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Implications of OKN suppression by smooth pursuit for induced motion

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Induced motion refers to the illusory movement of a stationary stimulus that results from the opposite movement of other stimuli in the visual field (for a historical review, see Duncker, 1929). A familiar example is provided by the apparent motion of the moon viewed through a surround of moving clouds. Although the moon is objectively stationary, it appears to move opposite to the cloud motion.

A variety of explanations have been offered to account for induced motion. Duncker (1929) proposed that changes in the apparent location of a stimulus relative to its surround produced the illusory movement. Specifically, movement of the surround was presumed to result in the perception of changed relative locations of the induced motion stimuli, which in turn would give rise to perceived movement. More recently, Brosgole (1968) and Bridgeman and Klassen (1983) suggested that induced motion resulted from changes in the perceived direction of the fixated stimulus relative to the observer. Specifically, the motion of the inducing stimulus was assumed to alter the direction of the apparent straight-ahead, which in turn would alter the perceived direction of the stationery stimulus. Changes in perceived direction are, in turn, inferred as movement of the fixated stimulus. These two accounts are similar in that the induced movement percept is mediated indirectly, that is, the illusory movement results from changes in perceived location or perceived direction.

To date, the possibility that oculomotor mechanisms contribute to induced motion has been rejected on the basis of experiments in which eye movements were measured during observation of the illusory movement. These studies (Mack, 1970; Brosgole, Cristal, & Carpenter, 1968; Bassili & Farber, 1977) consistently found that there was no significant amount of eye movement during fixation of induced motion stimuli. The absence of significant retinal image motion eliminates the possibility that the induced motion results from stimulation of afferent motion analyzers. Similarly, the possibility that the efference copy associated with activation of the pursuit system (Helmholtz, 1962, p. 234; von Holst & Mittelstaedt, 1950) is involved has not been considered, presumably on the basis of the observation that the eye is not moving.

Although it has been assumed that there is little or no activity in the pursuit eye movement system if the eye is stationary, this conclusion may not be justified. A substantial body of evidence now exists which suggests that the pursuit system is activated during the suppression of involuntary eye movements. In particular, pathologies or drugs that disrupt smooth pursuit also impair the ability to suppress nystagmus (Dichgans, von Reutern, & Römmelt, 1978; Schroeder, 1972; Troost, Dell'Osso, & Daroff, 1976; Welch, Schroeder, Thurgate, Erikson, Higgins, & Wait, 1977), which is presumed to depend on the inhibitory activity of floccular Purkinje cells (Melvill Jones & Gonshor, 1975; Robinson, 1975; Waespe, Büttner, & Henn, 1981; Waespe & Henn, 1981). Accordingly, floccular lesions result in both saccadic pursuit and impaired nystagmus suppression (Takemori & Cohen, 1974). This role of the flocculus in both nystagmus suppression and the generation of smooth pursuit is further supported by the results of Lisberger and Fuchs (1978), Waespe et al. (1981), and Waespe and Henn (1981), who demonstrated that the activity of single floccular Purkinje cells is similarly modulated during either pursuit eye movements or the suppression of the slow phase of nystagmus in the opposite direction.

A number of illusory movement phenomena are consistent with the active role of the pursuit system in the suppression of involuntary eye movements. Whiteside, Graybiel, and Niven (1965) proposed that the illusory movement of a fixated stimulus during equal acceleration of the observer and the stimulus (the oculogyral effect) resulted from the efference associated with the pursuit effort required to suppress nystagmus under these conditions. A similar mechanism was also offered by these authors and others (see Levy, 1972) to account for the apparent direction of autokinesis. More recently, Post and Leibowitz (1982) have shown that apparent concomitant motion (Gogel & Tietz, 1973) or the apparent loss of position constancy (Wallach & Kravitz, 1968) observed during lateral head movements results from the activation of the pursuit system to either suppress or enhance the reflexive counterrotation of the eyes to maintain fixation.

The thesis of the present paper is that induced motion also results (in part) from the activation of the pursuit system to suppress the slow phase of nystagmus in the interest of maintaining fixation. Specifically, it is assumed that the motion of the inducing stimulus would, if unopposed, result in reflexive following movement of the eyes and a loss of fixation from the test stimulus. To maintain fixation under these conditions, the pursuit system is ac-

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tivated in the opposite direction from the motion of the inducing stimulus. The test stimulus therefore appears to move as a result of the efference copy associated with the pursuit activity. In effect, the observer is making a pursuit effort for a stationary stimulus. Such an analysis is consistent with the findings of Wyatt and Pola (1982) that open-loop presentation of induced motion stimuli results in pursuit of the fixated stimulus.

Observations

A test was conducted to test the assumption that movement of a stimulus typical of those employed in induced motion studies is sufficient to elicit involuntary following eye movements, and to determine whether subjects could voluntarily suppress these movements without a fixation target. The stimulus display consisted of a luminous rectangle (luminance = .2 cd/m^2) that subtended 40° vertically and 60° horizontally, with edges 6° thick, when located 1 m in front of subjects. The rectangle was projected using a rotatable mirror and could be moved to either the right or left at 5°/sec. Within the rectangle, midway between the top and bottom edges, was a red spot of light, generated by projecting a low-power HeNe laser onto the screen. When present, this spot was located directly in front of the subject at eye level. An electronic shutter and timers controlled both presentation of the red stimulus and movements of the rectangle. A chinrest maintained the distance of subjects from the display.

Thirty-one subjects participated in each of 12 experimental trials. The first two trials were to confirm that movements of the luminous rectangle were capable of inducing apparent motion of the red spot. Prior to these trials, the position of the rectangle on the projection screen was adjusted so that the red spot was offset by a variable amount to either the right or left of the center of the rectangle. Of the two trials for each subject, one offset was to the right and the other was to the left. The subject was instructed to fixate the red spot, after which the rectangle was moved for 5 sec at 5°/sec. Movement of the rectangle was to the right if the spot was initially located to the right within it, or the reverse. At the end of the movement, the subject was asked to report any apparent movement of the spot that had occurred during fixation.

