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Research Report

VISUAL ILLUSIONS OF MOVEMENT *

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SUMMARY PAGE

1. It is shown that these illusions are related to involuntary eye movements, occurring either spontaneously as in the autokinetic illusion, or in response to the special stimuli associated with the other two illusions.

2. During fixation the visual sensation of movement seems to be produced by, or related to, the pattern of efferent activity aimed at the group of extraocular muscles which will act as antagonists to the involuntary eye movement referred to.

3. Under certain circumstances, when the stimulus change is rapid, an eye movement may be detected before the fixation reflex has time to operate.

4. Since the sensation can be caused by the pattern of antagonist efferent activity, it can arise during fixation with no demonstrable responsible eye movement.

5. The displacements of a visual after-image, as a result of the involuntary eye movements, are predominantly in the direction of agonist activity.

INTRODUCTION

In the three illusions considered in this report there is an appearance of movement or displacement of the visual field with respect to an observer. The autokinetic illusion, which refers to the apparent wanderings of a small light source observed in an otherwise dark environment, seems to be unrelated to any acceleration stimuli whatsoever. On the other hand, the oculogyral illusion arises when the observer experiences the stimulus of angular acceleration. Again this illusion is best seen when one looks at a small light source in an otherwise dark environment. By comparison, the oculogravic illusion, which is linked with the stimulus of linear acceleration, can be seen under any condition of illumination, although it too is best seen in the dark.

Since in each instance the illusion is observed during the visual fixation of a target or light source, it might seem that eye movements could be dismissed as a causal factor. Indeed, with regard to the autokinetic illusion the most generally accepted view is that there is no evidence of eye movements being responsible.

Of the earlier reports, that of Guilford and Dallenbach (14) gives a critical review of the theories held, and, in addition, after a series of photographic measurements of eye movement in which they were probably not able to detect changes smaller than one degree, they concluded that eye movements were not essential for the phenomenon. The slight tremors which they did record were considered to be too irregular and limited, to account for the illusory movement. Since this result was obtained apparently on only one subject, Graybiel and Clark (10) re-examined the problem, first, with a special target which became blurred if not fixated closer than 1-2 degrees, and secondly with the superposition of a real target and visual after image. By this means it was possible to detect subjectively much smaller movements, since these were seen as displacements of an after-image across the retinal image of a very small target. Their conclusion too, was that the autokinetic illusion could appear in the absence of appreciable movement of the body, head, or eyes.

More recently, Gregory (13) made use of the fact that the central fovea is blind to weak stimulation by far blue light to create a subjective demonstration, which again revealed no eye movement associated with the autokinetic phenomenon.

Although there is not such unanimous agreement as regards the role of eye movement in the production of the oculogyral illusion, yet the general consensus is that while eye movement may account for part of the illusion, it does not account for the entire phenomenon. For example, in 1946, Graybiel and Hupp came to the conclusion that a large part of this phenomenon was associated with nystagmus, whereas in 1954, van Dishoeck, Spoor and Nijhoff, referring particularly to the later stages of the illusion, showed that here at least one could experience the visual sensation of movement without any demonstrable eye movement, nystagmus apparently having stopped. These two views have to some extent been reconciled in a paper by Byford (4) who, by means of a contact lens and light source recorded eye movements, achieving a maximal sensitivity of 45" of arc per centimetre of trace deflection. He further employed a modification of this technique to present two of his subjects with a retinally stabilised image, and concluded that with a marked labyrinthine stimulus there was a small initial illusory displacement associated with eye movement, but that during slow continuous acceleration, the smooth undirectional illusory movement of the target was not associated with any demonstrable eye movement. Subjects employing a retinally stablilsed image likewise saw this displacement in the same direction as the fast phase of nystagmus.

While the two previous illusions have received much attention in the past, the same cannot be said of the oculogravic illusion, the investigation of which tends to be limited to experiments on the human centrifuge or in flight. None the less, the investigations in this field do show that, as in the previous two illusions, there is no demonstrable eye movement associated with the phenomenon. Graybiel (12) employed the technique of superimposing a visual after-image and real target while seated in a fixed end barrier facing the center of the centrifuge. The fact that the after-image and real target remained superimposed and that both appeared to rise during the increase in g, was taken as strong proof that the oculogravic illusion was not due to eye movement.

Under special circumstances, however, eye movement may occur. Thus, Niven, Whiteside, and Graybiel (20) have shown that, if a subject is suddenly exposed to a change from 1g to 0 g, the direction of acceleration being kept constant, he experiences an illusion (elevator illusion) which is associated with an involuntary upward deflection of the eyes. This eye movement can be considered as being due to the fact that the change from 1 g to 0 g has taken place so rapidly that the fixation reflex has had insufficient time to correct the reflex movement produced by the otolithic stimulus.

It is thus evident from the literature that in these three illusions the visual sensation of movement can arise unaccompanied by any demonstrable eye movement. But this does not mean that there is no eye movement, for a consideration of the fixation reflex on a servomechanical basis reveals the obvious fact that this reflex must depend on the detection and correction of an error signal. Such errors of fixation have been demonstrated by Barlow (1) as being of the order of 20' of arc, if optimal fixation is regarded as taking place when the image is placed at any point on the central foveal plateau which subtends an angle of 20' of arc.

