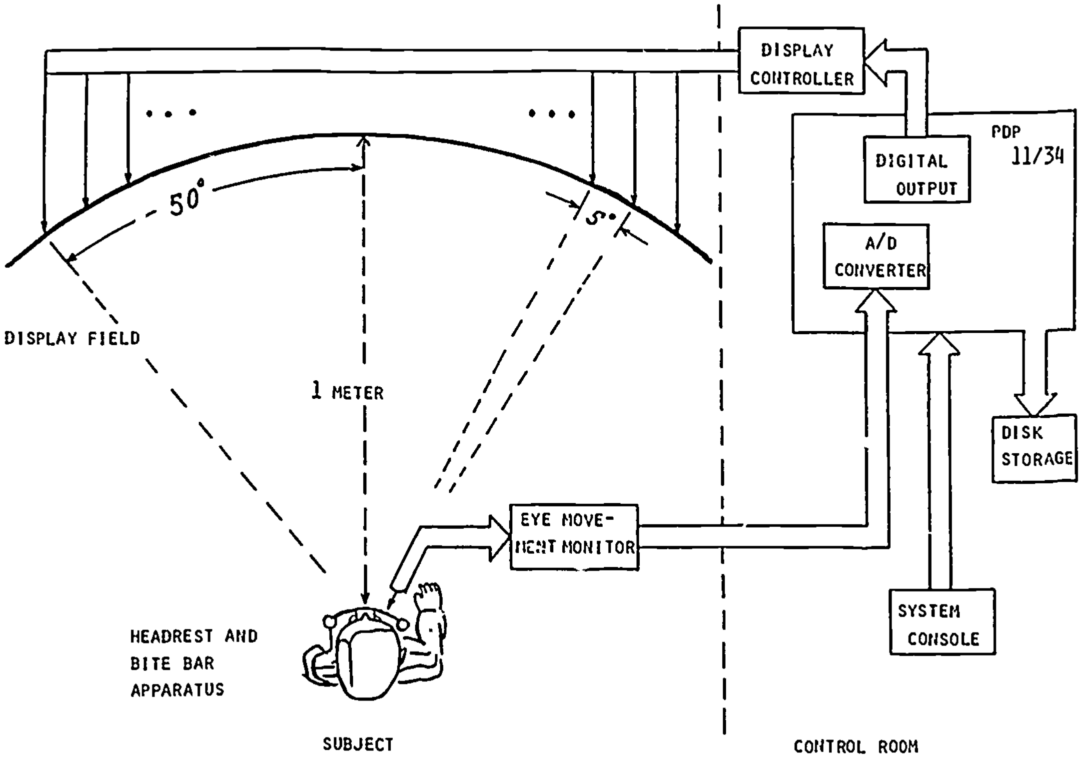

Figure 2. A Schematic Diagram of the Experimental Setup. The subject is shown viewing a perimetric display comprised of LEDs mounted 5 deg apart in the horizontal meridian. A laboratory computer controlled both stimulus presentation and data collection from the eye movement monitor.

of the eye position monitor was sampled at 100 Hz by a 12-bit analog-to-digital (A/D) converter and stored for later analysis by the PDP-11/34. Subjects' head movements were minimized with a combination of a dental impression bite bar and adjustable head and chin rests.

Procedure

The subjects were first seated in the apparatus and were asked to fixate the central LED. Next, the eye position monitoring system was aligned and adjusted. The eye monitoring system was calibrated by asking the subjects to fixate sequentially several calibration targets to both sides of the fixation point.

Subjects first fixated the central LED target, which was then extinguished and replaced either by one target which appeared at ±5, ±10, or ±15 degrees or by two targets which appeared symmetrically at those same eccentricities. For the two-target stimuli, one or the other target was delayed by 0, 5, 10, 20, or 60 msec. Subjects were instructed to foveate the newly appearing target(s) as rapidly and spontaneously as possible. Stimulus presentation was randomized with respect to type (single or double), eccentricity, delay, and interstimulus interval.

Each subject was tested in two experimental sessions, each of which lasted about 1 hour. There were 12 experimental runs per session. Each run lasted less than a minute, and the subjects were allowed a 2- to 3-minute rest period between runs. In addition, there was a longer rest period midway through the session, in which the subject was allowed off the apparatus.

