

EYE MOVEMENTS AND THE AFTER-IMAGE—II THE EFFECT OF FOVEAL AND NON-FOVEAL AFTER- IMAGES ON SACCADIC BEHAVIOUR

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INTRODUCTION

HEYWOOD and CHURCHER (1971) showed that subjects "tracking" a foveal after-image (AI) in the dark can produce sustained smooth eye movements, and it was suggested that the AI creates two conditions necessary for these movements: it inhibits searching saccades by fulfilling the function of a foveal target, and it eliminates the need for corrective saccades during smooth movement by being stabilized on the fovea.

If retinal information from AIs can be used in this way, the effect of a non-foveal AI by itself might be to facilitate searching saccades by combining information about a peripheral target with lack of information at the fovea; at the same time, if the AI is at an appropriate distance from the fovea, it might act as a stimulus for corrective saccades during smooth movement. If the foveal AI makes the corrective system redundant through absence of error signals, an extrafoveal AI would make it necessary but ineffective. Thus, whereas in the first case the tracking system behaves "perfectly", in the latter it should behave pathologically, and in particular there should be large numbers of saccades superimposed on smooth movement, whose amplitude and direction are determined by the location of the after-image on the retina.

This experiment was undertaken to see whether or not non-foveal after-images have systematic effects on saccadic behaviour, and to compare their effects with the effects of foveal AIs and with saccadic behaviour with no after-images. This experiment also compares eye movement behaviour with and without instructions to use the eyes in a specified way.

METHODS

The EOG recording system, the subjects lightproof room and the other apparatus were as described in a previous paper (HEYWOOD and CHURCHER, 1971). Briefly, subjects sat in a dark room that could be dimly lit by a red bulb. Calibration points were arranged in this experiment 3°, 15° and 30° to the left and right of a central 1° hole, from which a 1-msec white flash could be given. Subjects' head movements were restrained by a conventional chin-rest/bite-bar assembly. Horizontal eye movements only were recorded.

Each subject was dark adapted for 10 min without the bite-bar. At the end of the fifth minute, and unknown to the subject, a 36-sec sample of eye movements was recorded, which comprises the Dark Adaptation (D.A.) condition. After this 10 min period the red light was switched on, subjects moved onto the bite-bar and the EOG was calibrated. The light was then switched off for 1 min without any further instructions being given. Eye movements were recorded throughout this period, which comprises the Dark No Instruction (D.N.I.) control condition. The red light was then turned on again, the subject was told to fixate an appropriate point (the centre, or either of the two calibration points at 3° or 15° from it) and was warned of an

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imminent flash. The flashgun was fired and the red light turned off simultaneously, and the subject was left uninstructed for 1 min while his eye movements were recorded.

Each subject then received instructions as follows, according to the location of his after-image:

(F) "You can probably see an after-image. If the after-image moves, follow it smoothly with your eyes."

(E) "You can probably see an after-image slightly to the right/left of your line of sight. Without trying to look directly at the after-image, follow it smoothly with your eyes if it moves."

(P) "You can probably see an after-image to the right/left of your line of sight. Without trying to look directly at the after-image, follow it smoothly with your eyes if its moves."

The form (F) was employed if the flash occurred while the subject fixated the central point, and therefore had a foveal after-image, (E) in the case of an extrafoveal after-image (3° from the centre), and (P) a peripheral after-image (15° from the centre).

After he had been given the appropriate instructions, the subject's eye movements were recorded for a 1-min period before the red light was turned on, the calibration repeated, and the subject was allowed to rest for a few minutes. This procedure was then repeated twice, using the other two afterimage positions but omitting the "uninstructed" periods. Thus each subject yielded one minute of eye movement recording under each of five conditions, as well as a 36-sec sample during the dark adapting period. (One subject, M.W., did not provide data for the Dark N.I. condition nor for the peripheral AI condition.) Table 1 gives the order of presentation of after-images for the ten subjects (seven male and three female undergraduates who had not previously participated in eye movement experiments). The design was originally balanced, but data from two subjects had to be discarded for technical reasons.

TABLE 1. ORDER OF PRESENTATION OF A.I.S

Subject	First A.I. (without and with instructions)	2nd A.I. (with instructions)	3rd A.I. (with instructions)
T.H.	Foveal	Peripheral/right	Extrafoveal/left
A.R.	Foveal	Extrafoveal/right	Peripheral/right
M.W.	Extrafoveal/right	Foveal	Peripheral/left*
J.W.	Extrafoveal/left	Peripheral/right	Foveal
J.C.	Extrafoveal/right	Peripheral/left	Foveal
D.C.	Extrafoveal/left	Foveal	Peripheral/right
M.H.	Peripheral/right	Extrafoveal/left	Foveal
K.M.	Peripheral/right	Foveal	Extrafoveal/left
S.G.J.	Peripheral/left	Extrafoveal/right	Foveal
K.N.	Peripheral/left	Foveal	Extrafoveal/right

* Data missing.

