# Horizontal Saccades to Dichoptically Presented Targets of Differing Disparities

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Horizontal saccades were elicited to targets of various disparities displayed dichoptically. When the left eye and right eye targets were in the same hemifield, the resulting saccade demonstrated spatial averaging (42%, where 50% represents perfect averaging) between the left and right eye target positions. When the left eye and right eye targets were in opposite hemifields, the saccade was directed to one of the stimuli and was only minimally influenced by the presence of the other. This pattern is similar to that obtained when saccades are made to double targets, both of which are visible to both eyes. These data are discussed in terms of an ecological role for the global effect.

Saccades Disparity Depth Global effect Humans

## **INTRODUCTION**

Our eyes continually scan the visual world, moving from one fixation point to another. When changing gaze between objects at different distances and directions, the refixation movements must involve a combination of version (eyes moving in the same direction) and vergence (eyes moving in opposite directions).

Figure 1 shows a commonly-reproduced text-book figure purporting to describe how the eyes achieve refixation in the horizontal plane when a combination of version and vergence is required. This figure demonstrates Hering's law of equal innervation in showing that there is never independent movement of one eye alone: both eyes move equally although they can move either in the same or in opposite directions. The vergence may commence before the version movement but is, under some circumstances at least, much slower and consequently most vergence occurs following the saccadic movement. The version (saccadic movement) is assumed to be of the same size and direction in both eyes.

Accepting for the moment the validity of this description, the pattern of gaze changing shown in Fig. 1 raises a question about the programming of saccades in these circumstances. If the saccadic system is to bring the point of regard onto a route from which a symmetrical vergence movement can reach the target, then the amplitude required does not actually bring either eye onto the target. Instead the size of the saccade should correspond to the average of the eccentricities of the target as seen by the two eyes. Indeed, if one eye happens to be aligned with the target before refixation then Hering's law actually requires that eye moves away from the target as part of the version movement and then back again as part of the vergence movement.

Several workers have been aware of this calculation. Westheimer and Mitchell (1956) noted that the "bisector of the angle of convergence includes the new fixation point (following the saccade)". A point frequently made (e.g. Ono & Nakamizo, 1977) is that although the size of the saccade does not correspond to the position of the target in either individual eye, it nevertheless corresponds to the perceived direction of the target from the hypothetical *Cyclopean* eye, centred midway between the two eyes. Visual direction is perceived as originating from the Cyclopean eye, as Hering also noted (Ono, 1979).

An averaging process has been demonstrated in the saccade system by studies of saccade responses to two separate targets. When two targets are presented so that both eyes can see both targets either in rapid sequence (Becker & Jurgens, 1979) or simultaneously (Findlay, 1982), the evoked saccade often lands between the targets rather than on either one. This has been termed the global effect (Findlay, 1982). The global effect might appear to be a laboratory curiosity: a failing of the saccadic system under artificial laboratory conditions. But such averaging could serve a function in assisting the production of saccades between targets at different distances. For averaging to be relevant to this situation, the averaging needs to be over the stimulation produced by the left and right eyes' views of a single target, rather than over the stimulation produced by two separate targets. The latter case, essentially monocular, is the one in which the global effect has been observed to date. No

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systematic study has been made of the binocular situation. The monocular global effect may thus possibly arise as a by-product of a binocular system property.

If the two eyes' images are averaged, then it follows that information about the eye of origin of each image is lost. For many purposes the eye through which visual information arrives is of no significance and indeed utrocular discrimination (discrimination of the eye of origin) is often impossible (Blake & Cormack, 1979; Ono & Barbeito, 1985). Maybe the visual signal used in generating a saccade does not preserve the eye of origin information.

In order to investigate the hypothesis that global averaging takes place when targets are presented to separate eyes and that eye-of-origin information is lost, we systematically measured saccades produced when the eyes moved between targets with different disparities. We used dichoptic dot targets with a sudden onset appearing with unpredictable disparities and at unpredictable locations. This needs to be distinguished from the full stereoscopic situation. In particular, when the position of the target is predictable in advance, accurate refixation is achieved by a combination of non-conjugate saccades and rapid vergence movements (Erkelens, Steinman & Collewijn, 1989).

