The literature on human eye movements has been reviewed and summarized by Duke-Elder (1932) and Carmichael & Dearborn (1948); there is general agreement that the most usual type of movement is a rapid jerk, followed by a period of 0.1–0.3 sec during which the eye is relatively stationary, and terminated by another quick movement bringing the eye to a new fixation position. These fixational pauses separated by saccadic movements have led very naturally to a concept that the eye behaves like a camera taking a series of snapshots, the image being held still on the retina for periods of 0.2 sec or longer. Some reports suggest, however, that the eye is moving during the fixational pauses. If the retina behaved like a photographic plate, integrating intensity of light at a point with time, such movements would clearly 'blur' the image before it was transmitted to the brain. It has, on the other hand, been suggested (Marshall & Talbot, 1942) that movements, such as those described by Adler & Fliegelman (1934), occurring within a fixational pause, are functionally important and modify the information which the retina extracts from the image falling on it. Hartline (1938) found that many of the frog's optic nerve fibres only discharged when the illumination of their receptive fields was changed. A small eye movement would shift the image over the retina and change the illumination of all receptive fields covering part of the image which was not completely homogeneous. The corresponding nerve fibres would discharge, and this might form a basis for explaining the accentuation of contours and simultaneous contrast which are normally thought to be brought about centrally. It was hoped that a re-examination of eye movements might help to decide between the concept of the retina taking a series of snapshots, and the concept of continuous scanning.

Various methods have been used to measure and record eye movements. None of them appeared to fulfil all the requirements of this investigation and a new method was developed: the movements in one direction of a small droplet of mercury sticking to the cornea were photographed through a microscope on a moving film. The main conclusions drawn from these records were
confirmed by a method of measuring eye movements by observing the after-image resulting from two successive exposures of a bright test object.

METHOD

A method was sought that would detect the movement needed to shift the image across the retina by the distance separating two cones at the fovea. Hartridge (1947) summarized the literature on the size of the cones, and concluded that this distance subtended about 40'' of arc at the posterior nodal point. The method must also be capable of recording oscillations occurring at 50/sec or more, since Adler & Fliegelman (1934) have reported such movements. The normal condition of the eye should be interfered with as little as possible.

The principle of the method used here is that a small droplet of mercury is placed on the cornea, and the image of a small light formed in the droplet is photographed through a microscope on a moving film. Movements of translation of the droplet in one direction are recorded; to calculate movement of the image over the retina it is necessary that the centre of rotation should be stationary, and this necessitates keeping the head as still as possible. This was done by having the subject lying supine with his head resting on a stone slab let into the wall. A rigid iron frame fitted round the head, and wedges were driven in on one side. The head was thus fixed between the wedges and the frame at the sides, and was resting on the stone slab. In addition the teeth were fixed by a dental impression in gutta percha which was clamped to a crossbar of the frame. This arrangement never stopped all movements of the head, but in the best cases there remained only a slight movement with each heart beat. These movements were recorded at the beginning and end of each experiment by photographing a droplet placed on the forehead or on the bridge of the nose; it is possible that these records overestimate the movements, since contraction of the facial musculature could move the droplet.

Fig. 1. Diagram of recording apparatus. A, lamp; B, objective; C, mercury droplet; D, mirror; E, film; F, eyepiece; G, cylindrical lens.

Droplets of mercury about 0.1 mm in diameter were placed on the edge of the cornea by gently blowing them out of a piece of capillary tube held close to the eye. The subject held his eyelids open to prevent involuntary blinking, and felt nothing when the droplet was successfully placed. Lacrimation and a strong desire to blink usually ended the run in 3–5 min.

Fig. 1 shows the principle of the optical arrangement. A is a small ophthalmoscope lamp run at just sufficient current to expose the film adequately. It caused a rather unpleasant glare for the subject, but was seen in the periphery of the field of view. The microscope objective B is focused on the image of A in the spherical surface of the mercury droplet C. The mirror D enables
the operator to find and focus the image of the droplet using the eyepiece \( F \). The film \( E \) is so placed that the image falls accurately upon it when the mirror is swung aside for recording. The cylindrical lens \( G \) has its conjugate foci on the film and on a 3 mm slit placed at the backstop of the objective \( B \). Movements of the spot of light in the plane of the paper are not affected by the cylindrical lens, whilst movements in the direction of motion of the film (normal to the diagram) are eliminated. The film moved continuously at 25 mm/sec, and the image was photographed at a magnification of 35 ×.