The EOG records permitted measurement of saccades which were accurate to within one degree. They were analysed for the numbers and direction of all saccades and for amplitude of each saccade between 1° and 25° inclusive (saccades greater than 25° were omitted from amplitude analysis since EOG linearity falls off for excursions greater than this),² for all intersaccadic intervals (ISIs) and for the proportion of the total distance travelled by the eye that is covered by smooth movement (except in the dark adapting period (D.A.), where this measure was omitted because of the possibility of confusion with head movement). During D.A., saccadic amplitude was estimated on the basis of the first subsequent calibration. Since these measurements may have inadvertently included some eye movements compensating for fast head movement, and may also be distorted by the decrease in EOG potential level that occurs during the first 10 min of the dark adaptation process (KRIS, 1958), saccadic amplitudes during D.A. should be considered only approximate. Saccades were defined as step displacements of the EOG trace of one degree or more which conform to the durations given by YARBUS (1967).

The baseline drift of the recording system varied between subjects, ranging from negligible rates to an overall maximum rate in one condition of approximately $20'$ arc/sec. The overall rate for each subject in each condition was calculated, and was taken into account wherever necessary.

² 43/1719 (2.5 per cent) saccades were eliminated by these boundaries.

RESULTS

1. *Darkness*

The pattern of eye movements in the Dark N.I. condition consists in a large number of small saccades occurring at relatively short intervals (Fig. 1a). When the subjects' head movements were stopped (by biting the bite-bar) the pattern of eye movements changed. The distribution of ISIs shifted towards longer intervals ($\chi^2 = 38.63$, $p < 0.001$; Figs. 2a and b) and a higher proportion of small saccades occurred during Dark N.I. ($\chi^2 = 50.37$, $p < 0.001$; Figs. 2c and d, Table 2). There is no significant difference in the number of saccades made to the left and to the right during Dark N.I.³

Most of the observed smooth movement in this condition (Table 3) consists in very slow drifting of the eyes, shows no dominant direction and is of very small amplitude.

TABLE 2.

Condition	No. of saccades	Saccadic amplitudes		ISIs mode (msec)
		Mean (deg)	S.D. (deg)	
<i>No Instructions</i>				
D.A.	356	3.94	5.11	370
D.N.I.	357	3.52	3.84	370
Foveal AI	20	2.45	3.82	> 6 secs
Extrafoveal AI	201	4.04	3.09	750
(Towards AI	87	4.48	3.22)	
(Away from AI	114	3.7	2.97)	
Peripheral AI	210	2.9	2.52	370
(Towards AI	94	3.04	2.69)	
(Away from AI	116	2.78	2.39)	
<i>With Instructions</i>				
Foveal AI	152	2.67	3.65	370
Extrafoveal AI	330	3.35	2.49	750
(Towards AI	191	3.17	2.84)	
(Away from AI	139	3.6	4.22)	
Peripheral AI	409	4.64	4.92	370
(Towards AI	230	4.46	4.26)	
(Away from AI	179	4.88	5.66)	

2. *Foveal A.I.*

(a) *Without instructions.* The distribution of ISIs is different from Dark N.I. ($\chi^2 = 8.2$, $p < 0.05$) and is highly skewed towards long intervals (Fig. 3b). In a manner compatible with this, subjects make fewer saccades with a foveal AI ($U = 0$, $n_1 = 2$, $n_2 = 7$, $p = 0.028$). The distribution of amplitudes is not, however, different from that obtained in the dark (Fig. 4b, Table 2). The lack of a significant difference may be attributable to the very small number of saccades observed with a foveal AI.

One subject increased the proportion of smooth movement from 32 per cent in the dark to 82 per cent with a foveal AI; the other decreased the proportion by 9 per cent (Table 3).

³ All χ^2 tests are based on expected values derived from the distribution in the Dark N.I. condition or from the appropriate uninstructed AI condition by the following formula: $E(y_i) = (x_i)/(\Sigma X)(\Sigma Y)$. The class intervals used for the χ^2 tests do not necessarily correspond with the class intervals used in the figures because of the need for expected values in the χ^2 test to be ≥ 4 .