Furthermore, it is conceivable that the measurement of eye movement may not necessarily indicate what movement has taken place between the image and the retinal mosaic itself, for not only are the contact lens techniques open to the objections of slipping (2) but it may well be, particularly during small movements, that the crystalline lens may not exactly follow all movements of the eye.

It was therefore decided to re-examine these three illusions in order to determine the part played by retinal image movement of small amplitude, and by the other factor which could also play a part in the visual perception of movement - the knowledge of eye position.

EXPERIMENTAL OBSERVATIONS

MOVEMENTS OF THE RETINAL IMAGE

The technique employed, which has been described elsewhere (Niven et al), depends on producing a visual after-image by the successive flashing of each half of a line of light while the subject fixates the mid point of this line. As there is an interval of predetermined length (50 msecs.) between the right and left hand flashes, the subject whose eye moves at right angles to the line, will on introspection see not two after-images in line but two after-images out of line, the extent of misalignment depending on the extent of eye movement between the first and second flash. It has been possible by this means to detect movements of the retinal image of about 5' of arc under optimal conditions and 10' of arc with certainty, for the task of detecting misalignment is virtually one of vernier acuity.

Although this technique had on a previous occasion successfully demonstrated eye movements occurring during the elevator illusion, no distinct movement was detected during either the autokinetic, the oculogyral, or oculogravic illusions. Certainly on some occasions the images were not quite in line and occasionally a large movement of 10' - 20' of arc was found, but the appearance of this was inconsistent. It was therefore concluded, particularly in regard to the autokinetic and oculogravic illusions, that if there was movement of the retinal image, it must be smaller than 5' or slower than 5' of arc per 50 msecs (1 2/3°/sec.)

Since the technique described above did not completely exclude eye movements as a contributing factor, it was thought advisable to make an additional observation. Accordingly, the fixation light was exposed by means of a leaf shutter so as to be presented to the subject in flashes of one-hundredth of a second duration and at a frequency of 1-2 per second. During the observation of the fixation point, however, one still experienced the typical autokinetic, oculogyral, and oculogravic illusions, the light source moving and drifting as though it were seen continuously. A repetition of this observation but with a small neon bulb which gave a series of 2-3 msec. flashes, yielded the same result.

On the basis of this observation, therefore, it is evident that tracking of the image across the retinal mosaic is not essential for the appearance of movement in these illusions, or conversely that the visual sensation of movement can arise without movement of the retinal image.

How this sensation can arise is not clear, for although the human extraocular muscles contain spindles (6) which in skeletal muscle would signal changes in muscle length, the eye can be passively displaced without any visual sensation of movement of a fixed retinal stimulus, such as a visual after-image.

A similar type of observation was made by Brindley & Merton (3), who in addition found that if a subject with an anaesthetised conjunctiva tried to move his eyes while they were mechanically immobilized, he experienced a sensation of movement of his entire visual field in the direction of the attempted movement. In a subsequent paper, Merton (19), referring to these findings which agreed with the view of Helmholts (15) that knowledge of eye position was related to the effort of will required to produce the movement, went on to suggest that there is no reason why one should not be as capable of judging the size of an efferent volley as one is of judging the size of a sensory volley arriving at the brain.

Such a system would certainly have the advantage of stabilising the visual world, for in moving the eyes from left to right, the external scene, by reason of retinal image movement, would appear to move from right to left. Since the pattern of efferent activity would give rise to a visual sensation of movement in the opposite direction, the two sensations would tend to cancel one another.

This, together with the fact that in the illusions being considered there is no detectable causal eye movement, thus suggested the possibility that the sensations of movement might be associated with a pattern of efferent activity which, however, did not measurably move the eye since there was a fixation point to "lock on" to.

AUTOKINESIS OF VISUAL AFTER-IMAGE

A small light observed in darkness appears to wander but if a visual after-image, which is of course fixed on the retina, is observed in total darkness, it appears to move too, although usually in a more exaggerated way than the real fixation light. The general similarity of this after-image movement to autokinesis of a real light source suggested that it might be rewarding to determine whether these wanderings of the after-image were associated with any demonstrable eye movement, and secondly, if there was eye movement, whether it was related to the typical autokinesis of a real target during fixation. The following observations were therefore carried out.

After imposing on the retina an after-image of a circular source, the subject was given a fixation light straight ahead, on which to direct his gaze and center the after-image. This light was extinguished after a few seconds, and when the subject reported that his after-image had moved, the fixation light was switched on again. Any difference between the line of gaze and the fixation light was then noted.

It was found that when the after-image seemed to move, this sensation was accompanied by an eye movement of magnitude and direction approximately equal to that of the perceived shift in position. However, if this first movement were not monitored by switching on the fixation light, the subject apparently adapted to his sensation of altered direction of gaze in that he felt that his eyes were gradually returning to straight ahead. While still in darkness a subsequent but corrective eye movement could therefore be incorrectly sensed as a movement to the opposite side of the real fixation target.

