Vision Res. Vol. 13, pp. 1343–1353. Pergamon Pres 1973. Printed in Great Britain.

MOVEMENT PERCEPTION DURING VOLUNTARY SACCADIC EYE MOVEMENTS

GUY ORBAN, JAAK DUYSENS and MARK CALLENS

Laboratorium voor Neuro- en Psychofysiologie, Katholieke Universiteit Leuven, Dekenstraat 6, 3000 Leuven, Belgium

(*Received* 1 *November* 1972)

INTRODUCTION

THE VISUAL system can be considered as a feature extracting system consisting of several parallel channels each one of which deals with a particular visual perception parameter as, e.g. form or movement. As far as perception of movement is concerned, it has been suggested by GREGORY (1966), in his studies on movement after-effects, that at least two movement perception channels should be postulated to exist: a first one dealing with velocity (v) and a second one with displacement (Δx); and that each of these channels may consist of several directional subchannels.

On the other hand, several theories have been formulated to explain the stability of the visual world during saccadic eye movements, e.g. the saccadic suppression theory (ZUBER and STARK, 1966), the Efferenzkopie (von HOLST and MITTELSTAEDT, 1950) or corollary discharge theory (SPERRY, 1950), and the input overflow theory (MACKAY, 1970). To our knowledge all experiments on this topic explored the perception of a fixed stimulus (flash, luminous point, visual scenery) during the saccadic eye movement, the only exception being BEELER's (1967) confirmation of an earlier observation of DITCHBURN (1955) that in darkness a moving luminous point is not perceived during a microsaccade.

At the start of the present research it was felt that (a) the investigation of the perception of a moving object during a voluntary saccadic eye movement, and (b) the analysis of the results in terms of velocity and displacement channels might reveal some important aspects of the perceptual stabilization mechanisms. (It is to be noted that in the present study only the horizontal subchannel has been explored.)

METHODS

The experiments were performed on 12 naive male human subjects, 19–21 yr old, all with normal vision. The subject sat, with the head fixed, 2 m in front of a large black screen. A rectangular opening of 3 × 3 cm in the center of the black screen revealed the central part of a low persistence CRT-screen, on which the stimulus, i.e. a moving spot, appeared in conjunction with the eye movements of the subject.

Two fixation spots were mounted on the screen one on each side of the CRT, and 67 cm apart. At the same horizontal level and on both sides of the rectangle a small bulb at a mutual distance of 67 cm constituted a left and a right fixation point. In preliminary sessions the subject was trained to shift his gaze from one bulb to the other in a swift and smooth movement as soon as one of the bulbs was switched off whilst the other one was simultaneously lit. In these conditions the eye movement covered a visual angle of 20° and swept across the rectangular opening. (In the experimental sessions, at least in the dark condition, the bulbs were not lit in order to avoid any interference from stationary reference points, pupil-reflexes and after-images.)

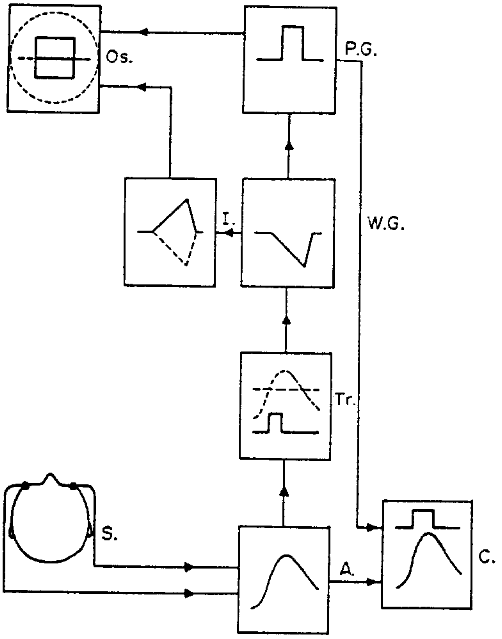

Fig. 1. Blockdiagram of the experimental setup. S.: subject; A.: a.c. preamplifier; Tr.: Schmidt trigger with 1 sec refractory period; W.G.: waveform generator; I.: inverter; P.G.: pulse generator; Os.: stimulus CRO; C.: control CRO.