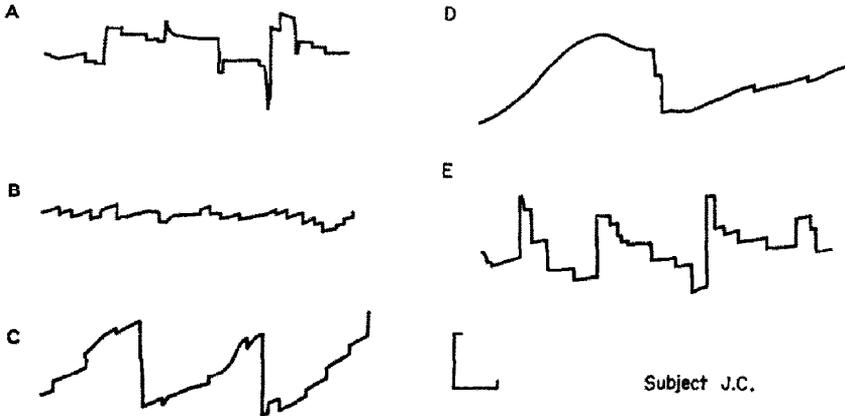


FIG. 1. Tracings of representatives samples of EOG records from subject J.C. in five conditions, A: Dark N.I., B: Extrafoveal AI without instructions, C: Extrafoveal AI with instructions, D: Foveal AI with instructions, E: Peripheral AI with instructions. Eye movements to the right indicated by upwards deflection of the trace. Calibration: Vertical—20°; Horizontal—1.5 sec.

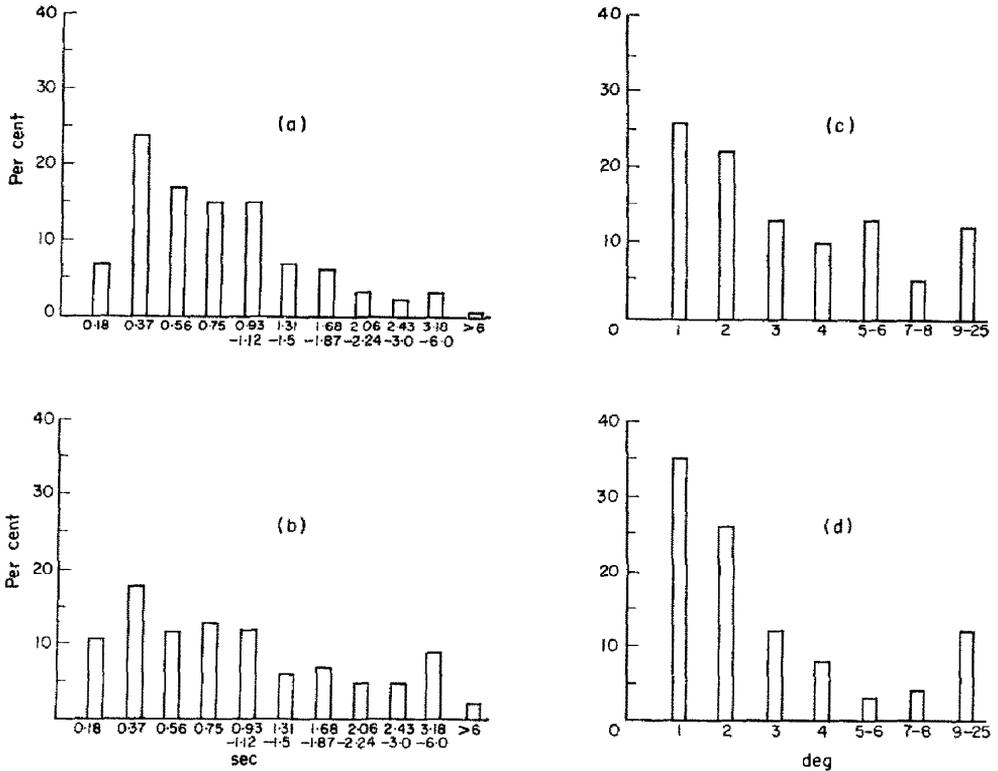


FIG. 2. Frequency distributions of saccadic amplitudes and ISIs in the dark adapting and Dark N.I. conditions. (a): ISIs during D.A., (b): ISIs during Dark N.I., (c): Saccadic amplitudes during D.A., (d): Saccadic amplitudes during Dark N.I.

The smooth movement showed a dominant direction; more saccades are made in the direction opposite to this ($\chi^2 = 5, p < 0.05$) and the variance of their amplitude is greater ($F = 16.08, p < 0.01$).

