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DIRECTION PERCEPTION AND HUMAN FIXATION EYE MOVEMENTS

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Abstract—The existence of involuntary movements of the eye during fixation gives rise to a problem concerning location in visual space. This has been investigated using a psychophysical task in which subjects judge the relative positions of two stimuli briefly flashed on a screen and separated by a temporal interval. It was shown, in line with the work of Matin (1972), that a subject's ability to compare two directions in space will decrease with time. This decrease occurs in a manner which suggests that the judgement is achieved on the basis of retinal position only and thus correspondence with external direction is subject to change as the eye drifts. Microsaccadic eye movements made by the subject were recorded whilst the same task was carried out and this showed a new phenomenon. When the subject makes a microsaccade, errors in location show that a shift in perceived direction occurs *towards* the direction of the microsaccade. This is exactly opposite to the result expected if only retinal position was used. A model to explain the results based on a form of corollary discharge is postulated.

INTRODUCTION

The existence of movements of the eyes produces a problem for theories of perception based on the processing of retinal information, arising from the lack of correspondence between position on the retina and direction in visual space. The suggestion is frequently made (e.g. Teuber, 1966) that eye movements are accompanied by some form of "corollary discharge" in which information about the movement is transmitted from the motor control centres to the visual sensory pathway in order to maintain constancy of perceived direction. A certain amount of evidence from psychophysical studies, reviewed recently by Matin (1972), is available to support this in the case of voluntary saccadic movements.

During fixation the eye moves with a characteristic pattern of drifts, tremor and microsaccades (Alpern, 1969) causing its axis to fluctuate over a region of about 10′ dia. Thus the same problem arises. Matin (1972, p. 359) argues that the compensation necessary to maintain an exact correspondence between retinal position and external visual direction does not exist "at least during [eye] movements away from the optimum position". His argument is based partly on the need for an error signal to activate the microsaccade generation mechanism and partly on results (Matin, Matin and Pola, 1968) which show that perception of direction in darkness is achieved almost entirely on the basis of retinal position alone. Since most subjects will make very few microsaccades in darkness (Cornsweet, 1956; Matin, 1972, Fig. 15) the existence of a compensatory signal accompanying microsaccades is still an open question and forms the subject of the present study.

EXPERIMENT 1

This experiment investigates the accuracy of perception of direction and is a necessary preliminary to experiment 2 in which eye movements are recorded, but the results are of interest in their own right.

A difficulty in investigating the perception of direction is to devise a task in which no other form of perceptual judgement may be used. The task used here is a variant of that used by Matin and Pearce (1965) in which the subject has to judge the relative positions of two lines (see Fig. 1) flashed in turn briefly on a screen with some temporal interval separating the two flashes. Caution is still necessary when the temporal interval is short. Firstly, it may occur that the parts of the stimulus are registered together to form a pattern, perhaps at the level termed iconic storage by Neisser (1967). The task then becomes a form of vernier alignment, and as discussed elsewhere (Findlay, 1973), this is perhaps better seen as a pattern recognition than as a location task. Secondly, the stimulus configuration may give rise to apparent movement effects, and once again a feature analytic approach in terms of movement detectors would be called for. A figure of 200 msec is often quoted as the upper limit of the duration over which perceived movement may be obtained (Graham, 1965) although it is problematic whether movement detection and displacement detection are operationally separable (Cohen and Bonnet, 1972).

The object of experiment 2 is to study this task when subjects make a microsaccade in between the two flashes constituting the stimulus. However, such a microsaccade will not be produced in the absence of a continuously visible target and this raises a further problem because if such a target is visible, judgements of spatial direction might be made relative to it. The experiment reported here investigates the possibility that a location task involving two briefly flashed stimuli in the centre of a large uniformly illuminated screen will be carried out without making use of the screen as a spatial reference for the judgement. It is known (Steinman, 1965) that subjects viewing such a target will make microsaccades, although with a reduced frequency to that obtaining when a central target is fixated.

Method

The subject was presented with the stimulus pattern shown in Fig. 1; the upper line was flashed on briefly, followed at a time t later by the second line which was also flashed briefly and could be positioned either to the right or to the left of the first line. The subject made a two choice judgement, indicating by pressing one of two buttons whether the second part of the stimulus appeared to be on the right or the left of the first.