#### METHODS

#### Subjects and equipment

Stimuli were presented on two display screens with P31 phosphor (Tektronix 604 and Tektronix 608equivalent for the present purpose), viewed through a



FIGURE 1. Schema for changing fixation between two positions at different distances. The movement combines a vergence component, in which the eyes make equal movements in opposite directions, with a version (saccadic) component in which the eyes move equally in same direction.



FIGURE 2. Plan view of the apparatus used in the experiment.

mirror stereoscope (Fig. 2) at a distance of 32 cm. Four laboratory workers (two male, two female) aged between 24 and 43 and naive concerning the purpose of the experiment served as subjects. The subjects used dental bite bars to reduce head movement.

The stimuli were small luminous dots which could be positioned at any desired location along a horizontal axis through the centre of each screen. These dots were matched for brightness using a subjective monocular comparison. The screens were carefully aligned and appeared to the subject as a fused single screen. The control of the stimuli and recording of the eye movements was accomplished using a CED 1401 interface, driven by a PC AT computer. The experiment was carried out in a dimly lit room with precautions taken to eliminate any back reflections off the screen or mirrors.

#### Stimuli and calibration

With fixation at the screen centre, the eyes (for an average interocular distance of 6.4 cm) converged at an angle of 11.4 deg. Dots could be presented to each eye in the range 9 deg temporally to 6 deg nasally. For each trial the dots on both screens were initially central (zero disparity). This stimulus was then replaced with the target stimulus for the trial (presented for 2 sec), following which the central point again appeared (for 3 sec). A brief warning signal (100 msec 1 kHz tone) was presented 300 msec before the target.

The stimuli were presented in blocks, each lasting about 5 min. The subjects performed 12 blocks with a brief pause at the end of each block and a more substantial break after each set of four blocks. Each block consisted of a random ordering of 36 different pairings of 6 left eye and 6 right eye stimuli. Preceding each block were four warm-up trials (randomly chosen from the set of 36) which were not recorded, and four trials for calibration. The possible left eye stimuli were at positions 9, 6 and 3 deg left, zero, 3 and 6 deg right. The possible right eye stimuli were at 6 and 3 deg left, zero, 3, 6 and 9 deg right. Zero indicates that the central spot did not move in that eye. Figure 3(a) shows the apparent positions simulated by the target pairs. For certain of the combinations, binocular fixation would have required absolute divergence of the eyes and thus could not correspond to actual depth locations. These combinations were nonetheless included for comparison purposes. The 36 combinations were classified as illustrated in Fig. 3(b).

In unilateral trials, the spots were in the same hemifield of each eye. There were 12 trials of this type, four of which had zero disparity (spots in corresponding positions in the two eyes). Paired-with-zero stimuli (10 in total) are ones in which the spot in one eye moved but that in the other eye remained at the fixation point. Bilateral stimuli have the two spots in opposite hemifields in the two eyes (13 in total, 4 with crossed disparity and 9 with uncrossed disparity). Finally, for one trial in each block, no movement occurred. The calibration trials were the four zero-disparity, unilateral trials with targets at 6 deg left in each eye, 3 deg left in each eye, 3 deg right in each eye and 6 deg right in each eye. The order of these four trials was randomized in each block.

### Instructions

When the subjects had been installed in the apparatus, they were told that the experiment involved tracking a spot target and given the following protocol. "I want you to track the spot with your eyes as accurately as possible when it moves. Just before it moves away from the central position, you will hear a beep from the computer. Sometimes the spot will appear double. If that occurs, look at one or the other; it doesn't matter which. You may find that the spots come together after a while."