The experiments were done in a darkened room, and the usual fixation point was the reduced image of a small bulb sharply focused on a ground glass screen lying 70 cm from the eye. The intensity was adjusted so that it could be seen clearly, but was not uncomfortably bright. About 1–1\( \frac{1}{2} \) min elapsed between putting the droplet on the eye and starting to record. The droplet was usually wiped off by blinking within 4 min of being placed. Most subjects did not complain of undue discomfort in preventing blinking for this period, but some had great difficulty, and these were discarded.

_Calibration._ The apparatus was calibrated by moving the fixation point through a distance subtending a known angle at the eye. The record consisted of a series of steps as in Fig. 2. The upper record of each pair is taken from the droplet on the eye, the lower from a droplet on the forehead. Since small eye movements occurred within the period when the fixation point was in one position, the final fixation position of the eye was always used, and the distance across the film for each of a number of steps was measured. The interval between the two fixation points subtended 87' at the eye, and the size of the jumps, together with their standard deviations, are given in Table 1. Since the calibrations done on different subjects only varied by a small amount, 9·3/mm was used subsequently for all subjects. A deflexion of the eye of 1' caused a 0·107 mm movement on the film, and this could be measured quite easily when the film was projected at 10 × enlargement. The film moved fast enough to record oscillations at a frequency well above 50/sec.

The method has adequate sensitivity, accuracy and recording speed. There are four disadvantages

Fig. 2. Tracings of calibration records of two subjects. The upper record of each pair shows the movement of the eye when the fixation point is moved a distance subtending 87'. The lower record shows amount of head movement in the same subject, same run, but not simultaneous with eye record. Time scale, 1 sec.

**Table 1.** Calibration by moving the fixation point through 87' and measuring the movement of the trace on the record

<table>
<thead>
<tr>
<th>Subject</th>
<th>No. of steps measured</th>
<th>Mean movement on film (mm)</th>
<th>Standard deviation of steps (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>R.M.</td>
<td>18</td>
<td>8·7</td>
<td>0·9</td>
</tr>
<tr>
<td>E.N.W.</td>
<td>23</td>
<td>9·0</td>
<td>0·7</td>
</tr>
<tr>
<td>I.B.</td>
<td>12</td>
<td>9·3</td>
<td>0·6</td>
</tr>
<tr>
<td>M.P.</td>
<td>26</td>
<td>10·1</td>
<td>1·0</td>
</tr>
<tr>
<td>All subjects</td>
<td>79</td>
<td>9·34</td>
<td>1·04</td>
</tr>
</tbody>
</table>
which remain: (i) movements of the eye of the same type as the residual head movements are difficult to detect; (ii) the subject has to restrain blinking for periods of about 4 min; (iii) the subject's eye is brightly illuminated from the side, causing a rather unpleasant glare; (iv) the image has a tendency to go out of focus and thus parts of each run are missed.

The analysis of the record was done by projecting at a magnification of 10 ×, making the total magnification 350 ×, and measuring the position to within 0·19′ of arc (0·2 mm on the enlargement) at intervals of 4 msec (1 mm on enlargement).

RESULTS

Gross features of the records

Fig. 3 shows a tracing of a record of the eye movements with a portion of head movement record for comparison. The subject was attempting to fixate a small, sharply focused spot of light. It will be seen that the head-movement record is almost a straight line, indicating that the head was well fixed. There is, however, a slight movement with each heart-beat, and this is shown in Fig. 4, where the record has been enlarged. By comparison the eye record shows various types of displacement, and examples of these types of eye movement

![Fig. 3. Tracings of records taken during attempts at steady fixation. (a) eye, blinks; (b) eye small saccadic movement; (c) head. L shows 100′ of arc and 1 sec. of time.](image)

![Fig. 4. Parts of the original record of Fig. 3 enlarged. (a) eye, blink; (b) eye, saccadic movement through 9′ arc; (c) head, wobble synchronous with pulse at the beginning of the record. L shows 20′ (arc) and 0·2 sec (time).](image)
are also shown enlarged in Fig. 4. The large, slow, spike-like displacement occurs when the subject attempts to blink. This was shown by observing the subject's eye, and marking the film whenever a blink was attempted. The smaller, quicker, step-like displacements are similar to the well-known saccadic movements. The record between the blinks and saccadic movements is almost as smooth and straight as the head record, indicating that the eye is moving little during these periods.