The stimulus was generated in the centre of the screen of a Tektronix Type 602 display oscilloscope. The screen area was 10 × 8 cm, and the screen was placed at a distance of 180 cm from the subject; thus the visual angle subtended by the screen was 3·2° × 2·5°. The visual angle subtended by each stimulus line was 6′. The stimuli were produced, and the timing controlled, by an IBM 1130 computer using a WDV interface. The computer also recorded the responses and the response latencies. The line stimuli were produced by generating a sequence of points on the oscilloscope; this process took about 1 msec and the decay time of the phosphor (P31) has a value similar to this.

In this experiment, two conditions were investigated. In the first, termed the "Light" condition, the whole screen was uniformly illuminated at a level of 30 cd m^{-2} by a separate tungsten light source. In this condition the stimulus lines had a luminance estimated at 45 cd m^{-2}. In the second, "Dark", condition, the tungsten light was absent and the intensity of the stimulus lines was reduced to about 0·8 cd m^{-2} at which level there was no noticeable afterimage. In the Dark condition the oscilloscope beam was shifted off screen, but not blanked. This had the consequence that the screen was visible as a faint, diffuse, phosphorescent patch (luminance 0·05 cd m^{-2}). Unless this was present the absence of any stimulus for approximate accommodation or location prevented subjects from carrying out the task. Reasons for believing that this condition is equivalent to one of complete darkness are presented later.

Procedure

In each session the computer presented the subject with 50 practice stimuli followed by 250 test stimuli, which consisted of five presentations of each combination of five values of t and 10 values of d, the distance separating the lines. The values of the time interval were multiples of some basic unit, (e.g. 100, 200, 300, 400 and 500 msec), and the values of d were equally spaced and distributed evenly to the right and the left of the first line. Stimuli were presented at intervals of about 3 sec, with a warning click preceding each stimulus by 0·5 sec. The sequence was randomized by the programme. Viewing was binocular (pilot experiments showed virtually no difference between binocular and monocular viewing).

Fig. 1. Details of the target used in the experiments.

Subjects

Three subjects were used (one being the author). All had normal or corrected vision.

Results

From two sets of 250 stimuli, a set of psychometric curves was constructed for each value of t by plotting the proportion of trials on which the second stimulus was judged to be on the right against the value of d. From such plots, the best straight line fit when plotted in probability co-ordinates was derived (using averaged z scores, Woodworth and Schlosberg, 1954 p. 205), and a measure of the slope taken, denoted d_{75}, which corresponds to one half the distance between the values of d for 75 per cent left judgements and 75 per cent right judgements. Thus for a subject with no systematic bias, presentation of a stimulus with the two lines separated by a distance of d_{75} should result in 75 per cent correct responses in either direction. This procedure was repeated for each value of t used and the results from a series of experiments are presented in Fig. 2.

Discussion

As would be expected, the longer the time elapsing between the two parts of the stimulus the more difficult the task becomes. This is shown in Fig. 2 by the steady increase with time in the curves for both the light and the dark conditions. A very similar experiment to the present one was carried out by Matin, Matin and Pola (1968). Their experimental situation was essentially identical to the dark condition of the present one except that they used a totally dark surround and circumvented the fixation problem to some extent by the use of a fixation point which was extinguished shortly before the first stimulus line. The results they obtained are both qualitatively and quantitatively similar to those obtained in the dark condition, which encourages the conclusion that the vestigial surround present in that condition does not influence the results. One purpose of the experiment was to establish the effect of the screen surround. It appears from Fig. 2 that for values of t below about 350 msec the surround does not assist the judgement, and thus it may tentatively be assumed that in this region the judgements are made solely with reference to the line stimuli.