Thus when there is nothing on which the eye can fixate, there is activity of the extraocular muscles which must be considered as involuntary since it occurs in spite of attempts to keep the gaze directed straight ahead. A similar finding was reported in 1953 by Ditchburn and Ginsborg. Since the apparent movement of the visual after-image was in the same direction as the real eye movement it seems probable that it is the pattern of efferent activity or perhaps the change in this pattern which is responsible for the sensation of movement of the after-image.

AUTOKINESIS OF REAL TARGET

Although these random drifts in eye position take place when there is nothing for the eye to fixate, it seemed likely that the associated efferent pattern might well still be present even when the eye was fixated on a visible target. In such a case one might expect that even though there was little demonstrable eye movement, these patterns of involuntary activity might still give rise to visual sensations of movement similar to those experienced when trying voluntarily to move the mechanically fixed eye, as reported by Brindley & Merton.

Attempts were therefore made to determine whether during a particular autokinetic illusory movement, there was at that instant any involuntary activity similar to that producing the slow drifts and, therefore, tending to move the eye. Initial results, however, were inconclusive for if one waited for a steady autokinetic effect to take place and then momentarily switched off the fixation light, one could not be certain that the autokinetic effect would have persisted in the same direction. Although it had been reported by Klystra (17) that by varying the tonus of neck muscles, an autokinetic movement of the target could be caused to take place in a specific direction, our attempts to make use of this observation again gave inconclusive results since all our subjects did not experience a sufficiently predictable autokinetic movement in response to altered tension in the neck muscles.

It was found, however, that the technique of directing the gaze towards a fixation light near the limits of the visual field resulted, after an initial period of 1-1 1/2 minutes of random autokinetic effect, in a consistent apparent movement of the fixation light toward the side to which the eyes were directed. This autokinetic illusion persisted as long as the eyes were directed to the side, and it was found that if the fixation light were switched off, and one still tried to keep looking at where it had been, the direction of gaze involuntarily moved away from the periphery toward a more central position. Thus in this instance the autokinetic illusion was in a direction opposite to that of the involuntary drift.

The same result was obtained when the autokinetic illusion was elicited by passing a direct current of one or two milliamps from mastoid to mastoid. This technique of galvanic stimulus, which had been mentioned by Klystra, gives rise to a sensation of turning or tumbling in a direction which is dictated by the polarity of the current. It does, however, also give rise to visual autokinetic movement in a predictable direction, and on six subjects with normal labyrinthine function who were investigated by the same technique as previously, it was again found that there was an involuntary drift of the eyes in a direction opposite to that of the predominant autokinetic movement.

These involuntary drifts which seem to be present when there is nothing on which to fixate thus have probably to be countered by antagonistic eye movements when there is a fixation point, and it seems to be this antagonistic activity which gives rise to the predominant sensations of movement probably through the pattern of associated efferent activity.

We have shown earlier that eye movements are not essential to the production of the illusions, but it is still possible that a slow image drift off the fovea in response to involuntary or agonist activity may contribute to the sensation of movement. Some of these small movements can be seen if one imprints an after-image on the retina, and then fixates the small light source. It is then observed that, although the two remain reasonably together, there are nonetheless drifts which show that there is a certain amount of tracking of the fixation point on the retina. During this period one may see simultaneously, autokinetic movement of the real target and after-image. On the other hand, it was noted that for some intervals of a few seconds, there may be no visible movement between target and after-image and yet during that period there may still be a marked autokinetic illusion.