In many of the early experiments where the subject was attempting prolonged accurate fixation on a small point, records similar to Fig. 9 (a) were obtained. The conditions where they appear were never fully elucidated, but they occurred much less often in later experiments. By this time the subjects had become accustomed to the procedure, the experiments themselves had been made less uncomfortable, and recording was confined to the period from 1 to 4 min after placing the droplet. Some subjects never gave records of this type, and even those who did in the early experiments failed to do so when experiments were done to determine the conditions under which they appear. Only when the subject had been fixating continuously for 3 or 4 min without blinking were records approaching this degree of irregularity obtained. All that can be said then is that they occurred in some subjects after prolonged attempts at accurate fixation with restraint of blinking.

Saccadic movements

The rapid movements in Figs. 3 and 4 must be genuine movements of the eye in its socket, and are similar to those described in the literature as saccadic movements, but of smaller amplitude. The duration of each twitch is about 0.04 sec, and it varies surprisingly little with the size of the movement. Fig. 5 shows several examples of these saccadic movements from different subjects performing different tasks. Both the amplitude and frequency of the move-

Fig. 5. Tracings of records showing saccadic movements in various subjects performing various tasks. (a) I.B. Two-point discrimination. (b) M.P. Attempting to fixate exactly on fixation mark. (c) E.N.W. Looking at a photograph which was revealed at the arrow. L shows 100' (arc) and 1 sec (time). The heads were well fixed in all these runs.
EYE MOVEMENTS DURING FIXATION

Attempts were made to correlate these variations with changes in the fixation mark, but they were not successful. Fixation on a small red point on a black background, a black point on a white ground, a cross on a white ground, and even a specified part of a photograph all gave approximately the same pattern of movements. Fixation on a point so placed that extreme upward deviation of the eyes was required impaired the steadiness of the fixational pauses slightly, but the pattern of saccadic movements was hardly affected.

It was noticed, however, that a change to a new fixation point was almost invariably accompanied by an increase in the frequency of the saccadic movements. A new type of fixation point was perhaps most effective, but changing the position also evoked a fresh outburst of movements. The rapidity with which the frequency of movements declined was extremely variable, but after 30 or 40 sec continuous 'fixation' on a small point there might be periods as long as 5 sec without any rapid jerking movements. It might be suggested that these movements are adjustments in the position of the eye which are made less frequently as the eye becomes more accurately fixed on the target. This is not likely, because, although the saccadic movements become less frequent, irregular wobbles and attempts to blink become more frequent. Furthermore, all that it is possible to see of these simple fixation points is seen within the first few seconds, during the period of greatest saccadic activity; if 'accurate fixation', judged subjectively, occurs later, it is of little physiological interest, for it does not then correspond to the period when information is being extracted from the retinal image most effectively.

It was thought that the interest of the subject in the task he was asked to perform might be an important factor determining the frequency of movements. Fixating a small light is, to most people, a dull and tedious procedure; it is extraordinarily difficult to maintain one's attention on the task for any length of time. The reduction in number of saccadic movements might be connected with this withdrawal of attention. This concept accounts, in a general way, for the variation in frequency. As soon as the visual task is changed, saccadic movements appear more frequently. Changing the fixation point as in Fig. 2 is one example. Placing a second point of light close to the fixation point, and asking if they can be resolved, is another (Fig. 5 (a)). Asking the subject to indicate, by pressing a bell-push, when he is satisfied that fixation is accurate, is another (Fig. 5 (b)). Tasks which capture the attention, such as showing a photograph, immediately produce a burst of saccadic movements (Fig. 5 (c)). They are also known to occur during reading. On the other hand, they occur less frequently when the attention is withdrawn from the visual field. In Fig. 6 the subject was looking at a photograph. At the second arrow he was asked to perform mental arithmetic, and at the third arrow he had got the answer. During the period during which his attention
was on the mental arithmetic it was, presumably, withdrawn from the visual field, and there was a striking reduction in the saccadic movements. In other subjects this effect was not so marked, but it was usually detectable. On the other hand, some subjects were undoubtedly able to inhibit the movements, for a few seconds at least, by making a strong effort to fix on a point in the visual field.