Movement of the eye on the basis of a random walk

This section considers the results in the light of a

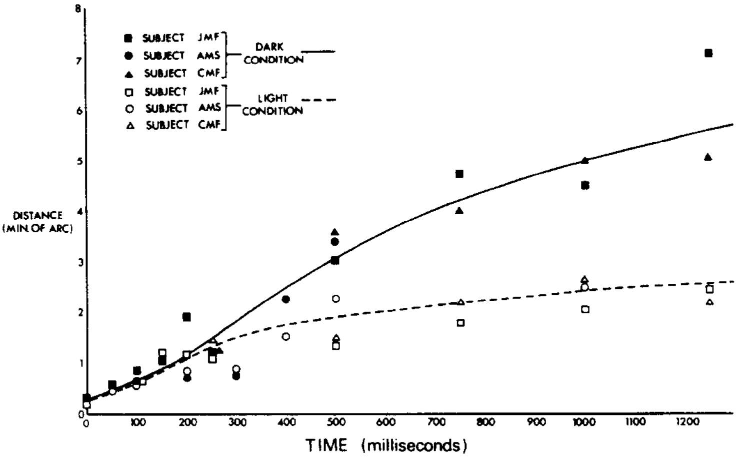

Fig. 2. Results from experiment 1, showing the decrease in accuracy in judging the relative positions of two briefly flashed stimuli as a function of the temporal separation of the stimuli.

semi-theoretical model of the drift movement of the eye, on the assumption that the task is carried out on the basis of accurate information about the retinal position of the stimuli. It has been suggested that the drift movement of the eye is analogous to a "random walk" (Cornsweet, 1956; Matin, Matin and Pearce, 1970); i.e. it can be considered to be the sum of a number of discrete steps of random direction. One way in which this might occur is if the movement is produced by random activity in individual muscle fibres (Findlay, 1971). Let us assume (ignoring such problems as the transformation between eye muscle activation and eye position) that the eye does execute a random walk in which the probability of a displacement of magnitude x (considering only one dimension of rotation) in time t is given by

$$P(x, t) = \left(\frac{2}{\pi k t}\right)^{1/2} \exp\left(\frac{-x^2}{2kt}\right).$$

The proportion of occasions on which a displacement greater than X will occur, and consequently an error in the direction judgement task, is given by

$$\int_X^\infty P(x, t)\,\mathrm{d}x$$

assuming as discussed above that the task is accomplished on the basis of retinal position.

For a given level of errors, this integral will be a constant, e.g. for the 75 per cent correct level discussed above, it will be 0·25. Evaluating the integral, it may be seen that

$$X \propto \sqrt{t}.$$

Thus on the random walk assumption one might expect to find that the distance for 75 per cent accuracy increased with the square root of the time interval between the two parts of the stimulus. It may be noted also that, if no systematic movements are present, this distance will also be the median distance moved by the eye when measured over a series of intervals of duration t.

Accordingly in Fig. 3 the data of experiment 1 are replotted, together with data from Matin (1972). Also plotted are the direct measurements of eye drift made by Riggs, Armington and Ratliff (1954) using a contact lens technique. With the axes used, the points would lie on a straight line if the square root relationship discussed above were obeyed. In fact, although there is reasonable agreement between the three sets of results,

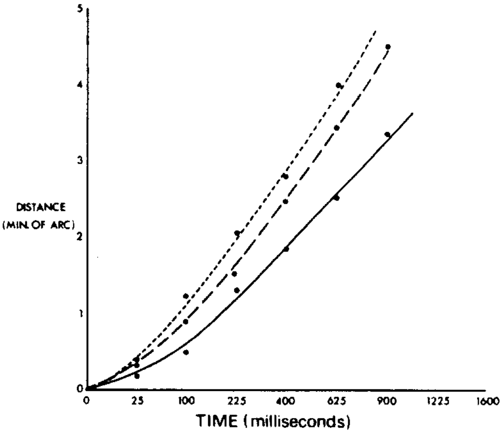

Fig. 3. Accuracy of relative location of two temporally separated stimuli. The axes are such that the movement of the eye predicted on the simple random walk model discussed will generate a linear function. The results plotted are those from the "dark" condition of experiment 1 (dashed line); results from the similar experiment reported in Matin (1972) (dotted line), and direct measurement of eye movement made by Riggs *et al.* (1954) (continuous line). The data in Fig. 16 of Matin (1972) represent a slightly different measurement to the present one and so have been scaled (by a factor of 0·6) to enable direct comparison.

in all cases there appears to be greater displacement at long durations than predicted by the random walk model. This may perhaps be attributable to the presence of a systematic component in the drift, which is variable between trials. It should also be noted that all the investigators used only a small number of subjects, and that the figures from Riggs *et al.* (1954) are of total eye movement in conditions in which microsaccades will occur.