### Eye movement recording

Recordings from both eyes of the subjects were made using a Biometrics Instruments SGHV/2 infra-red reflection eye movement monitor. This instrument had been modified so that the sensors were mounted on a platform with ready adjustment along three axes. By back viewing through the mirror system over the top of the CRT screens, the experimenter could position the sensors



The subject's initial fixation was central at a distance of 32 cm. This is represented by the open square. On each trial a combination of left eye and right eye stimulation was presented, equivalent to that generated by a target in one of the positions shown by the solid squares. (a) An overview of the set of stimuli used. As well as the 26 combinations shown, there were four targets simulated at about 200 cm distance and six representing absolute divergence of the eyes' axes. (b) Classification of the target types. In addition to the targets shown, there were two paired with zero targets at 200 cm and six bilateral uncrossed disparity conditions with absolute divergence.

accurately in relation to the limbus. The system had a noise level of about 0.1 deg and was linear to within 10% over the range  $\pm$  6 deg. On each trial, the first 900 msec of the record following target presentation was digitized at a sampling rate of 500 Hz and stored, together with an indicator of the trial type. An example of raw data is shown in Fig. 4.

### Analysis

Measurements were made of the saccade amplitudes and latencies using a computer assisted procedure. This procedure detected the initiation point of the first saccade in the record (using a velocity criterion—set in computer units but typically around 20 deg/sec). The record was then displayed on the computer screen with a cursor positioned at the estimated beginning and end of the first saccade. The operator could, if necessary, reposition these cursors. When the cursors were appropriately positioned, the amplitude was automatically calculated by subtracting the average eye position over the 16 msec following the termination of the saccade from the average eye position over the 16 msec prior to the initiation of the saccade (thus reducing any 60 Hz contamination). The angular rotation in degrees was computed using scaling factors evaluated from the calibration records, which were analysed prior to the test trials for each block. The calibration trials were analysed in a similar way to that for the test trials, except that the final cursor was moved to the position reached following any corrective saccades which was assumed to be the on-target fixation. The display also computed and displayed the difference between left and right eyes' position (vergence). A further cursor could be positioned at the beginning of any observable vergence movement, and a figure keyed in to indicate the direction of this movement (convergence or divergence). These measurements were stored in a second file for subsequent statistical analysis.



FIGURE 4. Examples of eye movements to our targets recorded with the infrared technique. Records from two trials are shown, (a) shows an example of each eye's response to dichoptic targets of eccentricity 3 deg in the left eye and 6 deg in the right eye, and (b) shows an example of responses to targets at 6 deg in the left eye and 3 deg in the right eye. The top diagrams show the dichoptic target configurations with an exaggerated scale. The central diagrams show the records from the right and the left eyes, with downward displacement corresponding to rightward eye movement. The lower diagrams show the difference between the two eye's movements with downward displacement corresponding to convergence. The scale is the same as for the individual eye records. In both cases, the initial saccades show global averaging, although the magnitude is greater in the right hand example. Note that in the right hand diagrams (convergence case), fusion occurs, wheras in the left hand example, only a small amount of divergence is found, insufficient to lead to fusion. A further interesting point is the saccade which takes the left eye back to its target.

Trials were rejected (a) if a saccade was detected with latency <100 msec, (b) if no saccade occurred before 800 msec latency, (c) if the saccade was in the wrong direction when both left eye and right eye stimuli were in the same direction, (d) if the record was unscorable because of blinks or other artefacts. Out of 432 trials for each subject, the numbers rejected were as follows: subject RK 4 [3(a), 1(c)]; TK 9 [3(a), 5(b), 1(d); SK 9[6(a), 3(c)]; HG 4 [2(a), 2(d)]. Only on one occasion (subject HG) did a detectable saccade occur to the combination with no movement in either left or right eye targets. Very small (0.2-0.6 deg) fast conjugate movements, presumed to be saccades, were occasionally (17/432 records) observed before the main saccade, which appeared in the normal latency range. The small saccades were ignored by our analyses unless their amplitude was greater than 0.5 deg. Around 80% of these small saccades occurred in the range 90-140 msec following target presentation and may well be related to the express saccade phenomenon reported by Fischer and Ramsperger (1984).

#### RESULTS

## Saccade direction

Whenever both left eye and right eye targets stepped in the same direction (unilateral trials), the subject made a saccade. This saccade was in the direction of the target in all but four cases (3% of these trials). In the pairedwith-zero trials, where one target stepped and the other remained at zero, a saccade always occurred in the direction of the target step.