(b) *With instructions.* The distributions of ISIs and saccadic amplitudes are both different from the uninstructed condition. ISIs are shortened ($\chi^2 = 122.52, p < 0.001$; Fig. 3B) and the distribution of saccadic amplitudes is flattened ($\chi^2 = 25.54, p < 0.001$; Fig. 4B Table 2).

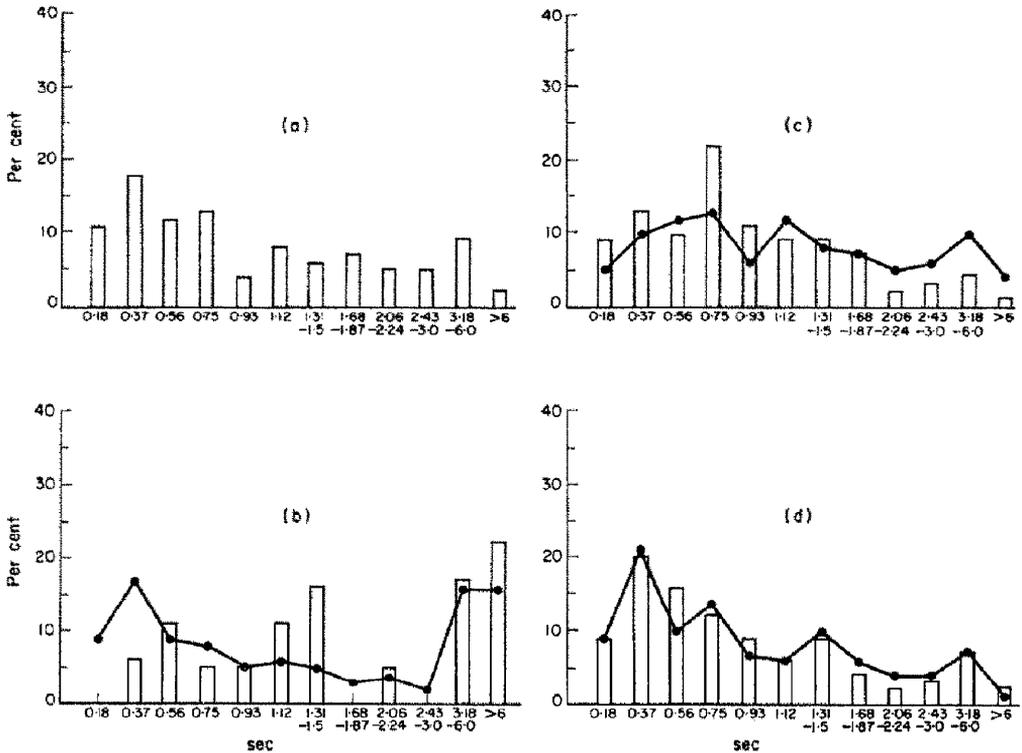


FIG. 3. Frequency distributions of ISIs under different conditions. In this and the following figures bars represent distributions obtained without instructions. The curves connect values at the same class intervals of the distributions obtained with instructions. (a): Dark N.I., (b): Foveal AI, (c): Extrafoveal AI, (d): Peripheral AI. Note that the abscissa scale differs from that used in Figs. 2, A and B.

Compared with the Dark N.I. condition, there is significantly more smooth movement ($T = 0, n = 10, p < 0.005$; Table 3, cf. Fig. 1(d)), and in 7/10 cases this has a clearly dominant direction (assessed by eye, Table 4). As in the uninstructed condition, more saccades are made in the direction opposite to this dominant direction ($\chi^2 = 5.01, p < 0.05$) and there is again greater variance of amplitude of these saccades ($F = 37.52, p < 0.001$).

3. Extrafoveal A.I.

(a) *Without instructions.* An extrafoveal AI tends to elicit more saccades than are made in the dark ($U = 3, p = 0.083$), but does not reliably increase the proportion of smooth movement (Table 3; cf. Fig. 1(b)). Any dominant direction of smooth movement is towards the AI, although this may be opposite to the direction shown with a foveal AI (Table 4).

TABLE 3. PROPORTION OF SMOOTH MOVEMENT

Subject	Without instructions				With instructions		
	Dark N.I. (%)	Foveal A.I. (%)	Extra-foveal A.I. (%)	Peripheral A.I. (%)	Foveal A.I. (%)	Extra-foveal A.I. (%)	Peripheral A.I. (%)
T.H.	32	82			37	70	19
A.R.	64	55			65	17	19
M.W.	—		59		94	29	—
J.W.	46		47		94	60	9
J.C.	24		39		81	59	1
D.C.	4		19		69	52	23
M.H.	28			14	62	36	36
K.M.	20			21	62.5	26	14
S.G.J.	4			16	90	47	11
K.N.	42			3	94	26	29
S.D.	19.5	9.55	16.81	7.59	19	17.49	10.65
Mean	29.3	68.5	41	13.5	74.85	41.1	17.89

The distributions of ISIs and saccadic amplitudes differ from those in the Dark N.I. condition. ISIs are longer with a clear mode at 750 msec ($\chi^2 = 34.07, p < 0.001$; Fig. 3(c)) and amplitudes are greater ($\chi^2 = 115.78, p < 0.001$; Fig. 4(c), Table 2).