Conclusion

The results from this experiment appear to be in agreement with those of Matin (1972) and provide further support for his view that the principal limiting factor in this type of direction judgement is the drift movement of the eyes. In addition, when the surround frame used in this experiment is visible (the "light" condition), accuracy of locational judgements are improved only for time intervals greater than about 350 msec.

EXPERIMENT 2

The purpose of this experiment is to study the effects of microsaccadic eye movements on judgements of visual direction. The rate of occurrence of microsaccades for most subjects is about 2/sec (Ditchburn and Foley-Fisher, 1967). The results of the previous experiment indicate that judgement of the relative positions of two stimuli separated in time by less than 350 msec is achieved on a "pure location" basis. Thus it was hoped that the use of stimuli of the same form as those of experiment 1, with a 250 msec interval, would provide a task in which a significant number of microsaccades occurred during an absolute judgement of spatial position. Since microsaccades are spontaneous and involuntary, it is necessary to use this apparently inefficient technique in order to study them.

Thus some trials will occur on which the subject makes a microsaccade in one direction, for example to the right, between the two parts of the stimulus. As discussed in detail later, microsaccades have greater magnitude than the stimulus displacements used, and so this will have the consequence that whatever the direction of displacement in the stimulus, the retinal position of the second line will be to the left (with reference to external space) of that of the first. Thus if the task is carried out solely on the basis of retinal position, an error will occur if the physical position of the second stimulus line was in fact to the right of the first. The pattern of errors thus provides a test for the occurrence of compensation for the eye movement.

Method

The same arrangement for the production of stimuli was used as in the "light" condition of experiment 1, but a single fixed value was used for both the distance parameter and the time interval parameter. On the basis of the discussion above, the value of the time parameter was chosen to be 250 msec, although results are also presented with a time of 1 sec elapsing between the two parts of the stimulus. The value of the distance parameter was chosen, on the basis of experiment 1, together with preliminary trials, to be that value at which 75 per cent of the responses were correct judgements of direction. Thus only two different stimuli could occur on any trial, with the second line either to the right or to the left. Equal numbers of each type of stimulus were presented, normally 25 of each type in a run which lasted about 5 min.

The subject's microsaccades were recorded using a photoelectric technique to assess the position of the iris–sclera boundary. The technique, which is described in detail elsewhere (Findlay, 1974), has a sensitivity of about 1′, and any microsaccades with magnitude greater than 2′ can be clearly distinguished. It was necessary to record from the opposite eye to that used for viewing the stimuli, and take advantage of the result that the direction of microsaccades is virtually always identical in the two eyes (Krauskopf, Cornsweet and Riggs, 1960). The eye position signal was recorded on a chart recorder. The occurrence of the stimuli was also recorded on a second track, together with coded pulses (generated by the computer), which enabled each stimulus to be readily identified and compared with the record of the type of stimulus and response.

Subjects

The subjects AS and CF from experiment 1 again served and in addition two other subjects (JE and DH) with normal vision. Unfortunately on account of apparatus difficulties, only a small section of the record from JE could be used.

Scoring

Microsaccades appear clearly on the records, their large magnitude and rapid time course distinguishing them from all other eye movements. Records were scored by noting whether a microsaccade had occurred between the two parts of the stimulus and if so, in which direction. It was, however, necessary to exclude a certain number of the records from further analysis for one of the following reasons: (i) a microsaccade occurred but was co-incident in time with one of the parts of the stimulus; (ii) more than one microsaccade occurred between the stimulus parts; and (iii) a small displacement occurred which could have been either a microsaccade with a small horizontal component, or a large rapid drift. This resulted in the exclusion of about 10 per cent of the data, and in addition certain parts of the record could not be scored because the subject was blinking excessively, or other difficulties were present with the eye movement record. It should be emphasized that this selection was all carried out prior to the comparison of the data with the stimulus–response record, which was recorded separately on the computer printout.

The scoring procedure resulted in all microsaccades with magnitudes greater than about 2·5′ being included. The magnitudes of the microsaccades were also recorded, but no detail is presented with the results here, since no effect of microsaccade magnitude could be found. In part this may be because the magnitudes of microsaccades are not perfectly correlated across the two eyes (Krauskopf *et al.*, 1960; St-Cyr and Fender, 1969).