For bilateral trials, symmetrical or otherwise, a saccade was nearly always made (on five trials of subject TK no detectable saccade occurred). In these cases, the different subjects showed idiosyncratic directional biases (the proportion of leftward saccades over all bilateral trials was 17% for RK, 66% for TK, 66% for SK and 41% for HG). Unexpectedly, all subjects produced a higher proportion of leftward saccades to stimuli with uncrossed disparity to those with crossed disparity. The overall percentage of leftward saccades was 55% to uncrossed disparity targets and 28% to crossed disparity targets.

## Saccade amplitude

The amplitude of the first saccade in each eye was measured (see Methods) for the twelve repetitions of each stimulus and the median amplitude calculated. The median was used as a measure because of occasional anomalous trials (e.g. staircase of small saccades). The first saccade in such a sequence would be included in the analysis provided its amplitude was >0.5 deg. For bilateral trials, since saccades could be to the left or right, a separate median for the saccades in each direction is presented. The means across the four subjects for this measure of saccade amplitude are given in Table 1.

The main features to be seen in the mean data of Table 1 were also present in the data from each of the individual subjects and can be summarized as follows. (i) Saccades to zero-disparity targets, i.e. ones with the same eccentricity in each eye, showed slight to moderate undershoot  $(14.3 \pm 2.8\%)$ .

(ii) Saccades to unilateral targets at different eccentricities showed an amplitude between that of saccades to either component target presented binocularly. This is an important finding and shows that the global effect is indeed found for targets presented in each eye. A detailed analysis is presented in the section on averaging below.

(iii) Saccades to bilateral targets were, of necessity, directed towards one or the other target. The amplitude of these saccades generally matched the eccentricity of the target in the hemifield to which they were directed. However the presence of the other target had an influence. The saccade amplitudes undershot the distance to the relevant targets by  $27.2 \pm 5.9\%$ . This undershoot is approximately twice the shortfall of saccade to zero-disparity targets. The difference is statistically highly significant (comparing the undershoot found in all the pairings involving 3 and 6 deg bilateral targets with the corresponding undershoot found on zero disparity trials gives t = 7.20, 23 d.f., P < 0.0001).

TABLE 1. Amplitudes of saccades in each eye to dichoptic stimuli

	RE						
LE	6 deg L	3 deg L	0 deg	3 deg R	6 deg R	9 deg R	
Left eye							
9 deg L	-6.28	- 5.37	-7.25	-6.88	-6.75	-6.97	
-				2.27	3.90	6.47	
6 deg L	-5.00	-4.07	-4.69	-4.35	-4.65	-4.81	
				1.93	4.29	5.36	
3 deg L	-3.33	-2.64	-2.56	-2.39	-2.26	-2.26	
				1.81	3.69	6.39	
0 deg	-4.65	-2.35	0.00	1.95	4.19	6.66	
3 deg R	-4.60	-2.18	2.47	2.57	3.23	3.23	
-	2.25	1.94					
6 deg R	-4.79	-1.95	4.81	3.80	5.09	5.36	
	4.54	4.80					
Right eye	2		_	г			
9 deg L	-6.74	- 5.46	-7.67	-6.29	-7.61	-7.45	
				2.40	4.20	6.15	
6 deg L	-5.31	- 3.86	-4.76	-4.28	-4.76	-4.41	
				2.21	4.48	5.73	
3 deg L	-3.54	-2.72	-2.29	-1.89	-1.80	-1.98	
				2.17	4.11	5.80	
0 deg	-5.14	-2.55	0.00	2.25	4.32	6.43	
3 deg R	-4.75	-1.79	2.53	2.61	3.53	3.52	
	2.68	2.22					
6 deg R	-4.99	-1.76	4.80	3.74	4.69	5.81	
	4.38	4.37					

The figures are means (across subjects) of medians (across trials). Negative values indicate leftward movements and positive values rightward movements. The axes of this table are the eccentricities of the targets in the right eye (horizontal axis) and left eye (vertical axis). The sections of the table dealing with bilateral trials (in which targets appear on opposite sides of the midline in the two eyes) are outlined. Saccades occurred in either direction to these stimuli and these have been analysed separately. (iv) Saccades to paired-with-zero targets were quite similar to those to the bilateral targets. They were directed to the target appearing in a new position in one eye but they showed an undershoot  $(21.7 \pm 5.0\%)$  which is greater than that found with the zero-disparity targets but smaller than that found with bilateral targets. Both differences are statistically significant (using the pairings involving 3 and 6 deg targets, comparison with zerodisparity t = 3.70, d.f. 20, P = 0.0014; comparison with bilateral t = 3.19, d.f. 38, P = 0.0028).