Data Analysis

The eye movement record for each response was visually inspected on a computer display to verify that a saccade had in fact occurred, and the saccadic latency was measured from that record. The means and standard deviations of the response latencies were computed for both the single and bifurcating targets at each eccentricity. All responses whose latency exceeded three standard deviations from the mean were excluded categorically. In addition, responses between 1.5 and 3 standard deviations from the mean were excluded from certain data sets when an analysis of the ratio of the mean to the standard deviation revealed an abnormally noisy data set.

III. RESULTS

All subjects exhibited a higher percentage of responses in one direction for simultaneously presented bifurcating targets. For subjects GG and MB, the response preference was to the right, and for subject BL, it was to the left (see Table 1 for percentages). For this reason, the data were pooled with respect to response preference rather than absolute direction, and this convention was adhered to in all data and figures presented in this report. The effects of retinal eccentricity on saccadic responses were not investigated *per se*. Eccentricity was varied only to prevent subjects from

Table 1. A Summary of the Latency Data for All Delays Except 60 Msec

Leading Stimulus/ Response Direction	Subjects GG	MB	BL	Mean ± sd
NP/NP	25.86 (n=28)	46.92 (30)	50.44 (5)	37.84 ± 22.62
P/P	11.57 (49)	39.53 (56)	18.64 (60)	23.63 ± 17.04
(NP/NP)-(P/P)	14.29	7.39	31.80	14.21 ($p < 10^{-4}$)
P/NP	29.15 (n=19)	61.29 (13)	77.60 (1)	43.28 ± 36.09
NP/P	28.29 (37)	40.12 (40)	22.71 (59)	29.25 ± 19.24
(P/NP)-(NP/P)	0.86	21.17	54.89	14.03 ($p < .04$)
NO/NP	39.17 (n=9)	44.85 (3)	--	40.59 ± 25.59
NO/P	9.35 (13)	35.79 (20)	10.36 (20)	19.75 ± 13.91
(NO/NP)-(NO/P)	29.82	9.06	--	20.84 ($p < .02$)
% responses in preferred direction	56.5 (n=23)	87.0 (23)	95.7 (23)	79.7 ± 20.58

Note. P - preferred
NP - nonpreferred
NO - no leading stimulus.

predicting where the target would appear. We have therefore pooled all data over the three eccentricities tested.

Shown in Figure 3 is the percentage of responses in the preferred direction, plotted as a function of the delay between the leading and lagging targets (with respect to the preferred direction). The data of Figure 3 represent the mean from all three subjects. The continuous curve was drawn by eye through the data and intersects the ordinate (representing 0 delay) at about 78%. This is representative of the mean response preference of our three subjects. The amount this curve must be shifted along the delay axis in order for it to intersect the ordinate at the chance level of 50% is approximately 40 msec (see broken lines).

The data of Figure 4 represent the mean data from three subjects and show the increase in response latencies to stimuli presented in both visual hemifields as compared to the response latencies to single point targets. The filled symbols on the left side of the figure represent the increase in response latency to the non-delayed bifurcating targets in the preferred (filled square) and nonpreferred (filled circle) directions. The difference of about 21 msec between these two data points was found to be statistically significant ($\underline{t} = 2.74$, df = 63, $\underline{p} < .02$).

The four data points on the right side of Figure 4 represent data in which one of the two target points was delayed by either 5, 10, or 20 msec. Since the amount of time allocated for selecting direction of response is less than 50 msec (see Figure 3 and Discussion), we have excluded from Figure 4 (and Table 1) the latency data obtained for the 60-msec delay. The two open symbols in Figure 4 represent responses in the nonpreferred direction, whereas the complementary filled symbols represent responses in the preferred direction.

The two square symbols in Figure 4 connected by a continuous line represent responses in the preferred direction. The circular symbols connected by a broken line represent responses in the nonpreferred direction. The filled symbols represent responses in the same direction as that of the leading target. The filled square represents the preferred direction, and the filled circle represents the nonpreferred direction. The difference of 14.21 msec between these data points was highly significant ($\underline{t} = 4.51$, df = 226, $\underline{p} < 10^{-4}$). The open symbols represent responses in the same direction as that of the lagging target. The difference of 14.03 msec between these data points is also significant ($\underline{t} = 2.16$, df = 167, $\underline{p} < 0.04$). Individual subject data and standard deviations relevant to the above statistical comparisons are given in Table 1.