Results

1. *Occurrence of microsaccades.* The first experimental condition investigated was similar to experiment 1, in that stimuli were presented regularly at intervals of 3 sec, with a warning signal presented 0·6 sec before

each one. The time between the two parts of the stimulus was 250 msec. Two subjects (CMF and AMS) were run. Under these conditions it was found that the subjects both failed almost completely to produce any microsaccades during the stimulus period, although at other times microsaccades were made at a normal rate. This is an example of an effect which has been found in a number of situations and will be reported in more detail elsewhere (Findlay, in preparation). For the purpose of this experiment it was unwelcome as it had the consequence that only on six occasions out of a possible 300 did a stimulus sequence containing a microsaccade occur. Because of this results were taken under two further conditions. In the first of these (C-250-R), the interval between the two parts of the stimulus remained 250 msec, but the warning signal was not presented and the stimuli occurred at intervals varied randomly (by the computer programme) between 2 and 6 sec. This achieved the object in that the subjects made an adequate number of microsaccades, nearly all within the first 100 msec of the stimulus period. In the second condition (C-1000), the interval between the two parts of the stimulus was increased to 1 sec, but the warning signal remained and the interstimulus interval was kept constant. In this condition the subjects also failed to make microsaccades at the beginning and end of the 1 sec period, i.e. when the stimulus was visible. However, on a large proportion of occasions, subjects made a microsaccade in the period between 200 and 500 msec after the start of the stimulus. These results demonstrate the microsaccades, although "involuntary" are nevertheless affected by the stimulus situation through a fairly complex timing mechanism.

2. *Errors in direction judgement and microsaccades.* Each trial was classified into one of four categories on the basis of the eye movement record. These were: (i) no microsaccade occurring during the stimulus period; (ii) a microsaccade to the left; (iii) a microsaccade to the right; and (iv) indeterminate (see scoring section). In addition on each trial just four combinations of the two possible stimuli (second part of the stimulus to the left or to the right) and the two possible responses (left or right) could occur. Table 1 presents, for each subject and condition, the distribution of responses under each eye movement category.

The effect of a microsaccade on the judgement can be assessed by comparing, for each subject and condition, the responses on trials with an intervening microsaccade to those on trials in which the stimulus is identical but no microsaccade occurs. Three possible outcomes of this comparison exist, listed as (A), (B) and (C) below.

(A) The proportion of errors on trials containing a microsaccade is identical to that on trials without one.

(B) For trials with a microsaccade in a particular direction, more responses are made (than to nonsaccade trials) indicating the second part of the stimulus is perceived in the *opposite* direction, (i.e. for microsaccades to the *left*, more "*right*" responses occur).

(C) As (B) but more responses are made indicating that the second part of the stimulus is perceived in the *same* direction as the microsaccade.

If the subjects were judging purely on the basis of retinal stimulation then the errors will tend to be of type (B). An error distribution of type (A) might occur, for example, if the direction judgement was made relative to the surround. Error distributions of type (C) will be discussed later but it may be noted that if (A) is taken as a null hypothesis, then a consistent finding of a significant difference from (A) in the direction (C) will entail also rejection of (B). These comparisons are presented in Table 1.

Table 1. Error patterns in direction judgement task

				Stimulus direction, left				Stimulus direction, right			
Subject	Condition	Distance (min arc)	Response direction	No microsaccade	Microsaccade to left	Microsaccade to right	Other	No microsaccade	Microsaccade to left	Microsaccade to right	Other
CMF	C-250-R	1·7	L	41	4	1	6	23	8	1	4
			R	16	1	1	2	38	0	2	0
					C	C			C*	C	
AMS	C-250-R	1·4	L	39	1	1	6	15	4	0	2
			R	17	0	4	3	51	2	2	2
					C	C*			C	C	
JME	C-250-R	1·8	L	8	0	1	0	1	1	0	0
			R	6	1	0	0	9	0	4	2
					B	B			C	C	
CMF	C-1000	2·8	L	14	20	0	5	5	17	0	2
			R	9	6	0	3	13	19	1	4
					C				C	C	
AMS	C-1000	2·6	L	12	8	2	4	1	6	0	1
			R	13	8	2	9	21	9	11	3
					C	B			C	C	
DH	C-1000	2·7	L	10	2	10	10	2	1	3	1
			R	12	0	18	8	27	4	25	13
					C	C			C	B	

The letters B and C after each set of results on the trials with microsaccades shows the direction of deviation of the error proportions from that in the trials with no microsaccades (see text). An asterisk indicates that the proportions differ significantly at the 5 per cent level.

