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EYE MOVEMENTS AND THE AFTERIMAGE—I. TRACKING THE AFTERIMAGE

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INTRODUCTION

YARBUS (1967) has claimed that smooth eye movements cannot be made in the absence of a moving visual stimulus. Experiments which apparently contradict this claim involve either a reduction in level of arousal, or some alternative information, or mechanical restraint. Smooth eye movements have been reported at the onset of, and during, sleep (MILES, 1929; DEMENT, 1964; FUCHS and RON, 1968). Kinaesthetic information from self-produced hand movement improves tracking (STEINBACH and HELD, 1968), an improvement maintained in the dark and enhanced by the addition of an afterimage (JORDAN, 1970). Smooth eye movements have also been reported with eyes closed (DECKERT, 1964; BECKER and FUCHS, 1969, Fig. 2e), i.e. when lid pressure may have damped normal saccadic movements.

WESTHEIMER and CONOVER (1954) did obtain smooth eye movements when fixation was repeatedly shifted between two fixed points. But the velocity and frequency of these movements were high (180°/sec; 3 c/s) in comparison with normal pursuit, and subjects were unable to make voluntary slow smooth eye movements.

However, in one recent report (MACK and BACHANT, 1969) there is a suggestion that slow pursuit-like movements may occur when a subject experiences an afterimage. The present experiment examines this possibility further.

METHOD

Horizontal eye movements were measured by binocular recording of the electro-oculogram (EOG). Electrodes (Ag–AgCl) were placed at the outer canthi of the two eyes and the resulting signals led through a d.c. amplifier type S.E. 4510 to a u.v. Galvanometer Recorder type 3006 (both S.E. Laboratories). The eye movements were written out on Kodak Linagraph photosensitive paper at a speed of 10 in./min.

Subjects sat in a lightproof room, 4 ft by 3 ft by 5 ft 6 in. high, painted matt black inside, and lit when necessary by a dim red light. Their heads were restrained by a conventional chin rest–bite bar assembly. They faced a flat surface 24 in. away on which a series of calibration points, each subtending 1°, were arranged 5, 10, 20 and 30° left and right of a central fixation point. This was a 1° black hole behind which was mounted an electronic flashgun producing a 1-msec intense white flash. The calibration points were visible only when the red light was on. The flashgun, light and EOG recording apparatus were controlled from outside by the experimenter.

The standard testing procedure was as follows. Each subject was dark adapted for 10 min with the red light on. The EOG was then calibrated with a series of fixations to each of the calibration points. The subject was now instructed to fixate the centre and maintain his fixation for 30 sec in the dark. He was then told to imagine a pendulum swinging in front of him and to try and track it smoothly with his eyes. This was continued for at least 30 sec. The light was switched on, and the subject refixated the central point. At the moment when the light was switched off, the subject was given an afterimage with the instructions "if it moves, try and track it smoothly with your eyes". His eye movements were recorded for at least 60 sec, and often longer. (The afterimage lasted several minutes under our experimental conditions.) At the end of the afterimage tracking period, the light was again turned on, the subject refixated centre and was instructed to maintain his fixation for thirty seconds in the dark. Finally the EOG was recalibrated.

Five subjects (including the authors) were tested under these conditions. Two additional subjects were told before receiving the afterimage that by moving their eyes they could cause the afterimage to move. Their task was to move the afterimage as smoothly and regularly as possible. One of these subjects had already participated in the standard experiment, and one was naive.

The records were analysed to compare the number of saccades, the intersaccadic interval, the proportion of smooth eye movement, and the mean amplitude and velocity of smooth eye movement under the different conditions. The recording system permitted measurements accurate to within 1° of eye movements of 2° or more, and all subsequent references to eye movements are to those greater than or equal to 2°. Saccades were defined as step displacements of the EOG trace of 2° or more which conformed to the durations given by YARBUS (1967, p. 132). The baseline drift of the system over one-half of an experimental session averaged the equivalent of 5·1′ arc/sec, and was taken into account in all subsequent calculations.

RESULTS

Figure 1 illustrates the typical eye movements of subjects trying to track an imaginary pendulum in the dark. There are very few smooth eye movements; these are mostly of small extent, occur at the end of horizontal excursions, and are very slow. The instructions

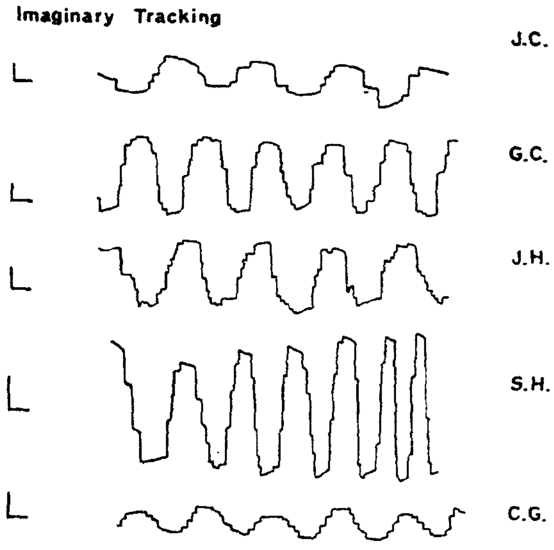

FIG. 1. Tracings of representative EOG recordings of subjects trying to track an imaginary pendulum in the dark. Calibration: vertical, 20°, and horizontal, 1·5 sec.

usually result in a series of saccades that are interrupted by fixation pauses. No subject showed any ability to make sustained smooth eye movements under these conditions. Table 1 shows the mean number of saccades per cycle of imaginary tracking and the percentage of the total distance travelled by the eye that is covered by smooth movement.

