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IS SACCADIC SUPPRESSION REALLY SACCADIC?

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INTRODUCTION

WHILE investigating the effect known as "saccadic suppression" a number of authors (LATOUR, 1966; VOLKMAN, SHICK and RIGGS, 1968; ZUBER and STARK, 1966) have found that visual performance decreases substantially before the onset of the saccade. This was the main reason (DUFFY and LOMBROSO, 1968; LATOUR, 1966; VOLKMAN *et al.*, 1968) to postulate the existence of a central mechanism of visual suppression, acting some moments before and during the saccade. In fact there exist other concepts (RICHARDS, 1968), but preference is given to the hypothesis of central suppression since it is attractive and fits with current ideas about the way the C.N.S. operates.

In two recent papers MACKAY (1970) demonstrated a phenomenon closely related to "saccadic suppression". In his experiments MacKay caused rapid motion of the circular, illuminated background on which a light spot was presented for a short time. He found an elevation of visual threshold for the spot. These experiments lead to the conclusion that the "saccadic suppression" is initiated not from the eye movement proper, but rather from the displacement of the visual image on the retina.

As we pointed out in a previous paper (MITRANI, MATEEFF and YAKIMOFF, 1970) the "smearing" of the retinal image during voluntary saccades gives a substantial contribution to the observed suppression. In order to verify the standpoint of MacKay it is important to undertake experiments on "saccadic suppression" in such a way that the smearing would be eliminated. It is true that the use of a flash lasting only a few microseconds can avoid the effect of "smearing", but such stimulus is far from being natural. In this paper we give the results of our experiments on the changes in the visual threshold during voluntary saccades. With a suitable experimental arrangement we are in position to measure separately the "smearing" and the pure "saccadic suppression".

EXPERIMENTAL ARRANGEMENT AND RESULTS

The subject was sitting in front of a circular, uniformly illuminated matt screen, his head fixed with a headholder. The screen was at 40 cm from the subject's eyes and had an angular diameter of 53°. On the screen, symmetrically on the left and right sides of its center, there were two fixation points with angular size of 40′. The angular distance between the two points which determined the size of the saccade was 8°. A diffuse reflecting sphere, placed behind the screen, was used for its illumination (Fig. 1). The position of the subject's eyes was measured with the device described earlier by us (MITRANI *et al.*, 1970). The resulting voltage was amplified and drove a pen motor from "Alvar" ink recorder in which the pen was

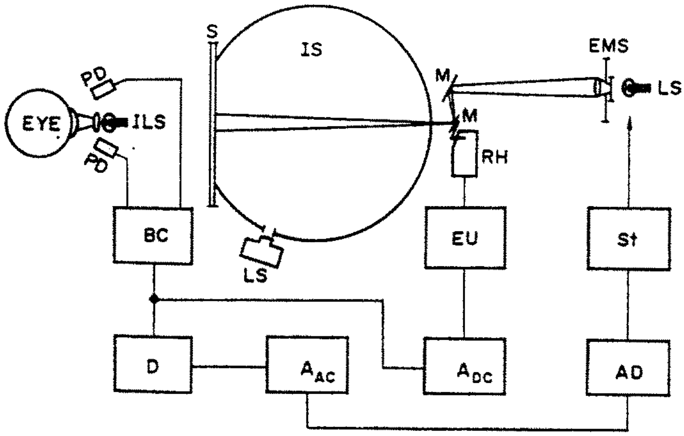

FIG. 1. Block diagram of the experimental arrangement: *PD*—photodiodes; *ILS*—infra-red light source; *BC*—bridge circuit; *D*—derivative circuit; $A_{a.c.}$—c.c. amplifier; $A_{d.c.}$—d.c. amplifier; *EU*—exit unite; *RH*—electromagnetic recording head; *M*—mirror; *LS*—light source; *St*—stimulator; *AD*—amplitude discriminator; *EMS*—electromagnetic shutter; *S*—screen; *IS*—integrating sphere.

replaced by a mirror. The position of the mirror was determined by the position of the subject's eyes. It is easy to obtain an exact correlation between the subject's line of sight and the position of a light spot projected on the screen by means of this rotating mirror (STARK, 1968). The frequency curve of the pen motor is almost linear up to 80 Hz and shows little distortion up to 100 Hz.