Shown in Figure 5 is the latency increase relative to the single-target condition as a function of the delay between the targets presented in the right and left visual hemifields. In Figure 5a, the responses in both the preferred and nonpreferred directions are combined. In addition to the increase in latency due to bihemifield stimulation as depicted on the ordinate, there is a further increase for intertarget delays up to about 20 msec. The data of Figure 5a are separated into responses in the preferred

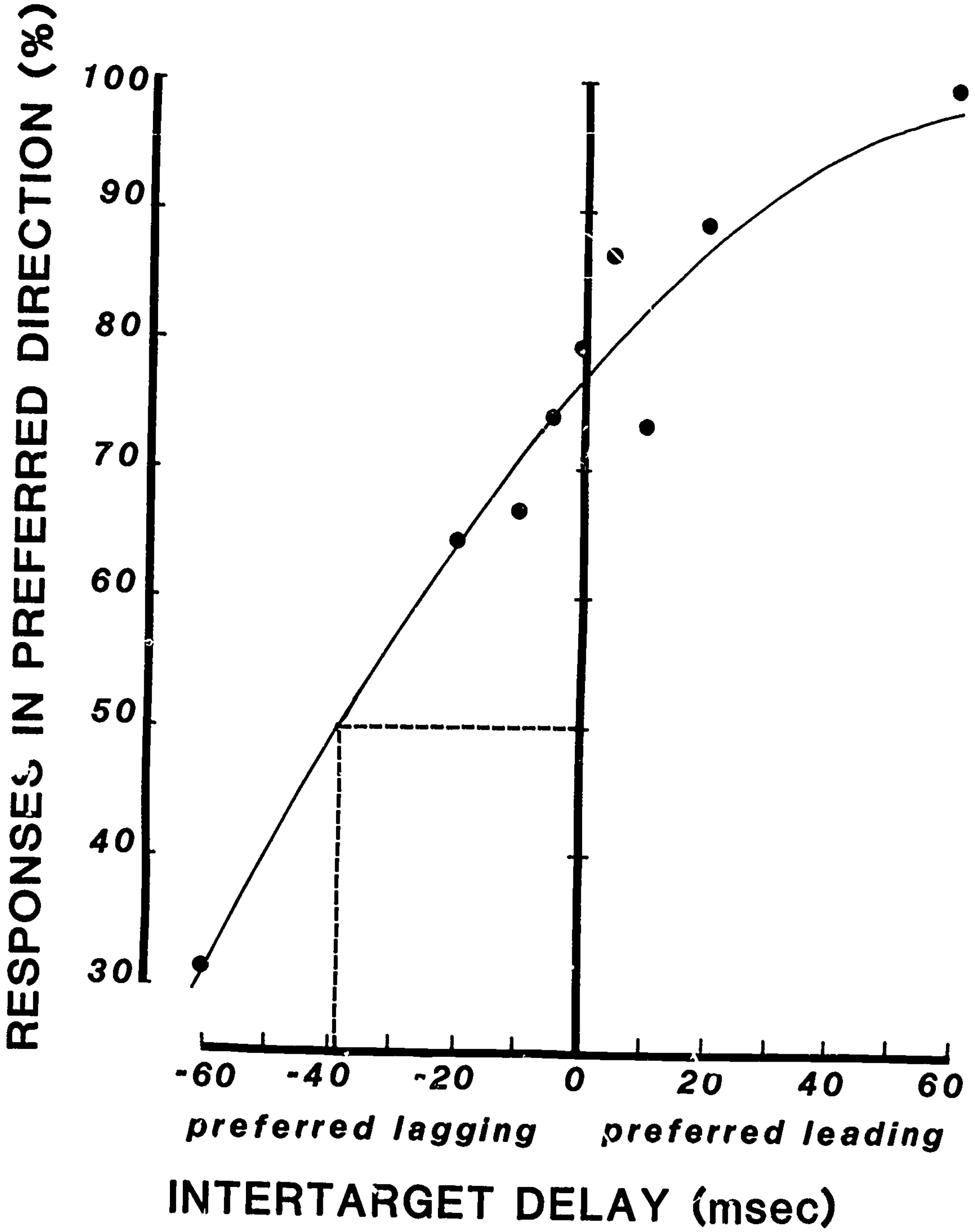

Figure 3. Percentage of Saccadic Responses in the Preferred Direction Plotted as a Function of the Difference in the Time of Appearance of the Two Targets. Data are pooled over the three subjects as well as over retinal eccertricity. Positive delays indicate that the target presented in the preferred visual hemifield appeared first (i.e., was the leading target). The broken line indicates the delay required to offset the subjects' response preference, thus equating the percentage of responses in each direction.