The direction of saccades in the extrafoveal AI condition is affected by the retinal displacement of the AI. Overall, more saccades are made *away* from the AI than towards it ($\chi^2 = 5.16, p < 0.025$). However, considering only small saccades, although more saccades

TABLE 4. DOMINANT DIRECTIONS OF SMOOTH EYE MOVEMENT WITH A.I.S

Subject	K.N.	M.H.	S.G.J.	K.M.	T.H.	A.R.	J.C.	M.W.	J.W.	D.C.
Dominant direction with foveal A.I.	R	—	—	R	R	L	R	L	L	—
Location of extrafoveal A.I.	R	L	R	L	L	R	R	R	L	L
Dominant direction with extrafoveal A.I.	R	L	R	L	L	R	R	R	L	—

$\leq 3^\circ$ go away from the AI, more saccades between 4° and 6° go towards it ($\chi^2 = 28.48, p < 0.001$). Furthermore, the variance of all saccadic amplitudes $\leq 6^\circ$ away from the AI is lower than of those towards it ($F = 1.82, p < 0.025$; Fig. 5(a), Table 2).

(b) *With instructions.* Instructions to track the AI change the patterns of saccadic behaviour (Fig. 1(c)). All four subjects who had previously received an extrafoveal AI without instructions now reduce the numbers of saccades made. There is an increase in the length of ISIs ($\chi^2 = 112.46, p < 0.001$; Fig. 3(c)) and there are more smaller saccades ($\chi^2 =$

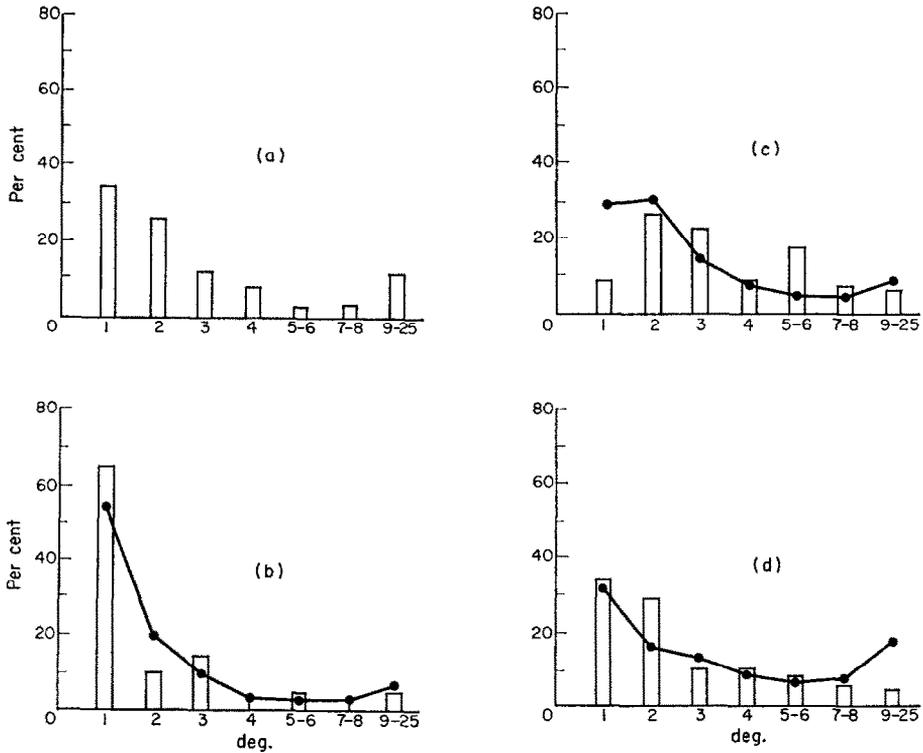


FIG. 4. Frequency distributions of saccadic amplitudes under different conditions. Conventions as in Fig. 3: (a): Dark N.I., (b): Foveal AI, (c): Extrafoveal AI, (d): Peripheral AI.