## Averaging

The principal hypothesis tested by the study was that global averaging would be found in saccades to two targets presented at different eccentricities in the two eyes. Table 1 and the raw data of Fig. 4 shows that this did indeed occur for unilateral targets. In all cases of unilateral presentation involving different eccentricities in the two eyes, saccades of intermediate amplitudes were generated. The cases involving 3 and 6 deg targets showed this phenomenon the most clearly and are reported in greater detail in Table 2 to confirm that the averaging shown in Table 1 really represents global averaging in the visual system and not, for example, averaging during the statistical analysis of the data. We have presented the left eye and right eye data separately in Tables 1 and 2 to avoid any artefactual additional source of averaging if the amplitudes of saccades differed in the two eyes. In fact, as we show subsequently, there were systematic differences between the eyes. However these differences were small in relation to the substantial averaging effect found.

Table 2 gives, for each subject, the median and inter-quartile range of saccade amplitudes to each target pair. The median amplitude to 3 + 6 combinations in all cases falls between the amplitudes to the zero-disparity

targets at 3 and 6 deg. The averaging effect is found in each subject tested. In Fig. 5 individual saccade amplitudes are plotted. While not every saccade to the 3 + 6combinations is directed to an intermediate position (especially for subject HG), most saccades arrive between the averages for each of the two presented alone. The effect is apparent even though there is considerable variability in the saccade end points both in the test and in the control conditions. It has been reported previously that target elicited saccades do show greater variability than voluntary ones (Lemij & Colewijn, 1989).

Averaging can be quantified as:

global effect percentage =  $100 * (A_{comb} - A_1)/(A_m - A_1)$ 

where  $A_1$  is the median saccade amplitude to the less eccentric target of the combination under consideration when this is presented to both eyes (e.g. the 3+3combination);  $A_m$  is the median saccade amplitude to the more eccentric target when this is presented to both eyes (e.g. the 6 + 6 combination);  $A_{comb}$  is the amplitude of the saccade elicited by the combination (e.g. the 3+6combination).

A global effect percentage of 0 or 100% means that the saccades are equivalent to those directed to the less eccentric (0%) or more eccentric (100%) target respectively and are uninfluenced by the presence of the other. A global effect of 50% indicates perfect averaging in which the saccade falls half way between where it goes when each target is presented alone.

Each of the four subjects received four combinations of 6 + 3 targets (Fig. 5), and a global effect percentage can be calculated for each eye. This gives a total of 32 separate (though not independent) measures of this measure. The mean of these 32 values is 42% (21/32 fall between 20 and 45%). The eye lands slightly closer to the "near target alone" landing position than to the

Subject		RK		ТК		SK		HG		
LE	RE	LE	RE	LE	RE	LE	RE	LE	RE	Average
6	-6*	-6.05	- 3.98	-4.13	- 5.25	- 5.35	- 5.92	-4.46	- 5.08	-5.15
		(1.37)	(1.22)	(0.51)	(1.01)	(1.15)	(1.35)	(1.30)	(1,96)	(1.23)
	-3	- 5.25	-4.64	3.68	3.47	-4.26	-3.77	-3.07	-3.55	-3.96
		(0.83)	(0.83)	(0.63)	(0.69)	(0.71)	(0.78)	(0.66)	(0.97)	(0.76)
-3	-6	-4.18	-4.40	-3.07	-3.18	-3.62	-3.60	-2.45	-2.97	-3.43
		(0.56)	(1.08)	(0.78)	(0.58)	(0.86)	(1.36)	(0.90)	(1.15)	(0.90)
-3	- 3*	-3.36	-2.91	-2.47	-2.66	-2.53	-2.75	-2.21	-2.56	2.68
		(1.12)	(0.40)	(0.26)	(0.67)	(0.53)	(0.88)	(0.38)	(0.76)	(0.62)
6	6*	4.76	5.48	6.21	5.19	4.89	5.06	4.51	3.01	4.89
		(1.94)	(0.78)	(0.76)	(0.85)	(0.68)	(0.89)	(0.97)	(0.94)	(0.98)
6	3	4.33	5.18	4.21	3.62	3.41	3.63	3.24	2.54	3.77
		(1.40)	(2.05)	(0.81)	(1.26)	(0.90)	(1.06)	(0.74)	(0.75)	(1.12)
3	6	3.35	4.14	3.31	4.24	3.47	3.67	2.78	2.05	3.38
		(1.34)	(1.40)	(0.59)	(0.48)	(1.16)	(1.35)	(0.58)	(0.67)	(0.95)
3	3*	2.80	3.13	2.61	2.63	2.60	2.92	2.27	1,77	2.59
2	C C	(0.62)	(1.21)	(0.66)	(0.58)	(1.63)	(0.40)	(0.77)	(0,70)	(0.82)