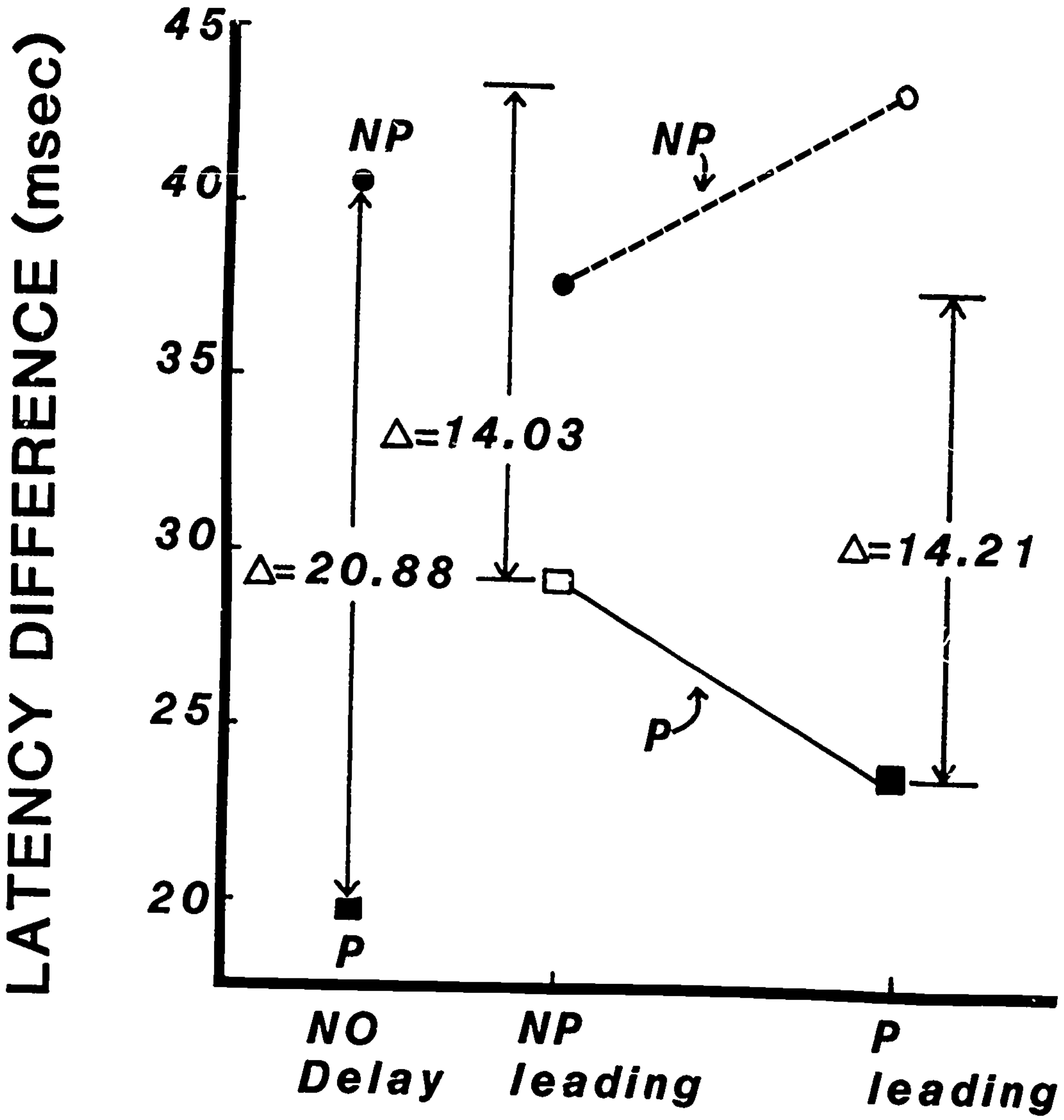

Figure 4. Latency Difference in Response to Bihemifield Stimuli Relative to Response Latencies to Single Targets. All data points represent weighted averages of the responses from all three subjects. The squares represent responses in the preferred direction, and the circles represent responses in the nonpreferred direction. The two filled data points on the left side of the figure represent the responses to simultaneously presented targets (i.e., 0 delay). The four data points on the right side of the figure represent weighted averages of responses to stimuli in which one of the two targets was delayed by 5, 10, or 20 msec. The filled symbols represent responses to the leading target, and the open symbols represent responses to the lagging target. Differences in the data indicating response direction preference are denoted by the arrows and are further described in the text.