The eye movement triggered a horizontal motion of the spot on the CRT-screen (Fig. 1). This was achieved by an EOG technique. AgCl electrodes, fixed to the outer canthi, were used. The eye movement voltage was amplified by a Tektronix 122 a.c. preamplifier and fed into a Schmidt-trigger with variable sensitivity level and a refractory period of 1 sec. This Schmidt-trigger was in turn connected to both a Tektronix 162 Waveform Generator and a Tektronix 161 Pulse Generator. A sawtooth wave of 100 msec produced by the waveform generator produced an x-axis deviation of the CRT spot. The direction of motion was either with the eye movement or in the reverse sense. A rectangular pulse of 50 msec produced by the pulse generator served as an unblanking pulse for the same CRO. This setup resulted in a spot motion in one or other direction across the visible part of the CRT-screen with the following characteristics: dia. of the spot 4′ velocity 40°/sec, visible displacement 52′, duration 20 msec, luminance (according to the beam intensity setting of the CRO)—0·5–1·9 log ft-L. The EOG trace was averaged on an average C Nuclear Chicago 7101 and the same equipment also recorded the unblanking pulse. This set up allowed us to set the Schmidttrigger so that the end of the spot's motion coincided with the end of the eye movement. All events were continuously monitored on a control CRO.

Eighteen separate experiments were carried out. In each individual experiment ambiant illumination and eye movement were kept constant: nine were done in light and nine in darkness. For each set of 9 there were five experiments with eye movements to the right and four to the left. Each individual experiment consisted of 105 trials; in 5 control trials there was no stimulus presentation, in the remaining 100 the spot moved to the left 50 times and to the right an equal number. The direcgion of spot motion was varied randomly and its luminance changed. Five different levels were used from . .0·5 to 1·25 log ft-L in darkness and from 1 to 1·9 log ft-L in light; thus each condition of spot direction and luminance occurred 10 times in each experiment. In some experiments the total number of trials had to be reduced to 50 or 40 trials with, however, the same distribution ratio over the various conditions. In total 1310 stimulus presentations were given.

The subjects were asked to respond to the stimulus presentations by one of the following statements: (1) "I did not see anything", (2) "I have seen something but I cannot decide upon the direction", (3) "I have seen a motion to the left" and (4) "I have seen a motion to the right". Only the last two responses (confident responses) were analyzed statistically.

Three-way contingency tables (Fienberg, 1970) were constructed with the pooled confident responses of all subjects (pooled responses and the individual responses showed a similar distribution) in order to test the dependence of the perceived movement direction on the saccade or stimulus movement direction. The analysis of the data by contingency tables is recommended over the analysis of variances approach since no assump tions as independence of the observations or equality of observation variances need to be satisfied. The trials were classified according to the variables A (stimulus movement direction) B (saccade direction) and C (perceived direction) with levels $\{A_i\}$, $\{B_j\}$ and $\{C_k\}$ where $i = 1, 2; j = 1, 2; k = 1, 2;$ (1 = left, 2 = right). Not all the mathematical models for expected cell frequencies in a three-way table were tested. From the nine possible models only those were chosen which take in account the fact that A and B are stimulus conditions (and hence interdependent) and C is the response.

The selected models are in the hierarchic order:

model (1): three variables A, B and C are independent
model (2): C is independent of A and B jointly
model (3): C is independent of B conditional on the level of variable A
model (4): C is independent of A conditional on the level of variable B.

More complex models than models (3) or (4) needed not to be tested since one of both these models fitted the observed data at the 5 per cent significance level. The goodness-of-fit of the models was tested with the "chi-square-test" statistic introduced by Pearson.

RESULTS

Since as well the velocity and the amplitude of the spot's motion were the same in all experiments, the influence of three variables was investigated: (1) the direction of the stimulus motion relative to the direction of the saccade, (2) the ambient illumination, and (3) the luminance of the moving spot. The first two variables have a definite influence on movement perception. Given the fact the second variable conditioned both other variables, results will be given successively for darkness and light. In these two conditions ambient illumination levels were −2 log ft-L and 0·1 log ft-L respectively.

1. *Dark condition*

In this condition no stationary visual references were available to the subject since the fixation bulbs were not used and the experimenter and all apparatus were hidden by the large black screen. Responses such as 3 and 4 were given in 86 per cent of the stimulus presentations. Among them 81·5 per cent ($n = 9$; $S = 14$) were correct if the stimulus movement coincided with the direction of the saccade, whereas 87 per cent ($n = 9$; $S = 13$) were wrong if the directions of the stimulus movement and the saccade were opposite. In other words the perceived direction was mostly the eye movement direction and not the spot direction.