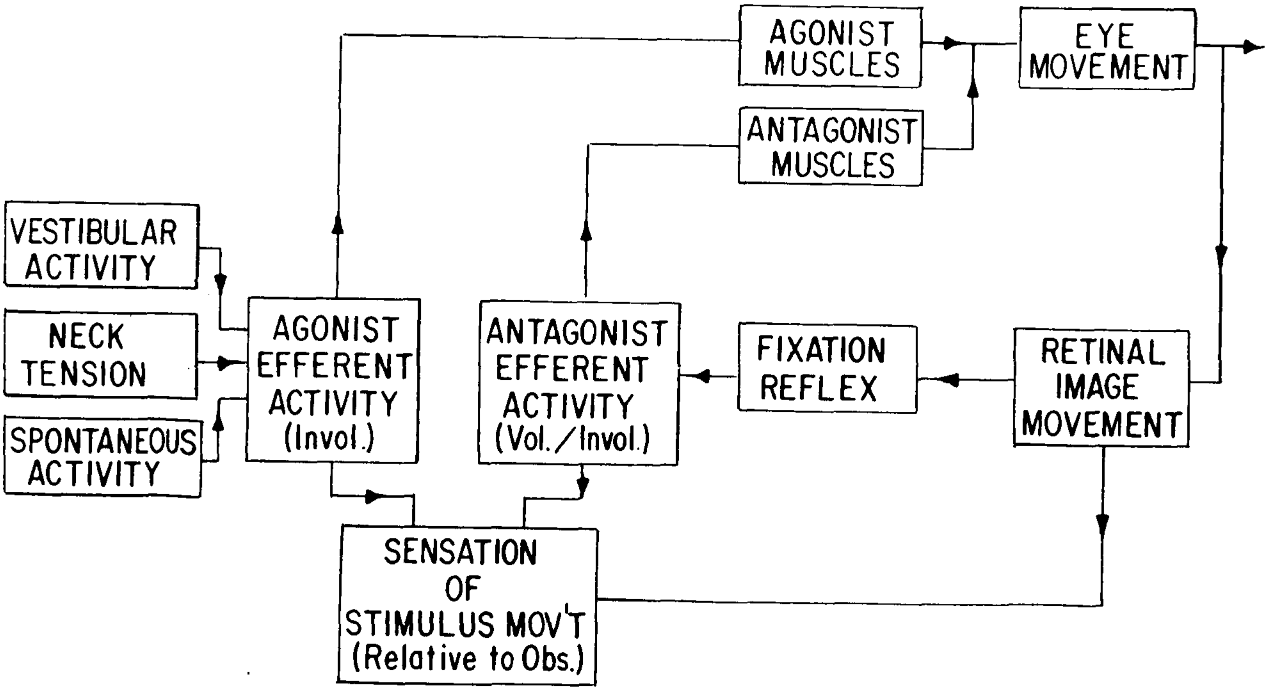


Figure 1

Observation of the movements of scleral vessels through a slit lamp microscope likewise revealed no pattern of micro-nystagmus, but the possible role of such small movements cannot be excluded without more satisfactory examination by an objective technique such as high speed cine photography.

If eye movement thus seems to play no essential part in the illusion, the same cannot be said of the efferent activity which is associated with the extraocular muscles causing such eye movements, for we now have the possibility of explaining the visual sensation of movement in an eye which is virtually fixed by being locked onto a real target.

One may regard the system of involuntary efferent activity resulting in drifts of eye position, as one in which there is an input of random activity (Figure 1). This activity will result in contraction of extraocular muscles and eventually in eye movement but, if there is a fixation light present, this effectively provides, through the change in the retinal picture, a misalignment detector which signals fixational errors. These errors, through the fixation reflex, result in signals which give rise eventually to contractions of antagonistic extraocular muscles, and so to a corrective eye movement. Thus, the presence of a fixation point completes a servo system for monitoring eye position.

The pursuit of this obvious fact leads one to the view that when there is no fixation light, or when one introspects on the drifts and apparent movements of a visual after-image, we have simply opened the servo loop and allowed free play to the involuntary efferent activity.

THE OCULOGYRAL ILLUSION

As with the autokinetic illusion, a satisfactory explanation of the phenomenon must take into account its characteristics under three different experimental circumstances, namely, while observing a real target, a visual after-image and the two simultaneously. Therefore, although the behavior of this illusion has already been described, the authors have repeated the observations, comparing particularly the durations of movement and displacement of the real target with that of the after-image.

The observer, with head supported, sat near the center of the Pensacola Slow Rotation Room observing a dimly illuminated cross in darkness. After rotating at a constant velocity of 12 RPM (counterclockwise) for one minute, the room was brought to a stop within 5 seconds. On deceleration, the target appeared to move rapidly to the right, at first jerkily during which good fixation was impossible, and then smoothly. After a period of 20 to 30 seconds, varying with the observer, the target appeared either to come to rest or to wander a little in an aimless fashion. After a further 2 to 5 seconds it appeared to move to the left, its velocity at first increasing and then diminishing. In some instances the apparent movement to the left ceased and in others the target began to wander in a manner characteristic of autokinesis. Observations were made twice by each of the three observers and there was agreement on the main characteristic of the illusion, although the duration of the different phases varied with individuals.

A similar procedure was employed in a second series of observations in which, instead of a real target, we used a visual after-image in the shape of a broken circle. This was impressed on the retina by means of a photographic flash bulb and suitable mask. It was found, in response to the same stimuli as previously, that the extent of apparent movement of the after-image was greater than that of the real target, but that in addition the direction of movement of the after-image was always opposite to that of the target alone. Initially it moved jerkily to and fro then to the left for some 20 to 30 seconds, after which the direction of movement was reversed.

When the after-image and target light were viewed together on deceleration, they separated momentarily owing to the difficulty of fixation, but as soon as the observer was again able to fixate the target, the after-image became superimposed more or less accurately, the two remaining together and taking on the direction of apparent movement of the real target.

The to and fro movements of the after-image produced by a strong vestibular stimulus are probably associated with the slow and fast phases of nystagmus and the sensation must therefore arise from the efferent activity associated with these phases.

The same relatively simple explanation cannot, however, be extended to the similar jerking motion exhibited by the real target for, during the slow phase of eye movement, neural activity may cause a sensation of movement to one side while tracking of the retinal image will cause a sensation in the opposite direction. These two may tend to cancel one another. In the fast phase, however, the neural volleys may create a sensation of movement unopposed by any sensation from the retina since the image may be, during this saccade, tracking too quickly to be seen. This may explain why one sometimes sees intermittently and after a strong stimulus, a target which is occasionally displaced towards the direction of the fast phase.