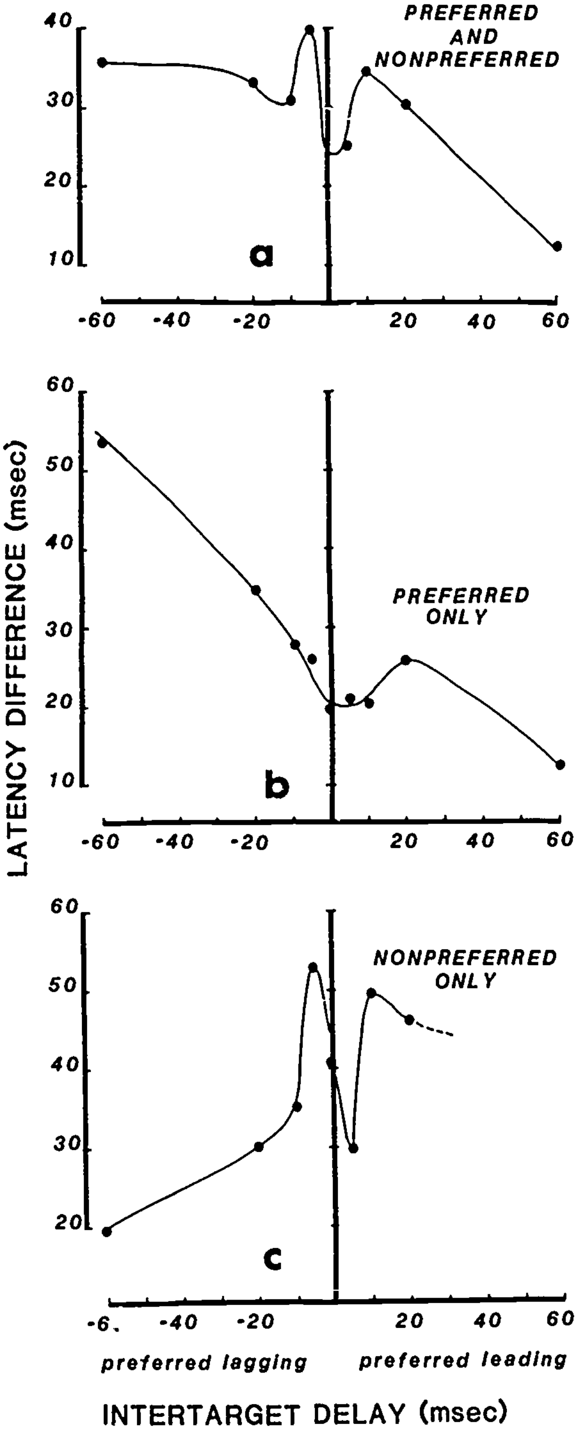

Figure 5. The Latency Difference, Indicating the Increase in Latency to Bihemifield Stimuli as Compared to Single Targets, is Plotted as a Function of the Intertarget Delay in the Upper Graph. Positive delays indicate that the target presented in the preferred hemifield appeared first. Each of the data points represents responses in both the preferred and nonpreferred directions. The latency of responses in the preferred and nonpreferred directions are shown in the central and bottom graphs, respectively.

direction (Figure 5b) and responses in the nonpreferred direction (Figure 5c). Here for longer delays the latency strongly depends on the response direction.

IV. DISCUSSION

The data of Figure 3 show that when the stimuli bifurcate symmetrically in time (that is, when the left and right field targets appear simultaneously), subjects exhibit a preference in one direction. The population average for this preference was found here to be about 80% (see Table 1) and may be compared to the preference of 80% to 88% reported by Zeevi et al. (1983). The existence of a response preference suggested that the target in the preferred direction could be delayed, thus eliminating the preference. As shown by the dashed lines of Figure 3, a delay of approximately 40 msec in the presentation of the preferred target is required to eliminate the preference shown by our subjects. This result indicates that in the sequence of events occurring prior to the execution of a saccade, a "window" of time of about 40 msec is allocated for decisions concerning direction of response. That is to say, to reach the chance level, representing an equal probability of response in either direction, requires that the stimulus in the preferred direction be delayed by this duration. A similar conclusion was reached by Zeevi et al. (1983), who also found a value of 50 msec for the window. It might be noted that a conclusion of this kind may be drawn also from pulse-step experiments in which only a single target is on at any one time (Becker & Jurgens, 1979; Wheeless, Boynton, & Cohen, 1966). The present data establish that the same mechanisms are active when the stimuli are projected to both hemispheres simultaneously.