TABLE 2. Saccade amplitudes to unilateral target pairs

\*Negative numbers correspond to leftward targets and eye displacements. Starred trials correspond to zero disparities. Target pairs which combine a 6 deg target in one eye with a 3 deg target in the other evoke saccades of amplitudes intermediate between those evoked by pairs with 3 deg targets in each eye and pairs with 6 deg targets in each eye. Figures show median amplitudes with inter-quartile ranges in parentheses below each entry. Also shown are the average amplitudes (in the right hand column) with the average inter-quartile range below. mid-point. There was no significant difference between those stimuli requiring a convergence (40.4%) and those requiring divergence (43.3%). There is no evidence for a bimodal distribution in the end-points of saccades for any one stimulus combination. However, it can be seen from Table 2 and Fig. 5 that the distribution of endpoints depends on the eye to which the stimuli are presented. That is, a target combination of 3 deg in the left eye and 6 deg in the right eye is not equivalent to one with 6 deg in the left eye and 3 deg in the right eye. The eye movements evoked by these pairs, differing only in which stimulus goes to which eye, are different in three of the four subjects at the P < 0.05 level. Paired-with-zero trials (not detailed in Fig. 5) showed a greater undershoot for the peripheral target than occurred when the eccentric target was present in both eyes. The global effect percentage (setting  $A_1$  to zero in the formula above) averages at  $91.3 \pm 5.5\%$ . Unlike other examples of averaging, the end-points fell closer to the furthest target.

The bilateral cases also showed weak evidence of averaging since the saccades undershot the target more than occurred when that target was present in both eyes. Treating leftward and rightward saccades separately, the global effect percentage can be measured using the principle of the formula above, but with the modification



FIGURE 5. Illustration of dichoptic averaging when targets are presented at different positions in left and right eyes. The end-points of saccades to four trial-types are shown for each subject as dots. Arrows indicate the median end-point positions. The open squares show the target positions. For each subject the records, in order from the top, are in response to (a) both targets at 3 deg, (b) targets at 3 deg in the left eye and 6 deg in the right eye, (c) as in (b) but with the stimuli in opposite eyes and (d) both targets at 6 deg. Note that if the system was completely unaware of the eye of origin, the data in lines (b) and (c) would be the same.

that the target treated as "less eccentric" is the one in the same hemifield as the saccadic response. The average global effect percentage is then  $7.2 \pm 3.6\%$  calculated for those targets for which zero disparity controls are present (all combinations of 3 and 6 deg targets).

## Saccade latencies

Saccades were always binocular and were almost always tightly synchronized in the two eyes to within the 2 msec sampling resolution. Table 3 shows the mean of the subject medians for the latency of the saccade initiated in the left eye. Two results are clear.

(i) For unilateral presentations, latency is shortest  $(215 \pm 5 \text{ msec})$  when the left eye and right eye targets fall on corresponding points in the two eyes and increases significantly with disparity (r = 0.71, d.f. 11, P < 0.005) at a rate of 2.5 msec per degree of disparity. There was no difference between trials requiring convergence and those requiring divergence. Paired-with-zero trials show a greater latency than predicted by the regression function: it is well known that saccade latency can be strongly affected by events at the fixation point (Saslow, 1967).