TABLE 1. CONFIDENT RESPONSES OF SUBJECTS FOR DIFFERENT STIMULUS CONFIGURATIONS IN DARKNESS

Perceived movement	Saccade to the left Stimulus to the left	Stimulus to the right	Saccade to the right Stimulus to the left	Stimulus to the right
To the left	102	97	24	34
To the right	14	12	101	92

This finding clearly indicates that in darkness the perceived movement direction depends not on the stimulus direction but on the eye movement direction. This dependence was evaluated in a three way table as described above. Table 1 shows the raw data in dark.

Table 2 gives the observed counts and the expected counts for the different models. Models (1–3) yield significant χ^2 values indicating (1) that variables A, B and C are dependent, (2) that C (perceived direction) depends on A and B jointly, (3) that C depends on B (saccadic direction) conditional to A (stimulus movement direction). On the contrary model (4) fits the observed data well (χ^2 not significant), hence C is independent of A conditional to B. The correlation between eye movement direction and response as given by the contingency coefficient calculated on the χ^2 value for model (3) is high ($C = 0{\cdot}55$ as compared to $C_{max} = 0{\cdot}707$).

In experiments on saccadic suppressions, changes of threshold cannot be demonstrated if the luminance of the stimulus is 1 log unit above threshold. For this reason in the present experiments the stimulus luminance was varied over a range of 1·6 log units. Figure 2 shows that a luminance variation over this range did not influence the movement perception responses and particularly, that the percentage of the wrong or illusory responses remains constant at all luminance levels: thus the phenomenon differs, in this characteristic, from saccadic suppression.

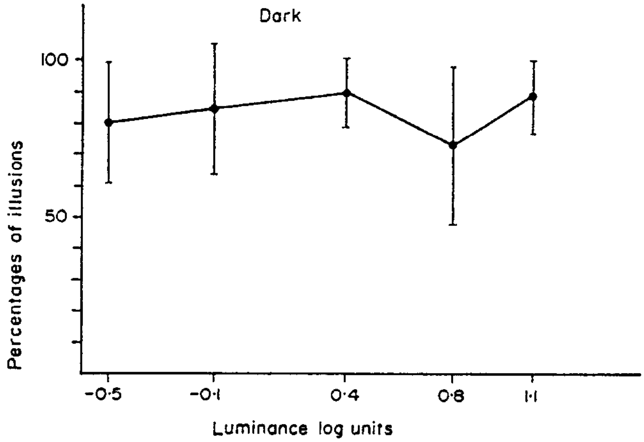

FIG. 2. Percentage of illusory responses (perceived motion opposite to stimulus motion) in function of stimulus luminance. The data approximate an horizontal line, indicating independence.

2. *Light condition*

In this conditions stimulus luminance levels higher than 0·3 log ft-L were used, this level corresponding to 75 per cent correct evaluations of the stimulus direction with stationary eyes. In 80 per cent of the stimulus presentations the subject gave a confident report of its direction. By contrast with the dark condition, in light the responses are dependent on the stimulus direction and not on eye movement direction. Table 4 shows the observed counts (based on the data of Table 3) and the expected counts for models (1–4). In this case C still depends on A and B jointly but this time C depends on A conditionally to B and not on B conditionally to A. The correlation, however, between the stimulus and the response as given by the contigency coefficient calculated on the χ^2 value for model (4), is small ($C = 0{\cdot}28$). This small correlation is due to the low percentage of correct responses, namely 64 per cent ($n = 18$, $S = 24$).