As the nystagmus becomes slower and decreases in amplitude, so the antagonist more readily succeeds in establishing fixation until eventually recordable nystagmus disappears. At this stage, however, the real target still seems to drift to the right. We can now dismiss tracking as the cause of the illusion, for a superimposed after-image shows that there is indeed little fixation movement.

Just as in autokinesis, an explanation can now be offered on the basis of efferent activity of the antagonist, for we now have antagonist activity which is in fact capable of dominating the involuntary slow phase nystagmus or agonist activity. That such nystagmus is still present but is merely being reined in by the fixation reflex mediated through the antagonist muscles, can easily be demonstrated by switching off the fixation light. When this is done, some small beats of nystagmus are again elicited.

To resume, with the exception of the phase in which there is obvious tracking of the image on the retina, the oculogyral illusion can be explained in the same terms as the autokinetic illusion; namely, that the apparent movement is associated with efferent activity in the antagonist to the slow phase efferent activity present as a result of labyrinthine stimulus.

THE OCULOGRAVIC ILLUSION

The term 'oculogravic illusion' embraces illusions of tilt, of displacement in a translational sense, and of movement, and indeed the many variations in the illusion depend simply on which of the physical parameters are varied, and which are controlled.

If one does not wish to introduce angular acceleration, or a change in the direction of action of linear acceleration into the stimulus pattern, the only way to examine changing magnitude of linear acceleration is to employ a vertical linear accelerator such as an elevator in which the subject is immobilised. The elevator then subjects him only to a change in mangitude of the acceleration, and the accompanying 'elevator illusion' consists of a visual sensation that, as acceleration increases, the object regarded seems to move upwards. The opposite takes place if the acceleration is reduced from 1 g to less than 1 g or even to 0 g, when the object regarded seems to move downwards.

Linear accelerators such as elevators have some advantage, but obviously they cannot be employed for accelerations lasting more than a few seconds, so if one wants to investigate the effects of a new steady linear acceleration, it is necessary to employ a radial accelerator such as a centrifuge.

During the increase in speed of the centrifuge, the subject, seated in a cabin which is free to align itself with the direction of the resultant force, experiences an increase in magnitude of linear acceleration, together with some superimposed angular accelerations. There is also a small change in direction, associated with the tangential component of the acceleration pattern. Once constant speed has been attained, however, and once the vestibular effects produced by the angular accelerations have subsided, the subject, whose head is immobilised, experiences a new steady linear acceleration which has been changed (increased) only in magnitude.

If the cabin in which the subject is seated is fixed in the horizontal plane, he will experience an increase in magnitude and a change in direction of linear acceleration, together with a superimposed angular acceleration which, however, will be confined to the horizontal plane. The change in direction again will be slightly affected by the tangential acceleration. When the steady state has been reached, and labyrinthine effects of angular accelerations have ceased, the subject will be in a steady state of linear acceleration of changed magnitude and direction.

If the subject is facing the center of rotation, he will first experience the illusion that the object regarded seems to move to one side (oculogyral illusion) then up (oculogravic illusion) - but slowly, and only some seconds after the acceleration has been applied. Thereafter it moves upward more rapidly, and after peak 'g' has been reached it may still seem to go upward for some time.

Obviously one feels tilted back, so an object in front of one is interpreted as also having been displaced upward, but in addition to this displacement, which temporally and spatially seems to be linked with the change in direction of the resultant force, there is an upward movement which seems to continue long after the steady acceleration has been reached. Nor can one attribute this to nystagmus since the angular acceleration was in the horizontal plane.

Deaf subjects with no demonstrable vestibular function have a tendency to equate this sensation of tilt - the sensation produced by non-labyrinthine proprioceptors - with an illusion that the light source in front of them must be tilted up. They do not however see movement upwards. It seems that by comparison the normal individual sees an accentuation of this apparent tilt - possibly because of associated apparent movement.

Another example of altered magnitude and direction of acceleration is afforded by the experiments in which the subject is on a fixed seat on the centrifuge arm, but facing the direction of rotation. The same physical stimuli are present as in the previous case, but if the subject now looks at a truly horizontal line of light, it will appear to tilt, tending to align itself with the direction of the resultant force as the latter approaches a 45 degree deviation.

The apparent complexity of the different types of oculogravic illusion is due merely to the different ways in which they are produced but they all appear to have two common factors. First, with an increase in magnitude of the force there is an illusion that an object observed straight ahead is either moved or displaced upwards. Secondly, with a change in direction of the force with or without a change in magnitude, there is an illusion that the visual scene is tilted to the horizontal through an angle approximately equal to the angle phi which the resultant g makes with the true vertical.

Under certain special conditions, eye movements have been recorded while the subject was fixating an object such as a light source. Thus it has been found that a reflex eye movement is evoked by a sudden change in magnitude of acceleration without any change in direction (Niven *et al*). It has also been shown that a change in magnitude of the force together with a lateral change in direction gives rise to reflex rolling of the eyes (24).

In the present experiment, however, in which, by means of a movable chair on the end of a centrifuge arm, the subject could experience either increased g alone or increased g together with changed direction of action, no eye movement was detected when the subject had a small light source on which to fixate. This experiment, using the two flashing lines of light, has been described earlier in this report.