(ii) Bilateral presentations evoke saccades with average latencies of  $259 \pm 9$  msec. There is no dependence of latency on disparity for bilateral presentations over the range investigated (6-18 deg).

#### Vergence movements and saccade nonconjugacy

No subject made consistent and appropriate vergence movements on all trials although each subject made vergence movements on some trials and also reported that the spots had fused on at least some occasions. The most regular vergence movements (about 75% of trials) were made by subject TK. However this subject also made frequent inappropriate anticipatory vergence responses.

Inspections of Tables 1 and 2 show differences in the size of the saccades measured in left and right eyes. These differences are systematic with the larger saccade being in the abducing eye with targets that simulated a divergence requirement and in the adducing eye for targets that simulated a convergence requirement. It can be concluded that the differences are, directly or indirectly, a consequence of the target disparity. The nonconjugacy was noted to be more marked on trials in which vergence movements were detectable. Its magnitude, however,

TABLE 3. The latency of saccades to dichoptic stimuli in milliseconds

LE	RE							
	6 deg L	3 deg L	0 deg	3 deg R	6 deg R	9 deg R		
9 deg L	227	227	228	252	257	257		
6 deg L	217	219	225	259	246	246		
3 deg L	228	213	228	271	276	259		
0 deg	253	253		248	252	242		
3 deg R	260	256	226	209	222	230		
6 deg R	254	274	249	235	221	229		

The axes are the same as for Table 1. The figures show the mean (across subjects) of the medians (across trials).

was often greater than that which could be attributed to the simple continuation of the vergence movement for the duration of the saccade.

## DISCUSSION

# Global averaging with targets in opposite eyes (dichoptic averaging effect)

We have demonstrated that saccades evoked by two targets presented in opposite eyes show an averaging effect. We are calling this the dichoptic averaging effect. The extent of averaging is determined by whether or not the targets fall in the same hemifield in the two eyes. When targets appear in the same hemifield, comprehensive averaging occurs (42%-where 50% would represent perfect averaging). In this case the saccades tend to take the eyes to a point from which a refixation could subsequently be achieved with a simple vergence movement alone, the traditional pattern ascribed to Hering's law as shown in Fig. 1. When targets are in opposite hemifields, a much weaker averaging effect is present (7%). In the paired-with-zero cases, the global effect percentage is 91%. This likewise represents a very weak averaging affect with the saccades going close to the more eccentric target which in this case is the only location where new stimulation occurs.

## Comparison with same-eye averaging (the global effect)

Dichoptic averaging, between targets presented in opposite eyes, is similar to global-effect averaging seen when two targets are presented to neighbouring positions in the same eye. In both cases the eye lands in between the two targets. When two targets are presented in the same hemifield, the saccade slightly undershoots the "perfect averaging" position both for dichoptic averaging and for the global effect. In both cases, the undershoot is around 10%. If the targets in the same hemifield are sufficiently far apart, global averaging is replaced by responses that are directed to the individual targets, with an intermediate region characterized by high variability (Findlay, 1982; Ottes, van Gisbergen & Eggermont, 1984). Evidence of a similar effect in dichoptic averaging may be seen in the responses to the 3+9 deg combinations, where both within subject and between subject variability was high.

When the left eye and right eye targets are in opposite hemifields, Findlay (1983) found that no averaging at all occurred with binocular presentation. In the dichoptic situation studied here, however, a weak but significant averaging effect occurred. Another difference may be noted between the results from dichoptic presentation and those from earlier binocular experiments. When the two targets are presented bilaterally at different distances from the fixation point, saccades have been found to be consistently directed towards the closest target (Lévy-Schoen, 1974; Findlay, 1980). Dichoptic averaging shows no such proximity bias. The probability of choosing a target appears independent of its relative eccentricity, although some idiosyncratic direction biases were noted. The increase in latency found when targets appear in opposite hemifields is comparable with similar differences found when both targets are presented to both eyes (Findlay, 1983). Figures 4 and 5 make it clear that there can be differences depending on which stimulus is presented to which eye.