To summarize, the saccadic movements tend to occur whenever the eye is in use; they occur less frequently both when an attempt is made to keep the eye on a point, and when attention is withdrawn from the visual field. They occur more frequently whenever a change is made in the visual task demanded of the subject.

![Fig. 6. Withdrawal of visual attention. Tracings from a record using corneal reflex method. No time interval between the lines. (a) Photograph revealed; (b) subject told to multiply 14 x 12 in his head; (c) subject signals that calculation is completed. Head was well fixed. L shows 300' (arc) and 1 sec (time).]

**Fixational pauses**

The periods between saccadic movements are known as fixational pauses. Inspection of the records shows that the eye is not always stationary, but the steadiest pauses show little more movement of the eye than of the head. Fig. 7 shows an analysis of four periods of 0.4 sec duration from four different subjects. A steady period was found in the record and the position of the trace measured at intervals, as described previously. Two of the records are shown in Fig. 8. Fig. 7 represents frequency distribution diagrams for the positions of (a) the eye, (b) the head; the zero point is the mean of the 100 measurements of position used to make each figure. The breadth of these diagrams gives an indication of the amount of movement of the mercury droplet on the eye or on the head during the period of measurement.

Clearly the movement of the head will also move the eye if this stays still relative to the head, but it is probable that the head is rotating about an axis much farther from the droplet than the axis of rotation of the eye. The range of movement of the eye indicated in these diagrams is therefore likely to be an overestimate of the actual rotation of the eye, and it is clearly rotation which moves the image over the retina. It will be seen that even the measured movement is very small; if the retina was replaced by a photographic plate,
the blurring of the image in this ‘exposure’ of 0·4 sec would be of the same order as that caused by diffraction and chromatic aberration in the lens. For about 65% of the time, the image is displaced by less than half a cone’s breadth in either direction.

Fig. 7. Diagrams showing frequency of occurrence of various deviations from mean position for eye and head in four subjects. 100 measurements at 0·004 sec intervals for each diagram. Mean position is zero on abscissa.

An attempt to correct for head movements was made by measuring the variance of the head and eye records. The figure for the eye record represents the sum of the variance of head alone and eye alone, and the variance for the eye alone can therefore be estimated by subtracting the head record variance from the eye record variance. This correction depends on the assumption that the eye movements are independent of head movements under the conditions considered. It reduces the estimate of the root mean square of the deviations from the mean from 0·37' to 0·25'.

The above results show that the eye is capable of keeping very still. They do not show that it does keep still within a fixational pause under ordinary conditions of use. Many of the fixational pauses show far more movement; Fig. 9 shows records of three types of movement within a fixational pause.
Steady drifts were frequently found after a big saccadic movement, and were usually in the direction opposite to that of the preceding saccadic movement. The rapid vibrations were seen on three separate occasions in one subject, but
were rarely of comparable amplitude in other subjects. Even in this subject they were not constantly present (compare Fig. 8 (a)). Slow oscillations have already been mentioned.

An attempt was made to see if these movements occurred while the subject was performing various tasks. Unfortunately the droplet almost invariably went out of focus under these conditions; possibly the increase in saccadic movements resulted in an increase in the tension of all the rectus muscles, thus pulling the eye farther into the orbit. Furthermore, visual acuity seemed to be uniformly poor under these conditions, presumably because the subject was not comfortable, and was not allowed to blink freely. For these reasons the results of these experiments were not satisfactory, but Fig. 8 shows two fixational pauses which are very still, taken while looking at a small photograph and while resolving two points of light subtending 3·5'.

It will be observed, however, that the eye moves considerably for the first few hundredths of a second in all the fixational pauses, and this must be borne in mind when considering the probable responses of the more rapidly acting pathways.