Three normal and three deaf subjects with reduced or absent vestibular responses (as measured by counter rolling) took part in the tests, in which, to allow the effects of angular accelerations to disappear, no observations were made until at least 30 seconds after reaching peak g. Furthermore, to eliminate Coriolis effects from head movement, and to reduce effects due to tonic neck reflexes, subjects were always strapped into the seat together with a plaster support for the head and neck.

When the fixation light was removed, however, and the experiments carried out in total darkness with the same acceleration stimuli, it was found that the eyes, particularly of normal subjects, tended to rotate downwards in response to an increase in g, particularly if this was associated with a change in direction corresponding to a backwards tilt of the subject. Some eye movement was also detected in the deaf subjects. After a number of observations essentially of a qualitative nature, in which it became evident that the change was probably a progressive one, the following technique was devised and employed on one experimental session so as to give a rough indication of the quantitative nature of the changes.

First, the subject fixated a small light source which was reflected to his eyes by means of a small clear glass plate so arranged that the image appeared superimposed on a photographic flash bulb. The bulb was partly masked so as to present only a small circle to the subject. When the illusion was observed as a result of the stimulus, the fixation light was extinguished, while the subject, now in darkness, tried to keep looking in the same direction. After a predetermined time, the flash bulb was switched on and then the overhead lights. The subject was now presented with a large card, at the same distance as the fixation light and flash, and was told to fixate a mark in the center of the card. While maintaining this fixation, he then pointed to the position occupied by the visual after-image. The orientation and angular separation between this point and the central fixation mark represented the direction and extent of eye movement which had taken place in darkness during the interval from switching off the fixation light to flashing the photographic bulb.

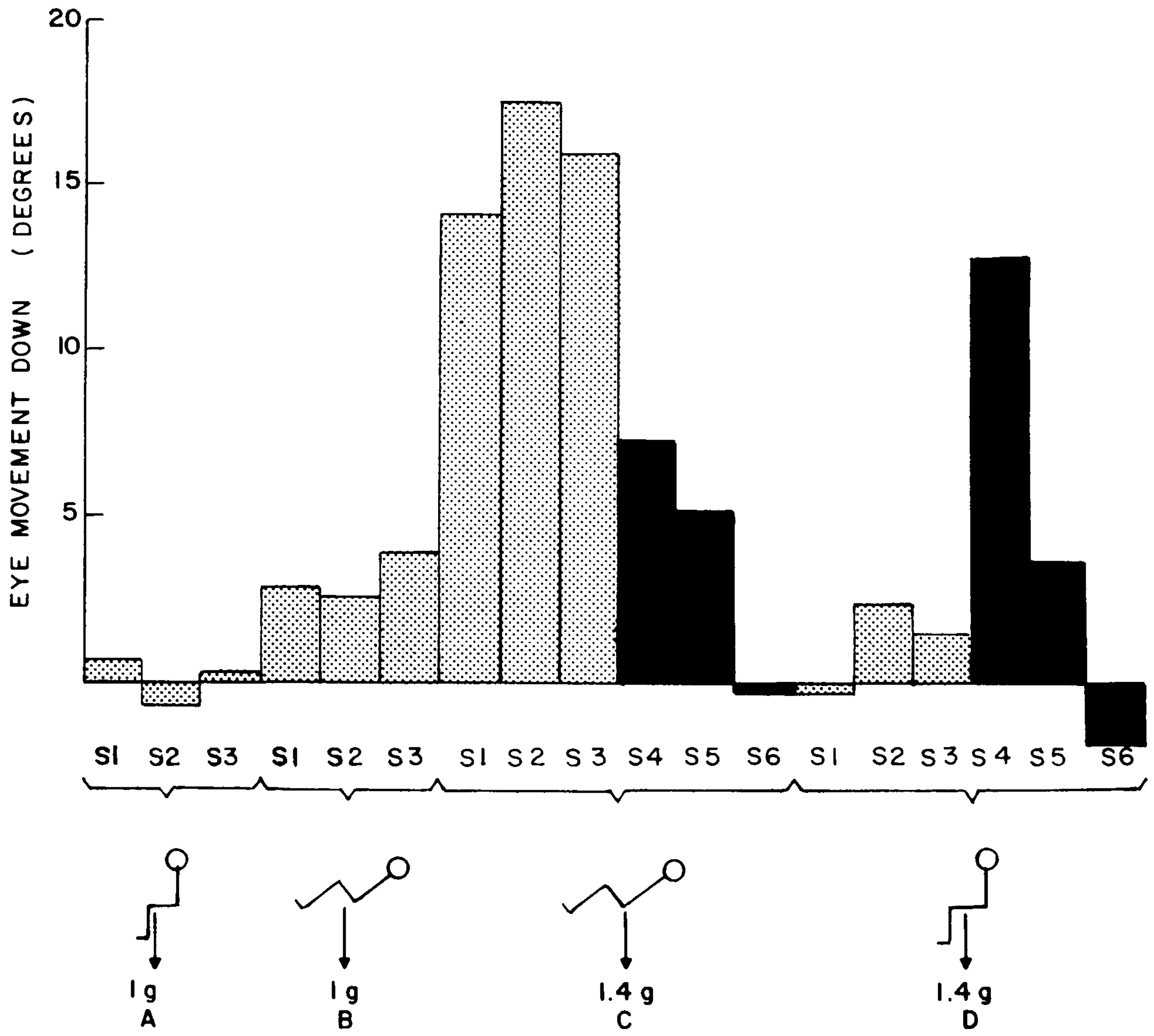
This technique however was not pursued because of its inability to provide the necessary continuous data on eye movements which it is intended to re-examine on similar subjects at a later date, and by a more sophisticated technique.