TABLE 2. OBSERVED COUNTS (BASED ON DATA OF TABLE 1) AND EXPECTED COUNTS FOR MODELS (1–4). BELOW THE COLUMNS THE χ^2 VALUE TESTING THE GOODNESS-OF-FIT FOR EACH MODEL. IN DARKNESS MODEL (4) FITS THE OBSERVED COUNTS

Cell	Observed	Model (1)	Model (2)	Model (3)	Model (4)
1,1,1	102	61,5	62,6	60,6	102,6
2,1,1	97	60	57,8	59,6	94,6
1,2,1	24	68,6	67,5	65,4	28,9
2,2,1	34	66,9	68	70,2	29,1
1,1,2	14	52,4	53,4	55,4	13,4
2,1,2	12	51,1	49,2	47,4	12,4
1,2,2	101	58,5	57,5	59,6	96,1
2,2,2	92	57	58	55,8	96,9
	$n = 476$	$\chi^2 = 205{,}1$ df = 4 S	$\chi^2 = 206{,}7$ df = 3 S	$\chi^2 = 206{,}2$ df = 2 S	$\chi^2 = 2{,}22$ df = 2 NS

The results are slightly dependent on the luminance of the stimulus: for increasing luminance levels the percentage of confident responses and that of correct responses both increase.

TABLE 3. CONFIDENT RESPONSES OF SUBJECTS FOR DIFFERENT STIMULUS CONFIGURATIONS IN LIGHT

	Saccade to the left		Saccade to the right	
Perceived movement	Stimulus to the left	Stimulus to the right	Stimulus to the left	Stimulus to the right
To the left	82	39	136	79
To the right	34	53	39	84

TABLE 4. OBSERVED COUNTS (BASED ON DATA OF TABLE 3) AND EXPECTED COUNTS FOR MODELS (1–4). BELOW THE COLUMNS THE χ^2 VALUE TESTING THE GOODNESS-OF-FIT FOR EACH MODEL. IN LIGHT MODEL (3) FITS THE OBSERVATIONS

Cell	Observed	Model (1)	Model (2)	Model (3)	Model (4)
1,1,1	82	68,2	71,4	86,9	67,5
2,1,1	39	59,8	56,6	42,8	53,5
1,2,1	136	110,9	107,7	131,1	111,3
2,2,1	79	97,1	100,3	75,4	103,7
1,1,2	34	42,6	44,6	29,1	48,5
2,1,2	53	37,4	35,4	49,4	38,5
1,2,2	39	69,3	67,3	43,9	63,7
2,2,2	84	60,7	62,7	87,6	59,3
	$n = 546$	$\chi^2 = 49{,}5$ df = 4 S	$\chi^2 = 49{,}4$ df = 3 S	$\chi^2 = 2{,}7$ df = 2 NS	$\chi^2 = 48$ df = 2 S

DISCUSSION

The results reported indicate (a) that during voluntary saccades there is no suppression of movement perception (movement was perceived in 86 per cent of the presentation in dark and in 80 per cent in light), and (b) that in darkness the direction of the perceived movement is that of the saccade (84 per cent) whereas in light the direction of the objective movement prevails (64 per cent; in this latter condition the performance of the subjects was much lower).

The finding of the persistence of movement perception during voluntary saccades contrast with the observation of BEELER (1967) of a suppression of movement perception during micro-saccades. It should, however, be pointed out that changes of movement perception during micro-saccades and voluntary saccades share a common feature, in that they are both largely independent of the luminance of the stimulus. This is not the case in saccadic suppression: this phenomenon is only observed for luminances within a range of 1 log ft-L above threshold. Therefore, since in normal vision luminance is well beyond this range, saccadic suppression cannot be considered as endowed with functional significance in contrast with the changes in movement perception observed during micro-saccades and voluntary saccades.

Both physical and physiological explanations can be proposed for the fact that in dark the perceived motion direction is that of the eye movement and in light that of the stimulus.

In physical terms the movement of the spot on the retina is the algebraic sum of the retinal movement induced by the saccade and the objective spot movement. If v_o is the velocity of the spot on the retina, v_r the velocity of the retina and v_s the velocity of the spot, then $v_o = v_r + v_s$. The sign of each velocity indicates the direction of movement in the hypothesis that the retina is stationary and the object is moving. Hence, since $|v_s| < < < |v_r|$, sign $v_o =$ sign v_r. This means that the perceived direction, i.e. v_o, would be eye movement dependent, and more precisely that the perceived direction should be opposite to the saccade direction. This was not confirmed by the experimental results.

It could be argued that in the against situation (eye movement and spot direction opposite) the illuminated retinal line length is shorter, and hence that a greater amount of quanta/unit line length could cause a backward masking. But it has to be noticed that in the against situation in darkness the movement is still perceived but in the wrong direction, which fact is hard to explain by masking. Moreover, as mentioned above, $v_o \sim v_r$ and hence the distribution of quanta/unit line length is quite similar in both "against" and "with" situations.