**Scatter of fixation positions**

Although the eye is held remarkably steady during a fixational pause, it is quite clear that the fixation position tends to be different for successive fixational pauses. This appears to be so even when the subject is asked to fixate a small point, and when he thinks that he is doing so successfully. The extent of this shift in position has been estimated in a number of ways. Consider first the original calibration of the apparatus, where a small fixation point was moved through a measured distance, and the distance the mercury droplet moved was measured on the film. This distance was found to vary considerably. This may be attributed to the scatter of fixation positions; the image of the fixation point was not returned to the same place on the retina when the eye followed the fixation point across the field of view. An estimate of the amount of scatter can be made from the figures in Table 1. Using the calibration for each subject, we can express the standard deviation of the measured jumps in minutes. On the assumption that each of the two fixation positions is an independent choice from the population of fixation positions, the standard deviation of the population is obtained by dividing this figure by $\sqrt{2}$. This gives 6·4' (R.M.), 4·8' (E.N.W.), 4·0' (I.B.), 6·1' (M.P.), of arc.

These estimates could be criticized on several grounds, and a more direct experiment was therefore attempted. The subject was asked to press a button, and thus mark the film, during the periods when he was satisfied that he was fixating the point accurately. The record was then measured and a set of figures for the position of the eye at the beginning of a series of such periods was obtained. In the only successful experiment the fixation positions were scattered with a standard deviation of 6·5'. Some of this scatter is contributed
by movements of the whole head which unavoidably occur during the minute or longer required for such an experiment. The amount of head movement was estimated by repeating the same procedure whilst recording from the head; the variance of head position during signalled periods was subtracted from the variance for eye-position, and this correction reduced the estimate of the scatter of fixation positions to 5·2'.

There is, finally, a third method of estimating the extent of this scatter of fixation positions. Saccadic movements occur in periods when the subject is satisfied that fixation is accurate. If these represent a random change of fixation within the area of scatter, then the size of such saccadic movements should be related to the area of scatter. Forty-one saccadic movements have been measured in periods of subjectively satisfactory fixation in three subjects. The root mean square of the size of jump was 5·7', and this would correspond to a standard deviation of fixation position of 4·0'. A correction for head movement is unnecessary, because it cannot move appreciably during the time occupied by a single saccadic movement.

After-image experiments

The results provided by the technique so far described point to the following conclusions:

(a) The eye moves very little during each fixational pause.
(b) It is difficult to reproduce fixation on a point with an accuracy greater than 5'.

The discomfort of the subject, the possibility of the mercury droplet shifting, the restraint of blinking, the residual head movements, and the selection of the records before measurement or reproduction, must all raise some doubts about these conclusions. An attempt was therefore made to check them by using an entirely different method, a comfortably seated, freely blinking subject, and a strict statistical technique.

The eye was briefly exposed twice to a brightly illuminated test object. An after-image resulted from each exposure; if the eye was in the same position for each exposure the after-images would be coincident, but if it had moved during the interval the after-images would be displaced relative to each other. The extent of this displacement was measured by matching the after-image to an adjustable replica of the original test object, and so the extent of the movement which occurred in the interval between the exposures could be estimated.

Preliminary experiments had shown that a misalignment of $\frac{1}{2}'$ could be detected easily in the after-image of a vernier test object, provided that the after-image was sufficiently intense, and the break lay close to the fovea. In order to detect small movements of the eye during a fixational pause the two halves of a horizontal, straight, brightly illuminated line were briefly exposed
one after the other within the period 30–150 msec following steady fixation of a small red point at the centre of the line. Small vertical movements of the eye occurring in the interval between the two exposures caused an apparent misalignment of the two halves of the straight line, and the subject could examine this misalignment at his leisure in the after-image.

The subject sits in front of the apparatus shown in Fig. 10. A lens L casts an image of a carbon arc A on to the artificial pupil E, to which the subject applies his eye. It was found that he could centre his pupil on the artificial pupil by using visual cues, and he then steadied his head by resting his chin on his hands. The subject sees the lens in Maxwellian view, but a blackened glass plate P lies just in front of the lens. This plate has a fine, straight, horizontal line scratched across it, and on looking through E the subject sees this line brightly and evenly illuminated. Between this fixed plate and the lens lies a shutter S. This consists of an opaque plate suspended by a thread; on releasing the thread it falls freely through the required distance until it is arrested by a stop. Three holes are cut in the plate so that:

(i) Before release a pinhole covered with red cellophane allows light to pass through the centre of the straight line on plate P. This is used as a fixation mark by the subject.
(ii) 30 msec after release the left half of the line on the plate is exposed for 20 msec.
(iii) 130 msec after release the right half of the line is exposed for 20 msec.