The data of Figure 4 summarize the results of the bifurcating target measurements. These data indicate a significant increase in response latency due to the presence of two targets, as compared to a single target. Previous studies (Findlay, 1982, 1983; Zeevi et al., 1983) have shown that this latency increase is not due to the number of targets but rather, to the way that they are distributed over the visual field. This was concluded from the finding that the response latency does not increase when the target bifurcates within one hemifield. The present investigation further differentiates between the effect of bihemifield bifurcation on response latencies in the preferred and nonpreferred directions.

As shown by the leftmost pair of points in Figure 4, the effect of bihemifield bifurcation on response latency in the nonpreferred direction is about twice as large as it is on responses in the preferred direction. It might be argued that this asymmetry could be due to asymmetries in saccadic responses to even single stimuli presented in either the left or right visual fields. It is important to stress, therefore, that these data have been corrected for the intrasubject differences between left and right response latencies to single targets. Thus, we must conclude that the existence of a response preference is due to interhemispheric interaction, since it is not apparent in either the single-target data of the present effort or the unidirectional, dual-target data of Zeevi et al. (1983).

The difference in response latency in the preferred and nonpreferred directions is apparent also in the comparison of responses to the leading target when the data are pooled over delays in the 5- to 20-msec range (compare filled symbols on right-hand side of Figure 4). It is interesting to note that a similar difference in the responses in the preferred and nonpreferred directions is obtained for the lagging target. These results suggest an asymmetry in the effects of disturbance on response from the counterhemisphere. Further, it appears that the (usually) preferred hemisphere (mediating response to stimuli in the preferred direction) exerts a stronger inhibitory effect on the nonpreferred hemisphere. Therefore, eliminating this effect takes longer, resulting in greater response latencies. It is important to note that these interactions and the corresponding processing time are not susceptible to predictive control and cannot be modified by training. This we infer from the similarity in the data obtained from subjects MB and BL here and in a previous study (Zeevi et al., 1983).

The response latency data of Figure 4 can be further analyzed by considering the response latency as a function of the delay between the left and right targets, as shown in Figure 5. The combined left and right response data of Figure 5a show a qualitative similarity with those of Zeevi et al. (1983), in that there is an increase in response latency from simultaneous bifurcation of the two targets to delays of about 20 msec between the two targets in either direction. However, unlike the results of Zeevi et al. (1983), there appears to be asymmetry for longer intertarget delays. That is, when the target in the preferred direction leads by 60 msec, the latency is less than for shorter delays or for simultaneous presentation. This is in accord with what one would predict based on the critical period of about 40 msec inferred from Figure 3. In contrast, when the target in the nonpreferred direction leads by 60 msec, there is a greater latency than is obtained for simultaneous presentation--a result inconsistent with the 40-msec "window" inferred from Figure 3. This asymmetry in the latency for longer delays is indicative of asymmetries in the interaction of the leftward- and rightward-driven saccadic responses. Therefore, to further refine the analysis, we have separated the data of Figure 5a into responses in the preferred (Figure 5b) and nonpreferred (Figure 5c) directions for the corresponding leading and lagging delays. This segregation of data further elucidates the asymmetry of responses in the preferred and nonpreferred directions. The data in the left-hand portion of Figures 5b and 5c show that the interaction beyond the duration of the direction processing "window" (i.e., the 60-msec point at the left in Figure 5a) is primarily due to the disturbing effect of the target in the nonpreferred hemifield on the responses in the preferred direction (reflected by the latency of response in the preferred direction when the target responded to lags by 60 msec [leftmost data point in Figure 5b]). To complete this comparison would require data points for responses in the nonpreferred direction when the target in the preferred direction leads by 60 msec. However, such responses are extremely rare and, in fact, none was obtained in the present effort.

The question becomes: What does the asymmetry evident in Figures 3 to 5 reflect? Considering the task of responding in one direction when targets are presented in both hemifields (and thus projected onto both cortical hemispheres, see Figure 1), it is obvious that one hemisphere must predominate and thus suppress the counterhemisphere. We assert that the mutual interaction of the two hemispheres in this mode of operation requires inhibitory signals for suppression of one or the other hemisphere. If this is the case, then we must conclude that there exists asymmetry in the inhibitory signals transmitted between the two hemispheres. This asymmetry is denoted by the filled arrows of different sizes in Figure 1.

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