176.67, $p < 0.001$; Fig. 4(c), Table 2). There are also changes in the directions of saccades, of which more, of all amplitudes, now go *towards* the AI ($\chi^2 = 10.44$, $p < 0.05$). Furthermore, these saccades now have significantly lower variance of amplitude than saccades away from the AI ($F = 2.21$, $p < 0.001$; Fig. 5(a)).

There is no difference in the mean proportion of smooth movement, which is lower than with a foveal AI and instructions ($T = 4$, $N = 10$, $p < 0.01$; Table 3). As in the uninstructed condition the dominant direction of smooth movement is in each case towards the AI (Table 4).

4. Peripheral AI⁴

(a) *Without instructions.* On several measures the peripheral AI condition cannot be distinguished from the Dark N.I. condition. Thus there is no significant difference in the number of saccades, nor in the proportion of smooth movement (Table 3). Nor is the distribution of ISIs different from that in the dark (Fig. 3(d)) There is no difference in the numbers of saccades towards and away from the AI. However, there are differences in saccadic amplitude ($\chi^2 = 19.69$, $p < 0.001$; Fig. 4(d), Table 2).

⁴ There is a possibility that the peripheral AI in this experiment may have fallen wholly or partly on the blind spot of one eye. It is therefore impossible to draw final conclusions about the effects of peripheral AIs on eye movements on the basis of these results, since we do not have controls for any specific effects of monocular images.

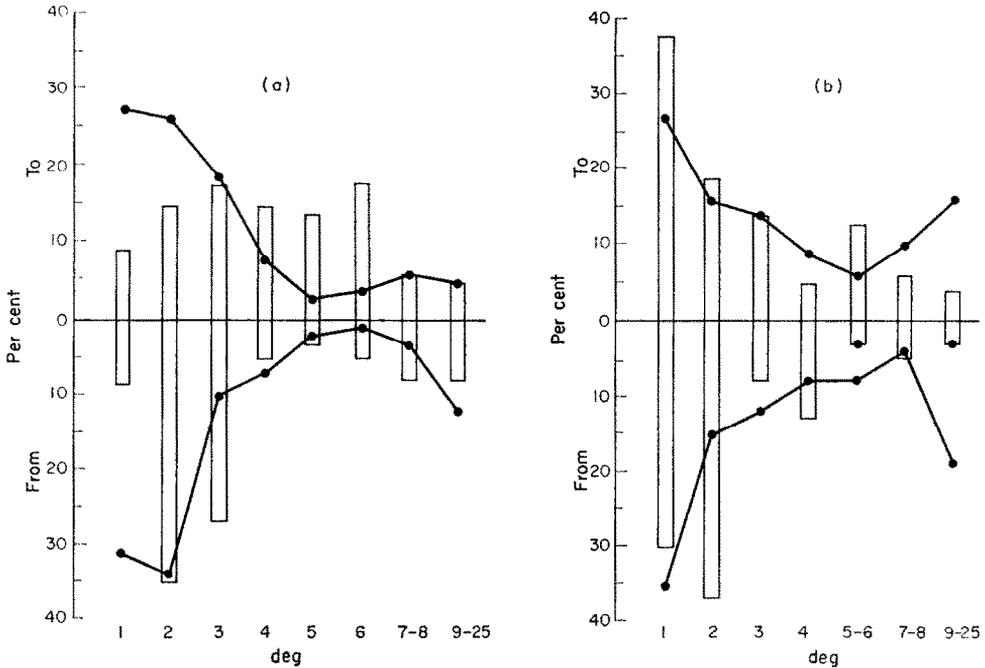


FIG. 5. Frequency distributions of saccadic amplitudes towards and away from eccentric AIs. Conventions as in Fig. 3. (a): Extrafoveal AI, (b): Peripheral AI. Note that the abscissa scale of (a) has been expanded to reveal the bimodal nature of the distribution of amplitudes towards the AI without instructions. This expansion does not occur in (b).

(b) *With instructions.* There is a change in the distribution of ISIs ($\chi^2 = 26.29$, $p < 0.001$; Fig. 3(d)) which is accompanied by an increase in large (9–25°) saccades and a decrease in small (<3°) saccades ($\chi^2 = 219.51$, $p < 0.001$; Fig. 4(d), Table 2).

There is no change in the proportion of smooth movement (Table 3).

As with the extrafoveal AI, the variance of saccadic amplitudes towards the AI is significantly lower than of those away from it ($F = 1.77$, $p < 0.001$), although there is no reliable difference in the numbers of saccades in the two directions (Fig. 5(b); cf. Fig. 1E).