The results of this session are shown in Figure 2. It will be seen that, in normal subjects, the tendency was for the eyes to move downward, either when the direction of resultant force was changed so as to correspond to a sensation of being tilted back, or when the magnitude of the resultant force was increased without a change in direction. Deaf subjects with no demonstrable labyrinthine function did not exhibit the same extent of eye movement in response to tilt plus increased g, but the experiment has to be repeated before it is assumed how much is of labyrinthine (probably otolithic), and how much is of nuchal origin.

One can, however, still suggest that in the oculogravic illusion the appearance of movement is due, as in the other two illusions considered, to the efferent activity of antagonists which correct an involuntary tendency for the eyes to move down with increased g or with backward tilt.

DISCUSSION

The process of fixation depends upon the presence of a fixation error and its correction. Thus to fixate, continual eye movements are required, which incidentally,



A – 10 sec AFTER LOSS OF FIXATION POINT;
B – 10 sec AFTER LOSS OF FIXATION POINT; 60 sec AFTER
C – 10 sec AFTER LOSS OF FIXATION POINT; 60 sec AT PEAK g.
D – 10 sec AFTER LOSS OF FIXATION POINT; 60 sec AT PEAK g.

▨ NORMAL SUBJECTS ■ L-D SUBJECTS

Figure 2

Eye Movement of Normal and Deaf Subjects are also essential to enable one to see the object fixated. It seems reasonable that these small eye movements may arise reflexly from spontaneous activity in the labyrinth or the neck muscles. In fact Cornsweet (7) suggests that the involuntary drifting eye movements may arise from instability in the oculomotor system, while the saccades may be caused by the displacement of the retinal image. Ten Doesschate (22) made a similar suggestion - namely that during fixation, involuntary contraction of some extraocular muscle will cause shifting of the retinal image so that there arises a reflex contraction of an "antagonist" muscle.

Clearly, the extent of this movement before correction by the fixation reflex, will depend in large measure on the size of the central foveal area over which the image may move without requiring a corrective saccade. Barlow (1) suggested that this area was 100 μ across, or subtended an arc of about 20', but more recently, Fender & Nye (9) concluded that inside a 6' arc, the eye was indifferent to image position, and that no corrective movement was made when the image was in this foveal area.

The suggestion that it may be the pattern of efferent activity which gives rise to the sensation of movement when there is no sensation arising from tracking of the retinal image is not really new for the same idea is echoed throughout papers on autokinesis and eye movement. Thus Charpentier (5) referring to the autokinetic illusion said that it might be explained by "efforts inconscients" produced in the brain. Helmholtz suggested that the sensation of movement associated with eye movement but without retinal tracking, may be due to the intensity of the effort of will to bring the muscles in action. Again, referring to the autokinetic illusion, Kleint (16) writing on researches into perception, suggested that since there is no eye movement detectable, tonus of eye muscle may be responsible.

Certainly there is no clear evidence as to the origin of the sensation. It does not seem likely that it should arise in the muscle since this sensation is experienced when a volley is dispatched to a paralysed (15) or partly curarised (3) muscle. The extraocular muscle of man was shown by Cooper & Daniel to have muscle spindles, but they do not appear to function as length misalignment detectors which is their function in skeletal muscle, for no stretch reflex can be elicited from them (25). Thus we use here the term 'efferent activity' without being able to specify how or where it gives rise to the sensation of motion. Is this a learned phenomenon; that is, does the infant, having learned to fixate, then learn to follow an object in motion, thus associating this form of motor activity with movement when the image of the object regarded remains on the fovea?

The fact that an autokinetic type of movement is still seen even if the fixation light is presented as a series of 2-5 msec. flashes at a frequency of 2 per second, shows that the sensation of movement cannot be due to the tracking of a retinal image. Nor can the appearance of this movement be explained on the basis of the Phi phenomenon, for it is accepted that the inter-flash period has to be of the order of 1/16 sec. and certainly shorter than 1/5 sec. to give rise to Phi movement. Furthermore, such a Phi movement would not give a smooth gliding motion characteristic of the autokinetic illusion, but would have saccadic jerky reversals if one were randomly sampling fixation errors.

This leaves only efferent activity as a causal factor, but, if that activity associated with a slow or agonist displacement were to give rise to a sensation of movement, its direction would be opposite to that found experimentally. We thus seem to be left with only one source from which this movement can originate: the efferent activity associated with the saccade or fast corrective movement. During that corrective movement any sensation produced by tracking, which anyway we know does not play an essential part, would cause a movement sensation in the opposite sense to that found experimentally.