Table 2. Correct responses and errors on trials with and without microsaccades

Subject	Condition		Trials without microsaccades	Trials with microsaccades	χ^2
CMF	C-250-R	Correct	79	7	4·15*
		Errors	39	11	
AMS	C-250-R	Correct	90	6	2·24
		Errors	32	8	
JME	C-250-R	Correct	17	5	(0·00)
		Errors	7	2	
CMF	C-1000	Correct	27	40	0·01
		Errors	14	23	
AMS	C-1000	Correct	33	30	0·08
		Errors	4	16	
DH	C-1000	Correct	37	41	0·71
		Errors	14	22	

The value of χ^2 for the comparison of the proportion of errors on trials with and without microsaccades is given. An asterisk represents a difference significant at the 5 per cent level.

In the C-250-R condition (i.e. the condition with 250 msec between the stimulus lines) the results clearly fall into pattern (C). In all of the individual cases, except two from subject JE in which only one response was made, the trend is in that direction, and in two of them this trend is significant at the 5 per cent level. In the C-1000 condition there appears to be the same trend, although it is not quite so clearly delineated. Of the error patterns, three are of type (B) compared with ten of type (C). A further breakdown of the results is shown in Table 2, in which the proportion of erroneous judgements is given for the trials containing a microsaccade and for trials without one. In each case the value of χ^2 for the resulting 2×2 contingency table is evaluated. The results demonstrate that in the C-250-R condition, for two subjects the presence of a microsaccade during the stimulus period increases the chance of an incorrect response being made. In the C-1000 condition the error proportions for all subjects are virtually identical for trials with and without intervening microsaccades.

To summarize the most important finding; in trials in which the two parts of the stimulus are separated by 250 msec, if the subject makes a microsaccade during this interval he is significantly more likely to make an erroneous direction judgement which will consist in reporting that the stimulus has moved in the *same* direction as his eye has moved.

Discussion

The argument to be presented rests on the assumption that, on trials with a 250 msec interval containing an intervening microsaccade, the direction of the displacement in the retinal image of the stimulus is determined solely by the microsaccade direction. The justification for this will be outlined first.

Riggs *et al.* (1954) present figures which show that the median drift movement in 250 msec is about 1·2′ (horizontal component), and only on 15 per cent of occasions is a drift movement in excess of 2′ observed. Their figures are supported by the compiled data of Ditchburn and Foley-Fisher (1967). These studies used a central fixation point but Steinman (1965) reports no difference in drift characteristics using a fixation target similar to the present one. The direction of drift is not generally believed to be influenced by the stimulus although many subjects exhibit an idiosyncratic preferred direction (Nachmias, 1961). In the C-250-R condition the stimulus displacements used were between 1·4′ and 1·7′. The microsaccades scored had a minimum magnitude of 2·5′ and a median magnitude estimated at 5′. (All figures refer to the horizontal component.) Thus only for the smallest microsaccades would it be possible for trials to occur in which the retinal stimulus displacement was in a different direction to that produced by the microsaccade and then only if a large drift occurred in the opposite direction. A further possibility which might influence the results would be any correlation between the direction of a microsaccade and that of the preceding or succeeding drift. However, no large effects of this type appear to be present in the author's records or those of other observers. Thus the assumption outlined initially appears tenable and confidence in this conclusion may be enhanced by the finding noted earlier that the pattern apparent in the results remains identical if only large microsaccades are considered.