The plate is arrested in a position where it obscures the whole line, and the subject therefore sees nothing after an exposure. The subject often detected a slight misalignment of the two halves. Most subjects agreed that the misalignment was seen more clearly when the after-image was deliberately inspected than when the subject tried to recall the fleeting impression he had during the exposure.

This apparent misalignment in the after-images of the halves of the horizontal straight line is presumably due to a vertical movement of the eye occurring in the interval between the exposures. In order to estimate the extent of this movement an adjustable vernier was set up at a fixed distance from the subject, who then tried to adjust this vernier until it matched the after-image

as closely as possible. The vernier was a black line on a white ground, and the negative after-image resulting from the exposure was made visible by switching the light illuminating the vernier on and off.

The accuracy of this estimation had to be carefully controlled, for the point of interest was the misalignment of the after-image, and this might have been obscured by errors in matching the vernier to it. The errors of the matching process were determined by altering the shutter and the fixed glass plate so that the nature of the after-image was accurately known. First a shutter was fitted which gave a single exposure of the whole line. The subject matched the vernier to a series of after-images which must, under these conditions, have been straight. Then the fixed glass plate was replaced by a plate having a vernier scratched on it, the single exposure shutter remaining in place, and under these conditions the after-image was always displaced by a constant and known amount corresponding to the angle subtended by the vernier scratched on the plate. This angle was 1-4', which was larger than the majority of the displacements observed with the double exposure shutter. The means and standard deviations of the settings obtained under these conditions enable one to estimate the errors in matching the vernier to the after-image.

Some further precautions should be mentioned. We are interested in getting an estimate of the amount of movement occurring in an unselected fixational pause when the subject is fixating a small point. The subject obviously had to know approximately when the exposure would occur, but it was thought desirable that he should not anticipate the exact instant. He therefore signalled when he was ready, and the observer released the shutter at the moment when the second hand of a clock passed the second division after he had signalled. The exposures were therefore randomly distributed in the interval more than 1 sec and less than 2 sec after he had signalled. The subject was never told which combination of plate and shutter was being used, but in fact he usually became aware of the improved consistency in the appearance of the after-images during a control series of observations. An attempt was made to prolong the interval between the exposure of each half of the straight line, but observations made with a shutter which moved the illuminated part of the line at an even rate from left to right indicated a rather consistent tendency for the eye to move after about 120 msec. This was attributed to a reflex movement resulting from the exposure of the first part of the line, and observations were therefore restricted to a period before this could interfere. It is conceivable that an oscillation at 10/sec or a multiple of this frequency might return the eye to its original position during the interval between the exposures of the two halves of the line. Observations with the shutter just mentioned had not revealed any such oscillation, which would have shown as a wobble in the after-image of the straight line, and a further check was provided by the use of a plate which gave a 75 msec interval between the exposures of the two halves of the straight line. This shutter gave results indistinguishable from those obtained with the 100 msec plate and in the final analysis the results were mixed. One subject was eliminated because his controls were unsatisfactory. The results of the remaining three, all of whom were normal-sighted people in good health who performed well on the controls, were consistent with each other and were mixed in the results presented in Table 2. Occasionally the subject was

<table>
<thead>
<tr>
<th>Object observed</th>
<th>Exposure</th>
<th>No. of exposures</th>
<th>Mean displacement in after-image (minutes)</th>
<th>Standard deviation of displacements (minutes)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Straight line</td>
<td>Single</td>
<td>58</td>
<td>0</td>
<td>0-31</td>
</tr>
<tr>
<td>Vernier of 1-4'</td>
<td>Single</td>
<td>51</td>
<td>1-3</td>
<td>0-29</td>
</tr>
<tr>
<td>Straight line</td>
<td>Half lines successively</td>
<td>85</td>
<td>0-07</td>
<td>0-54</td>
</tr>
</tbody>
</table>

Table 2: Estimation of movement of the eye within 75 or 100 msec by after-image method

dissatisfied with a match, which was therefore discarded. In eight out of ninety-three observations with the divided shutter one half-line of the after-image was noticeably broader than the other, and it was usually displaced a long way. These were thought to be the result of a saccadic movement occurring during the exposure, and they were rejected because an estimate was required of the movements occurring during a fixational pause.
Table 2 shows the results obtained. The mean of the readings taken when the after-image was known to be a straight line was taken as zero displacement. The difference between this figure and the figure for any other reading was taken as the apparent displacement of the vernier for that observation. These displacements are given as the angles they subtended at the subject's eye.