## Comparison with real depth targets: target elicited saccades

The dichoptic situation used here differs in several respects from real targets in real depth. No cues to accommodative responses were present, nor was there any visual framework to provide information about target depth (the "proximal" cue to vergence). Studies of target elicited saccades in situations where more cues were present have been made (Ono & Nakamizo, 1977, 1978; Ono & Tam, 1981). Ono and Tam (1981), using near and far LED targets, found that conditions resulting in bilateral presentation usually evoked multiple saccades with the second saccade in the opposite direction to the first. Our dichoptic bilateral stimulation evoked initial saccades which fell close to one or other target. Such saccades overshot the 50% point from which vergence could take the eye on to the final target position and thus required further corrective saccades in the reverse direction.

When Ono and Tam's stimulation was unilateral, a single saccade sometimes occurred (suggesting accurate averaging) but a more common pattern was of multiple saccades with the second saccade in the same direction as the first. Refixation tended to be achieved with a single saccade most often when the position of the target in one eye was unchanged [Panum's limiting case; similar to our "paired-with-zero" combinations-see also Ono and Nakmizo (1977, 1978)]. In our dichoptic pairedwith-zero trials, the saccades' amplitudes, instead of reaching the average position, tended to be closer to the target whose position had been changed. This would then require subsequent saccades to reach the average position. The difference between our pattern of results and that of Ono and co-workers may either reflect individual differences, or different strategies available.

## Comparison with voluntary refixations: nonconjugate saccades

Several workers have studied the eye movement patterns occurring when subjects make voluntary eye movements between stationary targets at different locations in depth (Enright, 1984, 1986; Erkelens *et al.*, 1989). Their work has shown that the movement patterns differ considerably from those portrayed in Fig. 1 in two major respects. Firstly, the vergence component has a much greater velocity than is found when the target depth is not predictable in advance. Secondly, considerable nonconjugacy occurs in the saccadic components. This results in a "vergence" shift during the saccade and, in many cases, the major part of the refixation is achieved by nonconjugacy of the saccadic components.

It has been frequently reported that saccadic nonconjugacy occurs during vergence (Ono, Nakamizo & Steinbach, 1978; Kenyon, Ciuffreda & Stark, 1980). We have shown here that appropriately directed saccadic nonconjugacy can occur on the basis of disparity information even when the subject has no advance knowledge of the position of the target. This complements the study by Enright (1986) who carried out two experiments in which subjects moved their eyes to targets at unpredictable positions. He found substantially more nonconjugacy in the binocular case and deduced that disparity was the major cause of nonconjugacy. We have confirmed that disparity alone can lead to nonconjugacy but have shown that substantial nonconjugacy occurs only if vergence is already initiated at the time of the saccade, although a small effect may occur for stimuli having uncrossed disparity even when no detectable vergence is present at the time of the saccade.

## Ecological role of saccadic averaging

The main features of the global effect are preserved during dichoptic presentation. This suggests that the global effect may actually represent a useful strategy: a way of automatically moving between targets at different distances by moving onto the route from which vergence alone can complete the gaze change. But then why do only unilateral stimuli show significant averaging? In fact, for real-life situations, most targets will be in the "unilateral area" (see Fig. 3). All same-plane targets are in the unilateral area. Thereafter it depends on distance. At 10 m, assuming an interocular distance of 6 cm and an initial fixation distance of 32 cm, the unilateral distance represents about 105 deg out of the 110 deg of the visual field: the bilateral cases corresponding only to the central 5 deg. Expressed as an area in which targets can appear, only targets in 0.16% of the total area within 10 m would be classified as bilateral. Furthermore, half of this central area corresponding to the bilateral targets will normally be obscured by the object at the point of regard.

Although it is rare outside the laboratory for targets to appear or disappear suddenly, rapid reorienting to such targets seems a desirable property for the oculomotor system. In the case of voluntary refixations, it has been reported that almost all the vergence component required can occur during the saccade (Enright, 1986; Erkelens *et al.*, 1989). This was not the case in our situation. It may be that different considerations apply to voluntary and target-elicited saccades (cf. Lemij & Collewijn, 1989) and that averaging contributes to the rapid alignment of eyes on to newly appearing targets whereas saccadic nonconjugacy is more likely to serve this role for more voluntary fixation changes.

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