Figure 2a shows the eye movements elicited by tracking an afterimage. They are large, slow and very smooth. For the most part they are also periodic. There are significantly fewer saccadic interruptions than in imaginary tracking ($t = 2{\cdot}205$, $p < 0{\cdot}05$) and most of these are very small (< 3°). One subject, J.C., made "recentering" saccades when the image had been tracked into the periphery, thus giving his record a nystagmus-like appearance. These recentering saccades have not been included in the analysis. The intersaccadic interval is

TABLE 1

Subject	Imaginary tracking: Mean No. of saccades per cycle	Imaginary tracking: Mean inter-saccadic interval (sec)	Imaginary tracking: Proportion of total distance covered by smooth movement (%)	Afterimage tracking: Mean No. of saccades per cycle	Afterimage tracking: Mean inter-saccadic interval (sec)	Afterimage tracking: Proportion of total distance covered by smooth movement (%)	Afterimage tracking: Mean velocity over a half cycle of smooth movement (°/sec)	Afterimage tracking: Mean amplitude of half cycle (°)
J.C.	4·8	1·244	22·5	0·116	8·625	86·1	7·81	27·6
S.H.	7·0	0·54	5·78	0	—	100·0	4·94	13·44
G.C.	6·46	0·55	8·57	1·8	6·7	83·18	5·46	15·4
J.H.	15·6	0·385	3·23	6	3·21	77·66	3·02	23·25
C.G.	6·43	0·67	18·32	1·11	12·0	87·5	2·84	17·5
Mean	8·06	0·678	11.68	2·42	6·88	82·89	4·81	17·27

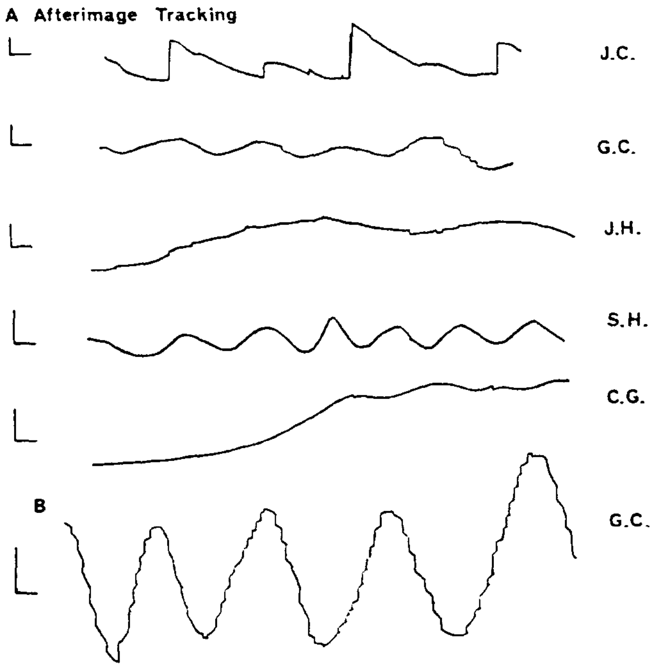

FIG. 2. (a) Tracings of representative EOG recordings of subjects tracking an afterimage. (b) Tracing of an EOG recording of a subject trying to move the afterimage with his eyes as smoothly as possible. Calibration for a and b: vertical, 20°, and horizontal, 1·5 sec.

significantly increased ($t = 7{\cdot}56, p < 0{\cdot}001$) compared with imaginary tracking. The increase in proportion of total distance travelled that is covered by smooth eye movement is also highly significant ($t = 27{\cdot}753, p < 0{\cdot}001$). One subject, S.H., made no saccades at all during 87 sec of afterimage tracking. Table 1 includes these data, as well as mean velocity and amplitude of smooth movement for a half cycle of afterimage tracking.

Most subjects reported that there were vertical components to the afterimage movement, and one, C.G., showed very much less horizontal movement than any of the others, apart from the common feature of a long smooth excursion to the periphery. Two subjects reported circular movements of the afterimage. In all cases the afterimage was reported perceived as ahead of the eye, and the tracking elicited by it was described as "compulsive".