The results thus indicate unequivocally that something more than the retinal image is used to make judgements of direction in situations in which microsaccades occur; the results are, in fact, the exact opposite of those expected on the basis of retinal stimulation. Consider next the situation resulting if the microsaccade is accompanied by a "corollary discharge" from the oculomotor system to the visual processing system. It may be noted here that Jeannerod and Putkonen (1971) have observed effects in the lateral geniculate nucleus which relate to the saccadic phase of vestibular afternystagmus. One way in which a corollary discharge has been considered to operate is by providing an exact specification of the eye movement so that a precise compensatory shift could be made. In this case, any effect of the microsaccade would be exactly annulled and so trials with microsaccades should be no different from trials without them, resulting in a type (A) error pattern on average. This can be rejected by the present data. Matin (1972), considering the situation with larger voluntary saccades, finds evidence for a compensatory signal which has a longer time course than the eye movement. A similar type of signal occurring with microsaccades would result in type (B) errors in the present experiment.

This also can be rejected, which is of interest since it suggests that, in some respects at least, voluntary saccades and microsaccades possess different characteristics. A corollary discharge signal which overcompensated might produce the observed results. It seems unlikely, however, that a corollary discharge of this type would fulfil the stabilization function assigned to it, and an alternative explanation is suggested.

The results demand an underlying mechanism which produces type (C) errors, i.e. responses to the same direction as that of the microsaccade. Now, it has been appreciated at least since the influential paper of Von Holst (1954) that the function of a corollary discharge could be "suppression" rather than "cancellation". The idea here is that visual information is transmitted in a number of pathways in parallel and when an eye movement occurs it is only necessary to suppress the signals in any channel which arise as a direct consequence of the eye movement, for example a movement sensitive channel. Of relevance here are the elevated thresholds commonly observed in various visual parameters during both voluntary (Latour, 1962) and involuntary (Beeler, 1967) saccades. With some weak additional assumptions, it appears that the present results are most satisfactorily accommodated by this type of theory.

The additional assumptions, illustrated in Fig. 4, are that at some point displacement to the left and displacement to the right are transmitted in separate channels and that these channels are "noisy", i.e. spontaneously active. If a microsaccade results in suppression in the appropriate channel (see Fig. 4) then in the experimental situation a response would be made in favour of the other direction, an argument similar to the explanation of movement aftereffects proposed by Barlow and Hill (1963). That is, a microsaccade to the left would have the effect of suppressing signals indicating displacement to the right (the visual consequence of the eye movement) and result in a decision of displacement to the left. The model of Fig. 4 leads to the further prediction that, if the suppression is complete, the response made would be independent of the actual stimulus. Considering the results from the C-250-R condition (Table 2), some support for this is found. When the results are pooled across subjects, on a total of 39 occasions when a microsaccade occurred, no fewer than 31 resulted in a judgement of stimulus displacement which was in the same direction as that of the microsaccade. On 21 occasions, the response was in the opposite direction to that of the stimulus displacement and on 18 occasions in the same direction.

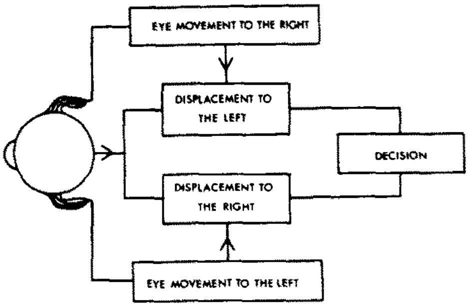

Fig. 4. A model providing a possible explanation of the results of experiment 2. The judgement is assumed to be made on the basis of two hypothetical channels signalling "displacement to the right" or "displacement to the left". The microsaccade has the effect of suppressing activity in one of these channels.

The above discussion refers only to the C-250-R condition. In the C-1000 condition (1 sec between stimulus flashes), the results of experiment 1 suggest that judgements are made with reference to the surround frame, since the subject's performance deteriorates when the frame is not visible. Nevertheless even here, 97 out of 145 trials on which microsaccades occur result in judgements in the same direction as the microsaccade. This result would not be expected if judgement is made relative to the frame, since the microsaccade would displace the retinal image of stimulus and frame equally. An alternative possibility is that judgement with the frame visible is still not made by using the frame directly as a spatial reference, but that the effect of the frame is to allow the eye to maintain more accurate fixation. The microsaccades themselves would fulfil this function (Steinman, 1965; Rattle, 1969).