There is difficulty in suggesting what constitutes the retinal stimulus which is seen to move during the corrective or antagonist activity. It may be the retinal stimulus present during the corrective movement itself, in which case this antagonist movement would have to be either sufficiently small or sufficiently slow to enable the stimulus to be seen and yet prevent a visual sensation of motion to be produced by tracking across the retina, since the sensation produced by such image movement would be in the wrong direction. It might well be however that during the fast phase what is seen is simply the after-effect of the retinal stimulus received immediately prior to the saccade.

Changing levels of activity of the antagonist can be envisaged without any muscle tension imbalance for, when the muscle becomes fatigued (as during prolonged fixation to one side) so more motor units have to be recruited to maintain fixation, and this recruitment will, of course, be effected by increased efferent activity, and therefore result in a visual sensation of movement in that direction.

This explanation of apparent movement during the autokinetic illusion fits the facts equally well, both in the oculogyral and in the oculogravic illusion, in both of which the maintenance of fixation of a real target requires that involuntary activity of extraocular muscles arising reflexly from either stimulation of the cupula, the otoliths, or of the neck tension receptors, be countered by antagonist extraocular muscles. The associated efferent activity is probably responsible for most of the movement seen.

Those who have therefore tried to explain these illusions purely in terms of eye movement have been unsuccessful for, although there is the component of involuntary movement present, it is controlled by the servo action of the fixation reflex. Only when this loop has been opened, therefore, can those involuntary movements of either random or reflex nature be uncovered.

The elevator illusion can be regarded as a special instance of oculogravic illusion in which the change in magnitude of the acceleration has been so rapid from 1 to 0 g that an upward eye movement has occurred reflexly and too quickly to be controlled by the fixation reflex. Under stable conditions of 0 g or of 1.4 g for example, no consistent eye movement has been demonstrated during fixation.

In the oculogravic illusion which is associated with a change in direction or magnitude, of the resultant force, one can consider two factors as playing a part. The first is a reflex eye movement which may arise from utricular stimulation such as has been exhibited in the changes from 1 g to 0 g or in counter rolling (24). It may also arise from nuchal tension, since reflex compensatory eye movement associated with stimulation of the cervical nerve roots, have been observed by Philipszoon (21) in both normal and labyrinthectomised rabbits, and in normal man. He found that turning the body while the head was immobilised, resulted in lateral eye movements with some superimposed nystagmus.

In order to maintain fixation, this eye movement has to be controlled by contraction of the antagonist muscles and it is probably the efferent activity associated with these whichgives rise to the apparent movement of the fixation point - upwards when the magnitude of the force increased, and downward when it decreased.

There is strong evidence from the work of Woellner and Graybiel that the extent of eye rolling is related closely to the lateral vector of the resultant force. In other words, the magnitude of the reflex eye movement seems to be related to the magnitude of the shearing force applied to the utricular hair cells. This in turn would imply that the subject on the centrifuge at a given acceleration would experience more utricular stimulation when the force was acting antero-posteriorly than when it was acting from head to foot. Conversely, one might argue that immobilisation of the head and neck was better, and therefore the stimulus for the neck tension receptors was likely to be less when the force acted antero-posteriorly instead of from head to foot.

Magnus (18) suggested that the vestibular and tonic neck reflexes may add algebraically to determine the final posture adopted, and indeed, this may be a reason for the difference in amounts of eye movement which we have observed. Thus, in a back tilt at 1 g there is a small eye movement which is greatly increased when, still with tilt, acceleration is raised to 1.4 g. That deaf subjects exhibit eye movement here may be due partly to residual otolithic activity. When the stimulus, however, is at 1.4 g but from head to foot, normal subjects show little eye movement while the deaf subjects show more - possibly because of their greater dependence on the reflexes associated with neck tension.

The other factor may be regarded as perceptual, being associated with a change in direction of action of the resultant force. One feels tilted back, a fixation point is seen dead ahead, therefore the fixation point is inclined so as to maintain a constant angle with the resultant force. This perceptual change could persist for as long as the resultant g acted antero-posteriorly, whereas the component of the illusion associated with eye movement would be expected to disappear gradually with adaptation either at the otolith or in the nuchal tension response.

The explanation of these illusions is not intended to be complete, for in the autokinetic illusion, for example, there are a number of facts still to be explained, especially in regard to the disappearance of this illusion when a bright square surrounds the fixation light. In spite of these gaps in our knowledge, however, the above hypothesis seems to offer a reasonable basis for further verification by more objective techniques.

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The autokinetic, oculogyral, and oculogravic illusions all involve apparent motion or displacement of the visual field with respect to an observer. It is shown that these illusions are related to involuntary eye movements, occurring either spontaneously as in the autokinetic illusion, or in response to the special stimuli associated with the other two illusions. During fixation the visual sensation of movement seems to be produced by, or related to, the pattern of efferent activity aimed at the group of extraocular muscles which will act as antagonists to the involuntary eye movement referred to.

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