The results of afterimage tracking do not contradict the hypothesis that smooth eye movements cannot be made to command. On a separate occasion two subjects were instructed to move the afterimage with their eyes as smoothly and regularly as they could. The results appear in Table 2, and in Fig. 2b. One subject, G.C., had already been tested on afterimage tracking. When instructed to move the afterimage, he showed a marked failure to produce smooth eye movements, although his performance was still greatly improved in comparison with imaginary tracking. The probability of order effects between testing sessions being the explanation for this improvement is reduced by the subject's repeated failure to make any smooth movement without an afterimage in the second testing session. The other subject, V.C., who had not already participated, reported almost total failure to move the afterimage at will. "Compulsive" tracking actually interfered with attempts to move the afterimage backwards and forwards. This subject's performance is thus much closer to afterimage tracking than to imaginary tracking, but is, nevertheless, slightly worse than any other subject's afterimage tracking.

TABLE 2

Subject	Voluntary movement of the afterimage: Mean No. of saccades per cycle	Mean intersaccadic interval (sec)	Proportion of total distance covered by smooth movement (%)	Mean velocity of smooth movement (°/sec)	Mean amplitude of smooth movement (°)
G.C.	12·5	0·599	46·27	7·06	4·35
V.C.	8·0	5·0	74·45	1·26	16·2

DISCUSSION

Our results suggest that for successful sustained smooth eye movements it is not necessary that there should be a really moving visual target or indeed a real target at all. Such smooth movements necessitate both the inhibition of "searching" saccades (occurring 1–3 times each second: FORD *et al.*, 1959; JEANNEROD *et al.*, 1968) and the absence of corrective saccades. The foveal afterimage fulfils the function of a target thus removing the need for searching saccades; also, because the afterimage is stabilized on the fovea there is no error signal generated by image displacement during smooth movement, and hence no stimulus for corrective saccades. (The effects of extrafoveal afterimages will be described in a subsequent paper.) Instructions involving the use of the eyes can, therefore, produce smooth eye movements without real target or image velocity, but only when the eye movements are under control of information from the retina and not under the voluntary control of the subject. In the latter case, saccadic behaviour is reintroduced.

How does this smooth movement start? Darkness, large targets ($> 1°$) and stabilized retinal images all tend to change the patterns of fixational eye movements towards a reduction in the frequency of compensatory flicks and an increase in drift rate (CORNSWEET, 1956; NACHMIAS, 1959, 1961; STEINMAN, 1965). With a 1° afterimage in the dark, therefore, the eye may start drifting without the usual compensatory mechanisms being activated. How this drift achieves pursuit velocities is unexplained [though YARBUS (1967) has shown that there is no discontinuity between the speeds of fixation drift and of pursuit of slowly moving real targets].

There are no proprioceptors in the eye muscles, etc., which could send the brain information about eye position or movement (BRINDLEY and MERTON, 1960). However, conditions for the perceived movement of the afterimage could be established if the brain can monitor the outflow from the oculomotor system, and can use the information that no apparent displacement of the retinal image occurs (cf. MACK and BACHANT, 1969).

This experiment shows, therefore, that smooth eye movements may involve two separable processes, one concerned with the inhibition of saccadic interruptions and dependent on the presence of information about a target, and the other concerned with maintaining the image of a moving target stationary on the retina and dependent on target velocity. The afterimage tracking condition makes the second process redundant, thus emphasising the role of saccadic inhibition in smooth eye movements.

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Abstract—Although subjects failed to make smooth eye movements when tracking an imaginary pendulum in the dark, when given an afterimage to track they exhibited sustained smooth eye movements despite the absence of a moving visual stimulus. These results suggest that smooth eye movements may be a product of two processes, one which stabilizes images on the retina, and one which inhibits saccadic behaviour.

Résumé—Les sujets ne peuvent pas suivre du regard un pendule imaginaire dans l'obscurité avec un mouvement continu des yeux, tandis que si on leur donne à suivre une image consécutive ils exécutent des mouvements réguliers du regard malgré l'absence d'un stimulus visuel en mouvement. Ces résultats suggèrent que les mouvements réguliers des yeux peuvent provenir de deux processus, l'un qui stabilise des images rétiniennes et l'autre qui inhibe le comportement saccadé.

Zusammenfassung—Obgleich die Testpersonen es nicht vermochten, gleitende Augenbewegungen zu machen, wenn sie ein imaginäres Pendel in der Dunkelheit verfolgten, zeigten sie gleitende Augenbewegungen so oft ein zu verfolgendes Nachbild gegeben wurde, trotz des Nichtvorhandenseins eines sich bewegenden Sehreizes. Diese Resultate weisen darauf hin, daß gleitende Augenbewegungen ein Produkt zweier Prozesse sein können; einer, welcher Bolder auf der Retina stabilisiert und einer, der saccadischer Verhalten hemmt.

Резюме—Испытуемым не удавалось плавно прослеживать в темноте воображаемый маятник, но "прослеживая" послеобразы, они оказались способны к плавным движениям глаз в отсутствие движущегося стимула.

Отсюда, повидимому, следует, что плавные движения глаз могут возникать в результате двух процессов: стабилизации изображений на сетчатке и угнетения саккадической активности.