In the dark conditions no fixation points were available to the subject and the exact eye position during spot presentation is unknown. It has to be observed that the subjects were trained to do the right eye movement and that before each experimental trial, a blank trial was given with fixation lights. Nevertheless it remains possible that in light and darkness different retinal areas were stimulated This fact would explain the difference between the light and dark results but not the differences in darkness between against and with situations.

The physiological explanation in terms of movement channels is based on three assumptions.

(1) The input to the movement channels is the movement of object image relative to the retina (absolute movement of the images). The retina is the stationary reference to which movement information transmitted by the cerebral channels is referred to. Even if the retina is moving during eye movements this is interpreted by the brain as visual scenary movement on a stationary retina.

(2) During saccades only the displacement channel is able to transmit movement information.

(3) In the displacement channel an evaluation is made of the changes caused by voluntary saccades. As MacKay (personal communication) suggested "the corollary discharge information serves not to subtract from or cancel parts of the visual input, but more generally to set criteria that determine whether and in what respect that input calls for readjustment of the perceptual map".

During saccades an expected value of movement is available to the higher cerebral centers. This expected value is used to evaluate the information transmitted by the movement channels. Figure 3 represents the expected value of velocity and displacement in function of time. These functions are constructed so that the movement of stationary images induced by saccades coincides with the expected value.

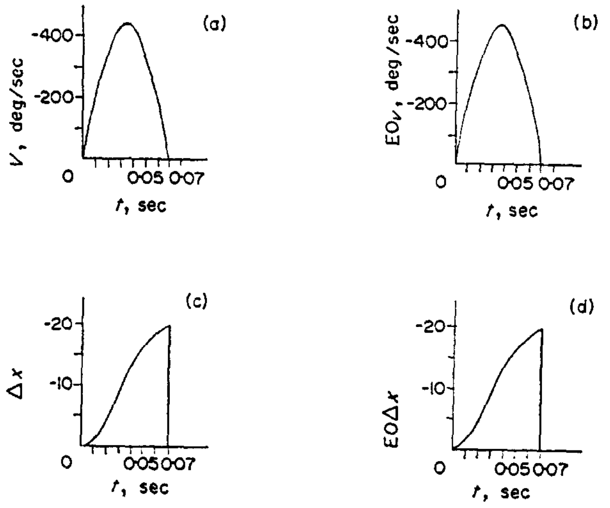

FIG. 3. Velocity and displacement expected values in function of time during a 20° saccade to the right. The curves of eye velocity and eye position in function of time are taken from YARBUS (1967). Although for a saccade of 20° these sinusoidal curves are only approximations, this has little bearing on the present discussion. (a) Stationary object image velocity in function of time. This function is the symmetrical image of the eye velocity function, relative to the time axis. (b) Eo_v velocity expected value. This function is constructed according to the principle that at each moment the zero translation equals the stationary object image velocity. (c) Stationary object image displacement in function of time. This function is symmetrical to the eye position time function. Note that at the end of the saccade the displacement falls to zero. Indeed displacement is a physiological movement parameter representing the amplitude of the movement. Hence it is zero when the object is stationary. (d) $Eo_{\Delta x}$ displacement expected value. Construction according to the same principle as in (b). Note negative values correspond to movement to the left in the physical world.

Since in dark condition no stationary reference was available to the subject, the spot image movement is the algebraic sum of the objective spot motion and the movement induced to the spot image by saccade. In Fig. 4 the evaluation of this input in velocity and displacement channels is represented. It is evident that the results support the hypothesis that during saccades information transmission and evaluation takes place only in the displacement channel.