In all of our experiments the light spot was projected with a delay of 10 msec after the onset of the saccade for 7 msec. The subject made voluntary saccades from the left fixation point to the right, following a command from the experimenter. During the course of the saccade the stimulus was presented either following the position of the eyes (i.e. on a constant retinal position), or immobile between the fixation points (i.e. moving across the retina). Control experiments were performed with both the subject's eyes and the stimulus immobile.

In a series of experiments these three different ways of stimulus presentation were used and the three thresholds were measured: (1) While the subject was making saccades, the stimulus being presented moving synchronously with the eyes; (2) while the subject was making saccades, the stimulus being presented immobile between the fixation points; (3) while the subject was fixing the center between the two points, the stimulus being presented immobile on the same place. Each series was repeated three times in three different days keeping the conditions unchanged. After that sequence the conditions were altered.

There were four different conditions. In three of them we had uniformly illuminated the screen with luminance of 4, 2, or 4×10^{-2} nt. In another the screen was made drastically nonuniform by means of black figures with sharp edges (Fig. 2). The total area of the black figures was one-half of the screen area. The luminance of the screen in this case was 4 nt and the total light from the screen was equal to that of an uniformly illuminated screen with luminance of 2 nt. The black figures were placed in such a way as to secure a free stripe around the fixation points. This stripe was left in order to eliminate any moving sharp contours on and around the place the stimulus was presented. It is known (MITRANI *et al.*, 1970) that there is an increase in the visual thresholds during a voluntary saccade when

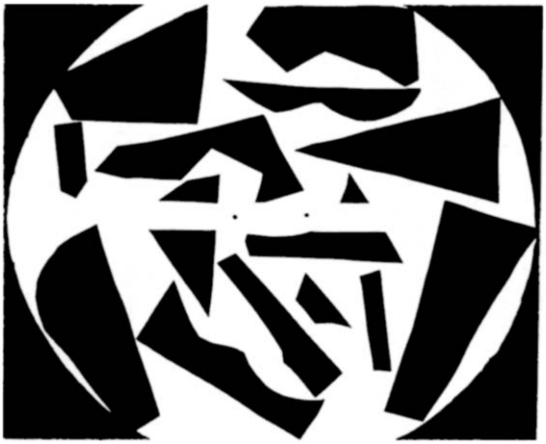

Fig. 2. View of the screen with the black figures and the fixation points on it.

the stimulus appears on a screen containing vertical end-to-end boundaries of different luminances.

In each series the changes in the visual threshold due to the "smearing" and the "suppression" for different luminances and structure of the screen were estimated. There were two subjects with normal sight aged 24 and 28 years. In Table 1 the measured thresholds under different conditions for the two subjects are given. I_m^m is the threshold for a moving stimulus presented during saccadic eye movements. I_m^r is the threshold for an immobile stimulus presented during saccadic movements. I_r^r is the threshold for stimulus presented in front of the eyes at rest. The change of the threshold due to the "smearing" is therefore $\Delta I_s = I_m^r - I_m^m$. The change of the threshold due to the "suppression" is consequently $\Delta I_t = I_m^m - I_r^r$. It should be noticed here that an imperfection of the stimulus—moving system would reduce the difference between ΔI_s and ΔI_t, and their absolute values. The values for ΔI_s and ΔI_t given in Table 1 are therefore maximal.

It is well seen from the data given that there is only a little difference between the changes ΔI_t (due to the "suppression") for 2 and 4 nt luminance of the screen. ΔI_s (the

Table 1

	4 *nt*		4*nt*-structured		2 *nt*		4×10^{-2} *nt*	
S_s	*T.M.*	*P.K.*	*T.M.*	*P.K.*	*T.M.*	*P.K.*	*T.M.*	*P.K.*
I_m^m	4·02 ± 0·47	2·82 ± 0·22	7·79 ± 0·61	4·73 ± 0·31	3·67 ± 0·35	1·89 ± 0·16	0·59 ± 0·06	0·47 ± 0·06
I_m^r	6·57 ± 0·37	4·45 ± 0·45	9·24 ± 0·84	7·57 ± 0·73	4·88 ± 0·41	3·14 ± 0·41	0·98 ± 0·1	0·90 ± 0·08
I_r^r	1·73 ± 0·08	1·18 ± 0·12	1·57 ± 0·12	0·9 ± 0·08	1·98 ± 0·16	0·90 ± 0·08	0·65 ± 0·08	0·41 ± 0·04
ΔI_t	2·29	1·64	6·22	3·83	1·69	1·09	0	0
ΔI_s	2·55	1·63	1·45	2·84	1·21	1·15	0·39	0·53