DISCUSSION

There are four main conclusions from the results obtained in this experiment. Firstly we have demonstrated a relationship between eye and head movements in scanning behaviour in the dark. Secondly we have shown that the presence of retinal information can have marked effects on eye movements if the feedback from eye movements is annulled. More particularly, we have shown that if a target is stabilized on the fovea the effects are qualitatively different from those obtained if it is stabilized just off the fovea and that these, in turn, differ from those obtained when it is stabilized in the periphery. Furthermore, we have shown that the effects of foveally stabilized images are not qualitatively changed by instructions but that instructions change the whole pattern of eye movements elicited by an extrafoveal AI.

The third conclusion is that a target stabilized 3° extrafoveally is a more specific stimulus for saccades than one at 15°. Finally, we find that saccades may show different distributions

in time when they are correcting for the displacement of an image, or compensating for the drift of the eyes, from when they are searching for visual information. In correction, they also show reduced variability in size. These results may reflect a distinction between saccades that are under central control (searching saccades) and saccades that are under the direct control of retinal information (correction saccades). In the latter case, the extrafoveal image becomes a "compelling" stimulus for saccades in a similar manner to the way in which a foveal image becomes a "compelling" stimulus for tracking.⁵

In the absence of instructions, foveal and extrafoveal AIs produce quite different patterns of eye movements. Whereas foveal AIs lead to marked inhibition of saccades and an increase in the proportion of smooth movement without reliably affecting saccadic amplitude, extrafoveal AIs tend to increase the numbers of saccades, to bias their direction, and to increase their amplitudes, without there being any reliable changes in the proportion of smooth movement. However, the direction of smooth movement is predominantly towards the extrafoveal AI. That eccentric AIs tend to drift in the direction of their eccentricity was also noted by REXROAD (1928) and by WALTERS and GRUNDLACH (1931).

HEYWOOD and CHURCHER (1971) suggested that uncompensated drift initiates the smooth eye movement of foveal AI tracking. This suggestion cannot explain the fact that the extrafoveal AI can bias the direction of smooth movement towards itself and can, in so doing, change the direction from that shown with a foveal AI, unless an eccentric AI, or real target, biases the direction of fixation drift sufficiently to overcome the individual differences (shown by NACHMIAS, 1961) in the distribution of drift directions with a central target. GAARDER (1967) has indeed shown that during fixation of a point on one edge of a complex pattern microsaccades are biased away from the pattern. As noted by MOLLON (1968): "The very strong suggestion is that drift is predominantly towards the pattern." Since our results show that, in the absence of instructions, saccades are biased away from the extrafoveal AI while smooth movement is directed towards it they appear to replicate Gaarder's finding, with *non*-fixational eye movements. Furthermore, since the mean amplitude of saccades away from the AI approximates to the displacement of the AI, and since these saccades show less variance of amplitude than saccades in the opposite direction, they may be compensating for this drift of the eyes towards the AI (see Fig. 1B).⁶

However, if subjects are instructed to track the extrafoveal AI eye movement patterns change. Now, instead of a preponderance of saccades which seem to be compensatory, there are more saccades correcting for "tracking error", as shown by variance changes and the close agreement between the reduced mean amplitude of saccades towards the AI (3·17°) and the retinal displacement of the AI.

⁵ Since completing this paper we have become aware of the results of KOMMERELL and KLEIN (1971) who have also investigated the effects of extrafoveal AIs on eye movements. Their results agree well with those reported here, and further suggest that the relationship between the displacement of the AI and amplitude of the saccades it evokes may be very close for all displacements between 2° and 10°, at least for the first few saccades made.

⁶ An alternative, or additional, hypothesis for the initiation of foveal AI movement derives from the results of CRONE and VERDUYN LUNEL (1969) who show that the pursuit of a slowly moving point (c.15' arc/sec) or the perception of autokinesis of a stationary point is a consequence of maintained eccentricity of fixation to the point. This eccentricity may be no more than 1' or 2' arc overall. According to this hypothesis, any slight initial eccentricity of the foveal AI would necessarily be maintained by image stabilisation and would be open to interpretation as movement of the AI leading to pursuit of it. Although MACK and BACHANT (1969) report that no movement of a foveal AI is seen during the small eye movements that occur while subjects try to fixate in the dark, enforced eccentricity of fixation may play a part in the perception of after-image movement.