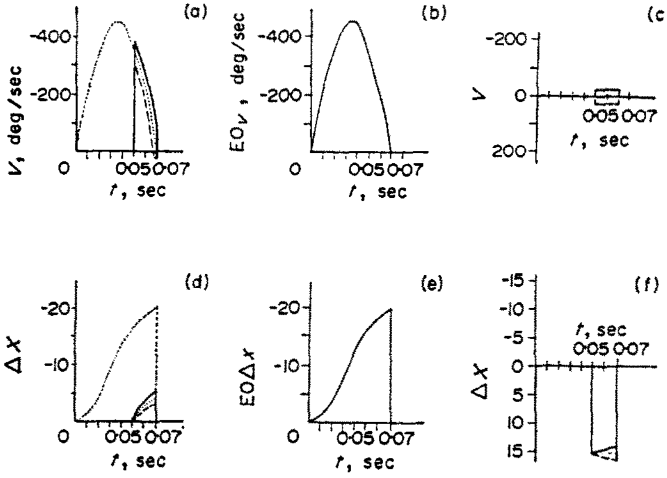

FIG. 4. Velocity vs. displacement subchannel evaluation hypothesis tested by the dark condition results (saccade 20° to the right). Upper row velocity channel, lower row displacement channel events. The stimulus was presented during the last 20 msec of the saccade. The stimulus image movement (*ad*) results of the superposition of the movement induced by the spot movement (*a*1) and the one induced by the saccade (*a*2). These three movements are relative to the reference plane bound to the retina (see text). Their velocities and displacements are $v_{ad}(t)$ and $\Delta x_{ad}(t)$, v_{a1} and $\Delta x_{a1}(t)$ $v_{a2}(t)$ and $\Delta x_{a2}(t)$ respectively. (a) Construction of $v_{ad}(t)$. $V_{a2}(t)$ (heavily dotted line) is equal, except the sign, to the eye velocity of the moment. Hence $v_{a2}(t)$ is symmetrical to the last part of the eye velocity function and equals the last part of the function $v(t)$ of Fig. 3(a) (this function is indicated by fine dots). Addition or subtraction, according to the stimulus motion direction, of the constant velocity v_{a1} yields $v_{ad}(t)$ (full line stimulus moving to the left, dashed line to the right). (b) Hypothetical velocity expected value function (see Fig. 3). (c) Perception: result of evaluating $v_{ad}(t)$ relative to the expected value given in (b). The perceived velocity is obtained by subtraction of the corresponding part of $Eo_v(t)$ from $v_{ad}(t)$ (full line stimulus moving to the left, dashed line to the right). In the velocity evaluating hypothesis the perceived direction should be that of the stimulus. This was not confirmed by the experimental results in dark. (d) Construction of $\Delta x_{ad}(t)$. $\Delta x_{a2}(t)$ (heavily dotted line) is opposite in sign and equal to the displacement of the eye *from the moment of stimulus presentation*. Hence $\Delta x_{a2}(t)$ can be obtained by translation by the last part of the $\Delta x(t)$ function of Fig. 3(c), which was symmetrical to the eye position function. The latter is indicated by fine dots. Addition or subtraction of the linear displacement $\Delta x_{a1}(t)$ yields $\Delta x_{ad}(t)$ (full line stimulus moving to the left, dashed line to the right). (e) Displacement expected value function (see Fig. 3). (f) Perception. Subtraction of the final part of $Eo_{\Delta x}(t)$ from $\Delta x_{ad}(t)$ yields the perceived displacement [full and dashed lines as in (d)]. In this hypothesis the perceived direction is identical to the saccade direction whatever the stimulus direction may be. Note that positive values mean movement to the right. In conclusion displacement evaluation hypothesis is confirmed by the experiments. Even if velocity evaluation occurs, the velocity information is canceled at least during the saccade by the displacement information.

In the light condition retinal image movement is subject to two reference systems: (a) a reference system bound to the retina (movements relative to this system are "absolute movements"; and (b) a reference system solidary with the image of the visual background which is absent in darkness (movements relative to that system are called "relative movements"). During the saccade the background reference system moves with respect to the retinal reference system. In this condition the absolute movement of a retinal image (*al*) is the sum of the relative movement of the image (*r*) and the (absolute) movement of the background reference (*o*) induced by the saccade. Stated in terms of velocity the resulting