Conclusion

It has been demonstrated that judgements of visual direction during fixation microsaccades show a systematic pattern of errors. When a microsaccadic eye movement occurs in one direction, errors are made indicating a shift in perceived location in the same direction. This is precisely the opposite result to that expected if the judgement was made on the basis of the retinal image, and to account for it, it appears necessary to invoke some form of corollary discharge.

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Résumé—L'existence de mouvements involontaires de l'oeil durant la fixation pose un problème de localisation dans l'espace visuel. Il est étudié au moyen d'une tâche psychophysique: les sujets évaluent les positions relatives de deux stimulus en éclats brefs sur un écran et séparés par un intervalle temporel. En accord avec le travail de Matin (1972), on montre que la capacité d'un sujet pour comparer deux directions dans l'espace décroît avec le temps. Cette décroissance se produit d'une manière qui suggère que le jugement est obtenu à partir de la position rétinienne seulement et qu'ainsi la correspondance avec une direction externe est sujette à changer avec les dérives des yeux. On enregistrait les microsaccades des mouvements d'yeux du sujet en même temps qu'il exécutait la tâche, ce qui a montré l'existence d'un nouveau phénomène. Quand un sujet fait une microsaccade, les erreurs de localisation correspondent à un décalage de la direction perçue *dans le sens* de la direction de la microsaccade. C'est juste le contraire du résultat prévu si la seule position rétinienne était en jeu. On suppose pour expliquer ces résultats qu'un modèle est basé sur une sorte de décharge corollaire.

Zusammenfassung—Die Existenz unwillkürlicher Augenbewegungen während des Fixierens führt zu einem Problem bei der Beurteilung der Lage im Sehraum. Dies wurde mit Hilfe einer psychophysischen Aufgabe untersucht, bei der Versuchspersonen die relativen Positionen von 2 Testreizen zu beurteilen hatten, die auf einem Schirm kurz und durch ein zeitliches Intervall getrennt aufleuchteten. In Übereinstimmung mit der Arbeit von Matin (1972) wirde gezeigt, dass die Fähigkeit einer Versuchsperson, zwei Richtungen im Raum zu vergleichen, mit wachsendem zeitlichen Intervall abnimmt. Die Art und Weise dieses Abfalls weist darauf hin, dass die Beurteilung nur aufgrund der Position auf der Retina erfolgt und so die Übereinstimmung mit der äusseren Richtung entsprechend den Driftbewegungen des Auges vermindert wird. Daher wurden während der Durchführung der gleichen Aufgabe die von der Versuchsperson ausgeführten mikrosakkadischen Augenbewegungen aufgezeichnet, und das zeigte ein neues Phänomen. Wenn die Versuchsperson eine Mikrosakkade macht, dann zeigen die Fehler in der Lokalisierung, dass die wahrgenommene Richtung in derselben Richtung verschoben wird, in der auch die Mikrosakkade erfolgt. Das steht in genauem Gegensatz zu dem nur aufgrund der Position auf der Retina erwarteten Ergebnis. Es wird ein Modell aufgestellt, das die Ergebnisse auf der Basis einer Art Nachentladung erklären soll.

Резюме—Существование непризвольных движений глаза во время фиксацин поднимает вопрос о локализации в зрительном пространстве. Зтот вопрос был исследован психофнзически методом с наблюдателями, которые должны были судить об относительном положении двух стимулов появлявшихся на зкране на короткое время и разделенных временным интервалом. Показано, в соответствии с работой *Malin* (1972), что способность испытуемого сравнивать два направления в пространстве уменъшается со временем. Зто уменъшение происходит таким способом, который заставляет предполагать, что сужаение основывается только на локализации стимула на сетчатке и, поэтому, соотношение с внешнии направлением подвергается изменению, когда глаз смещается (дрейф). Микросаккадические движения глаза делаемые испытуемым были зарегистрированы в то время когда такие пробы доводили до конца и при зтом обнаруживалось новое явление. Если испытуемый совершает микросаккаду, ошибко в локализации показывает, что сдвиг в воспринимаемом направлении происходит по надравлению Ммкросаккады. Зто прямо противоположно ожидаемому результату получеамому если бы было использовано только положение на сетчатке. Предлагается модель, которая объясняет полученные данные основываясь на форме результирующего разряда.