The scatter of the readings with the double exposure shutter is 0·54'. This is the standard deviation of the figures obtained by observing the difference between two positions of the eye, neither of which is the mean position. If one regards the two positions as independent choices from the population of eye positions, one can obtain the standard deviation of the population by dividing by √2. This gives 0·38'. Some of the scatter, however, is contributed by errors of the matching procedure, and this can be corrected for by subtracting the variance of the control readings. This correction reduces the estimate of the standard deviation of the eye from its mean position to 0·31'. The measurement of the records, after correction for head movements, gave an estimate of 0·25'.

These results confirm the conclusion tentatively arrived at by the other method. During use the eye is held still for short periods; the unsteadiness during these periods is not sufficient to 'blur' the retinal image appreciably, and there is no evidence for any kind of 'scanning mechanism' within the fixational pauses.

After-images have also been used in an attempt to confirm the estimate of the scatter of fixation positions obtained by direct measurements of the records. For these experiments a brightly illuminated line, the image of which fell in the parafoveal region, was briefly exposed while the subject attempted accurate fixation on a small red spot. The subject attempted a second fixation, and a second exposure was made. The after-images of the lines would only be coincident if the two fixation positions were the same, and the separation of the lines could be used to measure the discrepancy (in one direction only) between the two fixations. Only one subject has so far given satisfactory controls, and his results indicated that the distribution of fixation positions had a standard deviation of 6·3' in the vertical direction. Other subjects have given lower figures, but their controls have shown that they consistently underestimate the separation of the after-images, and until this difficulty has been overcome these results cannot be considered decisive.

DISCUSSION

The records which have been reproduced and analysed in this paper have been selected from several hundred feet of film. It would have been possible to show examples of almost all the types of movement that have been described in the literature, and it is reasonable to doubt that the steady fixational pauses separated by rapid saccadic movements are the most important functionally.
The records which differ most from the ‘typical’ records shown in Figs. 3 and 4 are those showing large irregular wobbles, as in Fig. 9 (c). Movements of this type have been described by Lord & Wright (1948), and there can be little doubt that they do occur in supine subjects asked to fixate a small point. The reasons for believing that they may result from fatigue, discomfort, or failure of visual attention, have already been given, but the possibility that they are functionally important has certainly not been eliminated.

Another type of movement that has been observed is the 50/sec vibration described by Adler & Fliegelman (1934). Many records showed a trace of ‘underdamping’; after a saccadic movement there was an overswing followed by a rebound, and occasionally the sequence was repeated for another cycle at a reduced amplitude. The tendency to show an underdamped oscillation of this type was possibly greatest in the younger and more energetic subjects, and one in particular showed them on three separate occasions. The oscillation sometimes persisted for many cycles and sometimes developed in the middle of a fixational pause. Fig. 9 (b) shows a period where the oscillation reached an amplitude of 3’. This subject was an apparently healthy undergraduate who neither smoked nor drank excessively. He showed no tremor in his hand, and there was no suggestion of neurological disease, excessive anxiety or hyperthyroidism. His vision was 6/6 in both eyes tested with a Snellen test chart. Examination of other records showed that a small, sustained tremor was not infrequent (see Fig. 8), but except in this subject it was never more than 1’ in amplitude (peak to peak) and rarely as large as this. The small amplitude and inconstant appearance do not support the suggestion of Marshall & Talbot (1942) that it is important in achieving good resolution.

Another type of movement commonly occurring within a fixational pause is a slow drift. It might be suggested that this is a deliberate movement analogous to the type of movement done by the fingers in feeling the details of the shape of an object, or testing the smoothness of a surface. Furthermore, the movements of the eye have been recorded in one direction only, and it is possible that when the record is straight the eye is moving in a direction perpendicular to this. Two arguments can be advanced against this suggestion. First, the occurrence of drifts in the eye movement records was on one occasion correlated with the appearance of movement of the fixation point (autokinesis); this phenomenon does not occur under normal conditions, and the correlation suggests that drifts are abnormal also. Secondly, calculations show that a steady linear drift of 2.5/sec in a random direction would account for the whole of the observed movement in the after-image experiments designed to detect movements within a fixational pause. This is equivalent to a movement of a point on the image over 3.5 cones/sec in the fovea and is unlikely to be important during a short fixational pause.