contribution of the "smearing") is also almost unchanged for these two cases. There exists a striking difference for the case of luminance 4×10^{-2} nt. Here the "suppression" does not exist ($\Delta I_t = 0$ in the 95 per cent confidence limits). The change in the threshold when the stimulus is immobile during a voluntary saccade is due entirely to the "smearing". There is almost a complete absence of "suppression".

The discontinuity in the screen luminance gives rise to a sharp increase of the "suppression". Even when during the saccade no contours pass across the fovea the mere presence of such moving contours in the peripheral field makes "suppression" dominate "smearing". The "suppression" is entirely different from that in the case of uniformly illuminated screen with luminance of 4 or 2 nt. It should be noted that at 4 nt the luminances are equal, while at 2 nt the total light energies are equal with the case with figures on the screen.

CONCLUSIONS

Our results confirm MacKay's assumption that the shifting of the visual image on the retina and not the eye movement is the cause of the "saccadic suppression". It is quite obvious that the signal for suppression does not arise from the saccade-programming system in the brain, as there is a complete lack of "suppression" for saccades made in darkness (4×10^{-2} nt). Evidently the presence of borders on the screen, even located in the peripheral visual field and not directly interfering with the stimulus, gives rise to a considerable increase in "suppression". Most probably it results from the movement of the entire visual pattern during the saccade. When the complexity of the pattern increases "suppression" increases too. One can expect a substantial diminution of the visual ability if MacKay was to shift an illuminated background with black figures on it instead of the uniformly illuminated circle.

We have not measured the time relation between the "suppression" and the onset of the saccade but even so we can drive quite firmly the conclusion that the "saccadic suppression" is not saccadic.

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Abstract—Visual thresholds were measured during voluntary saccades of 8° under different conditions. From the experimental data the contributions of the "smearing" and the propre suppression were evaluated. It was found that the suppression disappears when the luminance of the screen was 4×10^{-2} nt. On the contrary, the suppression increases when the screen was made nonuniform by means of black figures on it. Conclusion is made that the "saccadic suppression" is not saccadic but merely depends on the motion of the entire visual pattern on the retina.

Résumé—On mesure le seuil visuel durant des saccades volontaires de 8° dans diverses conditions. Les résultats permettent de faire la part relative de l'estompage et de la suppression proprement dite. La suppression disparait pour une luminance de l'écran de $4 \cdot 10^{-2}$ nt. La suppression augmente au contraire quand on rend l'écran non uniforme en y inscrivant des chiffres noirs. On conclut que la "suppression saccadée" n'est pas saccadée mais dépend simplement du mouvement sur la rétine du dessin visuel tout entier.

Zusammenfassung—Es wurden Unterschiedsschwellen während willkürlicher Saccaden von 8° unter verschiedenen Bedingungen gemessen. Aus den experimentellen Werten wurden die Beiträge einer "verwischten" und einer korrekten Unterdrückung ausgewertet. Man fand heraus, daß die Unterdrückung verschwand, sobald die Leuchtdichte auf der Leinwand 4×10^{-2} nt betrug. Im Gegensatz dazu wuchs die Unterdrückung an, wenn die Leinwand mittels dunkler auf sie abgebildeter Figuren ungleichmäßig gemacht wurde. Daraus wurde die Schlußfolgerung gezogen, daß die "saccadische Unterdrückung" nicht saccadisch ist, sondern lediglich von der Bewegung des gesamten Testmusters auf der Retina abhängt.

Резюме—Во время произвольных восмиградусовых скачков глаз измерялись зрительные пороги в разных условиях. были определены вклады "смазывания" сетчаточного изображения и "истинного" саккадического подавления. Оказалось, что подавление изчезало при яркости фона в 4×10^{-2} нт. С другой стороны, подавление нарастало зачительно при скачках на фоне структурированного поля. Делается вывод, что "саккадическое попдавление" не является саккадическим, но зависит главным образом от движения целостного зрительного изображения по сетчатке.