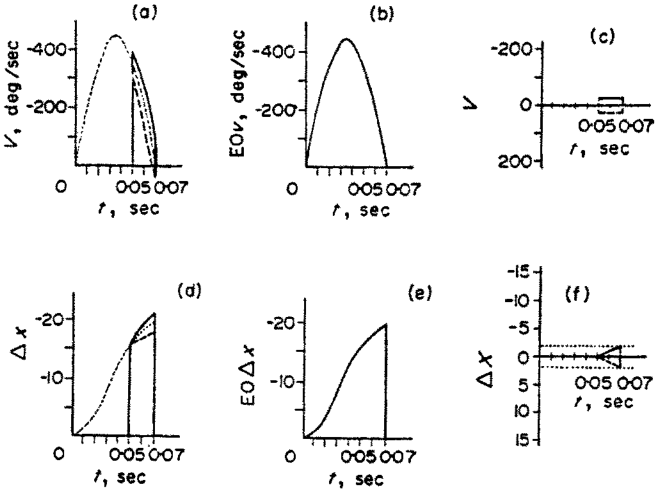

FIG. 5. Light condition results interpreted in function of the displacement evaluation hypothesis. Although they have but little importance, velocity changes are given in the upper row. Displacement data were displayed in the lower row. In light the stimulus image movement ($a1$) is the algebraic sum of the background reference movement (o) and the relative movement of the stimulus image in the latter reference (r). The corresponding velocities and displacements are indicated as $v_{al}(t)$ and $\Delta x_{al}(t)$, $v_o(t)$ and $\Delta x_o(t)$, v_r and $\Delta x_r(t)$. (a) Construction of $v_{al}(t)$. Here $v_o(t)$ (heavily dotted line) again is equal, except the sign, to the eye velocity of the moment, and $v_o(t) = v_{a2}(t)$ of Fig. 4(a). Given $v_r = v_{a1}$, $v_{al}(t) = v_o(t) + v_r = v_{a2}(t) + v_{a1} = v_{ad}(t)$ (full line and dashed line as in previous figures). (b) Expected velocity value (see Fig. 3). (c) Perceived velocity: as in darkness (see Fig. 4). (d) Construction of $\Delta x_{al}(t)$. $\Delta x_o(t)$ (heavily dotted line) is equal, except the sign, to the eye displacement *from the beginning of the saccade*. Hence $\Delta x_o(t)$ is the final part of the $\Delta x(t)$ function of a stationary object image (Fig. 3(c)), which is indicated by fine dots). $\Delta x_{al}(t)$ results from the addition or subtraction of the linear $\Delta x_r(t)$ to $\Delta x_o(t)$ [full and dashed lines as in Fig. 4(d)]. (e) Expected value as in Fig. 4(e). (f) Perceived displacement: subtraction of the final part of $Eo_{\Delta x}(t)$ from $\Delta x_{al}(t)$. In this situation the perceived direction is that of the stimulus as actually was observed. The perceived displacement ($= \Delta x_r(t)$) however, has a final value of 52′. This value being near or below the evaluator tolerance ($\pm 1°$ indicated by dotted line) can account for the bad performance of the subjects.

velocity ($v_{al}(t)$) is the same as that in dark (Fig. 5). Since velocity is an instantaneous property of a mobile, the velocity $v_{a2}(t)$ induced to the stimulus image by the saccade in dark equals the velocity $v_o(t)$ induced to the background reference by the saccade in light. Given that $v_{a1} = v_r$, it results that $v_{ad}(t) = v_{a1} + v_{a2}(t) = v_r + v_o(t) = v_{al}(t)$. On the other hand, with respect to displacement the situation is quite different in light and in dark. Although $\Delta x_r(t)$ still equals $\Delta x_{a1}(t)$, the equality $\Delta x_o(t) = \Delta x_{a2}(t)$ does not hold any longer (compare Figs. 4 and 5). Displacement is function of the preceding inputs to the system. $\Delta x_o(t)$ is the final part of the displacement function of the background since the displacement of the background reference starts at the beginning of the saccade. On the contrary $\Delta x_{a2}(t)$ was the translation of this final part since displacement of the spot image induced by the saccade started only when the spot was presented. The difference between $\Delta x_{al}(t)$ and $\mathrm{EO}_{\Delta x}(t)$, which results in perception, is $\Delta x_r(t)$. This means that the perceived movement direction and the stimulus movement direction coincide. The final value of $\Delta x_r(t)$ is 52′ and this may explain the bad performance of the subjects for it being near or below the tolerance of the evaluator.

REFERENCES

BEELER, G. W. (1967). Visual threshold changes resulting from spontaneous saccadic eye movements. *Vision Res.* 7, 769–775.

DITCHBURN, R. W. (1955). Eye movements in relation to retinal action. *Optica Acta* **1**, 171–176.