Instructions to track a foveal AI produce patterns of eye movement that are in agreement with the findings of HEYWOOD and CHURCHER (1971). Saccades are inhibited (all subjects show a reduction in the number of saccades compared with Dark N.I.) and sustained smooth movement is made. In contrast to the extrafoveal condition, patterns of saccadic behaviour with a foveal AI are determined by the direction of smooth movement. Thus, both with and without instructions, a foveal AI elicits more saccades in the direction opposite to that of smooth movement, and with greater variability of amplitude. With an extrafoveal AI, on the other hand, the patterns of saccadic activity depend on whether or not the AI is being tracked, although the direction of smooth movement remains the same in both cases. And whereas with a foveal AI increased numbers of saccades are associated with greater variance of amplitude, with an extrafoveal AI increased numbers of saccades in a particular direction are associated with reduced variance of amplitude.

The eye movements of subjects sitting in the dark without instructions indicate that in the absence of any visual input saccadic searching takes place, with most saccades occurring at short intervals. The modal interval of 370 msec agrees well with the values of ISIs found in visual search tasks or in the scanning of pictures (FORD, WHITE and LICHTENSTEIN, 1959; JEANNEROD, GÉRIN and PERNIER, 1968). Eliminating one degree of freedom in searching behaviour by preventing head movements has marked effects on eye movements. The increase in intersaccadic intervals and the decrease in saccadic amplitude presumably reflects the importance of head movements in normal scanning behaviour.

An extrafoveal AI, however, both with and without instructions (though less clearly defined in the former case) gives a modal ISI of 750 msec. This is substantially longer than the modal ISI either for the conditions in the dark or for the foveal AI with instructions, and suggests that if the saccades we observe with an extrafoveal AI are compensatory or corrective for error during smooth movement, these may be distinguishable from searching saccades by requiring more time for their initiation. It would also follow that accumulation of error over time is unnecessary for correction saccades during tracking, and that elapsed time plus the presence of error is sufficient.

Finally, the presence of a peripheral AI does not affect the temporal patterns of eye movements, and in particular does not affect the ability of the eye to make smooth movement. Indeed, without instructions the peripheral AI seems to be ignored as a stimulus for eye movements. However, when instructions are given, the patterns of saccades change although there is no improvement in tracking. It is clear, nevertheless, that the peripheral AI in this experiment does not affect eye movements to the same extent as, or as systematically as, the extrafoveal AI.

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Abstract—Foveal and non-foveal after-images affect saccadic behaviour in different ways. Foveal after-images inhibit saccades and facilitate smooth eye movements whether or not instructions to track the after-image are given. Parafoveal after-images are effective stimuli for eliciting consistent eye movement patterns, but these patterns change when instructions are given. Peripheral after-images have little effect on eye movements. Eye movement patterns with extrafoveal after-images suggest that corrective saccades (under retinal control) have different temporal properties from searching saccades (under central control).

Résumé—Les images consécutives fovéales et non fovéales affectent différemment le comportement saccadé. Les images consécutives fovéales inhibent les saccades et facilitent les mouvements réguliers des yeux, que l'on ait ou non donné des instructions pour suivre l'image consécutive. Les images consécutives parafovéales sont efficaces pour engendrer des types donnés de mouvements des yeux, mais ces types changent avec l'instruction qu'on donne. Les images consécutives périphériques ont peu d'effet sur les mouvements des yeux. Les types de mouvements d'yeux avec des images consécutives extrafovéales suggèrent que les saccades de correction (sous contrôle rétinien) ont des propriétés temporelles différentes des saccades de recherche (sous contrôle central).

Zusammenfassung—Foveale und extrafoveale Nachbilder beeinflussen Sakkaden unterschiedlich. Foveale Nachbilder hemmen Sakkaden und erleichtern kontinuierliche Augenbewegungen unabhängig davon, ob die Versuchspersonen die Nachbilder verfolgen sollen oder nicht. Parafoveale Nachbilder sind wirksame Reize, um konsistente Augenbewegungen hervorzurufen, aber diese Muster ändern sich, wenn Instruktionen gegeben werden. Periphere Nachbilder haben nur wenig Einfluß auf Augenbewegungen. Augenbewegungsmuster mit extrafovealen Nachbildern lassen vermuten, daß korrektive Sakkaden (unter Kontrolle der Netzhaut) ein unterschiedliches Zeitverhalten zeigen von Suchsakkaden (unter zentraler Kontrolle).

Резюме—Фовеальные и внефовеальные последовательные образы влияют на саккадическое поведение различным образом. Фовеальные послеобразы тормозят саккады и облегчают плавные прослеживающие движения глаз, независимо от того оудет или не будет дана инструкция следить за послеобразом. Периферические послеобразы оказывают малое влияние на движения глаз. Паттерн движений глаз при наличии внефовеальных послеобразов заставляет предполагать, что корригирующие саккады (под контролем сетчатки) имеют временные характеристики, отличающиеся от саккадических движений поиска (под центральным контролем).