The experiments designed to test how accurately the eye was retrained on
a given fixation point indicated that individual fixation positions were scattered around a mean fixation position with a standard deviation of about 5' measured in one direction. The three methods of deducing this figure by measurement of the records agreed reasonably well, but it might be objected that the subject was not placed in the most favourable circumstances for performing a delicate neuromuscular task. The after-image experiment designed to test this point gave a figure of 6', but there was only one successful subject, and he had not had a great deal of practice. Possibly the scatter of fixation positions might be reduced, but there is a considerable difference between the accuracy of re-fixation, and the accuracy with which fixation is maintained within a single fixational pause. This contrast is less remarkable if one considers the possibility that the nervous system treats the volley of nerve impulses resulting from each fixational pause as a separate unit. A steady image would be required to make full use of the temporal and spatial summation occurring in the retina, but there would be no need for the eye to be held steady in exactly the same position during the next fixational pause; indeed it might be advantageous to move the image to a new position on the retina to avoid adaptation or fatigue of the receptors. Polyak (1941) describes a 'small central island, measuring not more than 100μ across, where the cones are thinnest and practically uniform'; this subtends 20', and the observed scatter of fixation positions would be large enough to disperse the positions of the image of the fixation point over this area, but small enough to ensure that the image rarely fell outside it.

These experiments have given no support to any hypothesis postulating scanning movements within a fixation pause. Indeed the speed of the movements and steadiness of the fixational pauses are the most remarkable features of the records. The retina will be receiving a stationary image for the majority of the time, and this may indeed be necessary for it to function properly. This would certainly be consistent with various types of reflex movement made by the eye, such as the labyrinthine reflexes. These seem to be aimed at keeping constant the orientation of the eyes and the images of distant objects are thereby kept in the same position on the retina. Reflex following movements obviously do the same thing for moving objects.

The necessity of a steady retinal image seems to fit in well with a number of familiar observations, such as the movements of a pigeon's head as it walks over the ground, and the quick, jerky movements of a bird's head when it is looking around. This is suggestive of the saccadic movement-fixational pause pattern of movements in the human. A visit to the zoo is sufficient to convince one that movements of this type are common amongst all vertebrates. I have seen them, for example, in a young crocodile, and they are particularly obvious in a vegetarian lizard, Uromastix acanthinurus. Animals with non-foveate retinae usually make few spontaneous eye movements (Walls, 1942), but a rudimentary form of saccadic movement can perhaps be identified when the

visual attention of a toad is aroused by an edible object; it performs a succession of rapid but separate adjustments in its position, the movements being separated by stationary periods lasting one or two seconds, until it is in a position to strike. A pointer attached to the toad would trace a record remarkably similar to those of Fig. 6, slowed down to half or quarter the speed.

It was suggested in the introduction that the eye might either work like a camera, taking a succession of snapshots, or that the image might be moved deliberately over the retina in order to facilitate the extraction of certain types of information. The evidence that has been produced indicates that the first alternative is correct, in which case the fixational pauses must be regarded as the units from which visual sensations are built up, in the same way that a cinema film is built up of individual frames.

SUMMARY

1. A method is described for measuring the movements of the human eye by photographing the movement of a droplet of mercury placed on the cornea. The method is sensitive to rapid rotations of less than $\frac{1}{2}$' amplitude.

2. The records showed many types of movement, but when visual attention was aroused, and the subject was reasonably comfortable, the usual pattern of saccadic movements separated by fixational pauses was found.

3. Selected fixational pauses showed very little movement; the r.m.s. deviation from the mean position during 0-4 sec was 0-25' of arc.

4. When the subject was fixating on a small fixation point the individual fixation positions were found to be scattered round a mean position with a r.m.s. deviation of about 5' of arc.

5. A method is described of checking the last two points using after-images. The results confirm the figures obtained by direct measurement of the records.

This work was done when I held a Research Studentship from the Medical Research Council. I would also like to thank Prof. Adrian who suggested the work, and the subjects who remained patient and co-operative under somewhat exacting conditions.

Note added in proof. Since this paper was prepared for publication I have seen papers by Ratcliff & Riggs (1950) and Ditchburn & Ginsborg (in preparation). My results agree substantially with theirs.

REFERENCES