FIENBERG, S. E. (1970). The analysis of multidimensional contingency tables. *Ecology* **51**, 419–433.

GREGORY, R. L. (1966). *Eye and Brain, The Physiology of Seeing.* 251 pp. World University Press, London.

MACKAY, D. M. (1970). Elevation of visual threshold by displacement of retinal image. *Nature, Lond.* **225**, 90–92.

SPERRY, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *J. comp. physiol. Psychol.* **43**, 482–489.

VON HOLST, E. and MITTELSTAEDT, H. (1950). Das Reafferenzprinzip: Wechselwirkungen zwischen Zentralnervensystem und Peripherie. *Naturwissensch.* **37**, 464–476.

YARBUS, A. L. (1967). *Eye Movements and Vision.* Plenum, New York.

ZUBER, B. L. and STARK, L. (1966). Saccadic suppression: elevation of visual threshold associated with saccadic eye movements. *Exp. Neurol.* **16**, 65–79.

Abstract—In order to elucidate the stabilization mechanism of the visual perception during voluntary eye movements the perception of a moving object during a eye saccade was investigated in human subjects. The results were analyzed in terms of velocity and displacement perception channels. The experimental results indicate that during voluntary saccades there is no suppression of movement perception, and, on the other hand, that in darkness the direction of the perceived movement is that of the saccade whereas in light the direction of the objective movement prevails. The latter discrepancy can be explained by assuming that the perceptual analysis of movement during the saccade occurs in the displacement channel and that this channel is provided with a channel evaluation mechanism controlled by the oculomotor centers.

Résumé—En vue d'éclaircir le mécanisme de stabilisation de la perception visuelle pendant les mouvements oculaires volontaires nous avons étudié chez l'homme la perception d'un objet en mouvement pendant une saccade oculaire. Les résultats en ont été analysés dans le cadre des concepts de canaux perceptuels de vitesse et de déplacement. Les résultats expérimentaux montrent, d'une part, qu'il n'y a pas de suppression de la perception du mouvement pendant les saccades volontaires, et, d'autre part, que dans l'obscurité la direction du mouvements perçu est celle du mouvement oculaire tandis que dans la lumiére la direction du mouvement objectif est dominante. Cette divergence peut être expliquèe en admettant que le canal de déplacement est responsable de l'analyse du mouvement pendant la saccade et que ce canal est muni d'un mécanisme d'évaluation controlé par les centres oculomoteurs.

Zusammenfassung—Der Zweck der Untersuchung war der Stabilisierungsmechanismus der visuellen Wahrnehmung während freiwilligen Augenbewegungen zu erklären. Dazu wurde, bei Menschen, die Wahrnehmung eines bewegenden Objecktes während einer Augensakkade untersucht und wurden die Ergebnisse mittels der Begriffen Geschwindigkeits- und Verschiebungswahrnehmungskanälen analysiert. Die experimentelle Ergebnisse zeigen, einerseits, dasz während freiwilliger Sakkaden es keine Unterdrückung der Bewegungswahrnehmung gibt, und, anderseits, dasz im Dunkeln die Richtung der wahrgenommenen Bewegung diejenige der Augenbewegung ist während im Hellen die Richtung der Objektbewegung vorherrscht. Dieser unterschiedliche Befund kann erklärt werden durch die Annahme dasz die Wahrnehmungsanalyse eines bewegenden Objektes während einer Augensakkade vorgeht in dem Verschiebungskanal und dasz dieser Kanal mit einem durch die oculomotorischen Zentren kontrollierten Einstellungsmechanismus ausgestattet ist.

Яезцме—С целью выяснения механизма стабилизации брительного восприятия во время произвольных движений глаза было исследовано восприятие движущегося объекта во время саккадического движения глаза человека. Результаты были проанализированы в терминах скорости восприятит и смены каналов восприятия. Экспериментальные результаты оказывают, что во время произ вольных саккад нет подавления

восприятия движения, и, с другой стороны, что в темноте направление воспринимаемого движения совпадает с направлением саккады в то время как на свету превалирует направление объективного движения. Последнее расхождение может быть объяснено при допущении, что перцептуальный анализ движения во время саккады имеет место в канале смещения, и что этот канал обеспечивается механизмом каналч оценки, контролируемого глазадигвательными центрами.