At the conclusion of these preliminary trials, each subject participated in 10 trials to determine whether movements of the luminous rectangle elicited reflexive tracking eye movements if the red spot was removed. An afterimage was employed to monitor eye movements. This was generated prior to each trial by having the subject fixate the center of a photographic flash that was marked to generate a disk-shaped foveal afterimage 1° in diameter. With a fresh afterimage, the subject was then instructed to fixate the red spot that was located to the left or right of the center of the surrounding rectangle. Upon affirming that the spot was fixated (the afterimage was now superimposed on the red spot), the subject was instructed that although the spot was about to disappear, he or she should attempt to maintain his or her gaze on where the spot had been. At this point, the fixation spot was turned off and, after a delay of 1 sec, the luminous frame was moved either left or right in a manner similar to that of the first two trials. At the end of the 5-sec motion, the spot reappeared in the same location where it had been previously (directly in front of the subject) and the subject reported the location of the spot relative to the afterimage. In this manner, the direction of any involuntary eye movement that occurred during the frame motion could be specified. Of these 10 trials, five frame motions were to the left and five were to the right. Both directions of frame motion were used to insure that any tendency for the subject's eyes to move systematically in one direction in the dark (a drift bias) could not produce the appearance that his or her eyes were tracking the frame motion, as this tendency would be in the wrong direction on one-half of the trials.

Of the two preliminary trials for each of the 31 subjects, there were 30 reports of induced motion (that is, apparent movement of the fixated spot opposite to frame motion). On two trials, apparent motion of the spot in the same direction as the frame's motion was reported. This difference ($\chi^2 = 24.5$, $p < .0001$) demonstrates that the rectangle was an adequate motion-inducing stimulus, since the direction of apparent movement of the fixation target would otherwise be independent of the direction of frame motion.

On the eye-movement assessment trials, there were 231 trials (75%) during which the direction of involuntary eye movement was in the direction of the frame motion. On 51 trials (16%) the direction of fixational loss was opposite to the direction of frame motion, and on the remaining 28 trials (9%) there was no leftward or rightward fixational loss. The large difference between the frequencies of fixational loss in the same and opposite direction as frame motion ($\chi^2 = 114.9$, $p < .001$) indicates that the movement of the luminous frame which was effective in generating induced motion also elicited involuntary tracking movements when no fixational stimulus was present. Since these movements occurred in both directions, they cannot be attributed to drift-bias tendencies of the subjects.

These results demonstrate that movements of induced motion stimuli are effective in eliciting reflexive tracking oculomotor responses. Additionally, subjects are not able to suppress these responses if only an open-loop fixation stimulus is present. This is perhaps related to the role of the smooth pursuit system in nystagmus suppression. Neither smooth pursuit (Robinson, 1976) nor nystagmus suppression (Körner & Dichgans, 1967) is easily accomplished in the absence of a fixational stimulus.

The preceding findings are consistent with the proposed oculomotor account of induced motion. Movements of a luminous rectangle will, if unopposed, elicit reflexive following movements of the eyes. If, however, a fixation stimulus is also present, these movements are suppressed or opposed by pursuit activity in the direction opposite to potential fixational loss. The stationary fixated target is therefore seen as moving in the direction opposite to surround motion as a result of the pursuit activity.

The preceding results demonstrate that stimuli typically employed in studies of induced motion do produce the predicted involuntary tracking reflexes if unopposed. There are, however, potential objections to the suggestion that the suppression of these reflexes by means of the pursuit system produces induced motion. Specifically:

(1) Although the luminous frame employed in the present study produced involuntary fixational losses, induced motion may also be elicited by movements of substantially smaller displays, such as two dots moving in one direction. Although it has been reported that similar small displays are also capable of eliciting nystagmus (Cheng & Outerbridge, 1975), it is not known whether the stimuli investigated also generate induced motion if a fixation target is present.

(2) An alternative explanation of the present results is that subjects attempted to maintain fixation on a locus within the moving frame and therefore pursued this imaginary locus in response to the motion of the frame. Such pursuit would be similar to that reported by Steinbach (1976), in whose study subjects demonstrated pursuit tracking of invisible spatial loci perceived to be moving.

In order to address these possibilities, EOG records of eye movements were obtained while a pair of dots moved through the subjects' visual fields. This was first done with a fixation target present to confirm that the moving dots elicited induced motion. With EOG recordings, it would be possible to specify the characteristics of eye movements elicited by movements of the inducing stimuli. If subjects in the previous study were attempting to maintain gaze by fixating an imaginary locus within the moving frame, a smooth or slightly saccadic pursuit eye movement would be expected. However, if the fixational loss resulted from involuntary nystagmus, a nystagmic pattern of slow phase in the direction of surround movement alternating with opposite saccades would be expected. Additionally, the retinal eccentricity of the stimuli was varied. This was done because it is a reliable finding that stimuli moving near the fixated stimulus in induced motion displays are more effective in inducing motion than are stimuli positioned remotely in the field (Gogel & Koslow, 1972). The present study investigated the expectation that stimuli near fixation would therefore be more effective in eliciting OKN.

Subjects were seated inside a vertical rotatable cylinder 76 cm in diameter. A chinrest maintained viewing distance to the wall of the cylinder at 34 cm. The moving stimuli consisted of two red light-emitting diodes (LEDs) attached to the wall of the cylinder above and below the spot of laser light. Vertical separations of the LEDs were 2°, 20°, and 40°. Rotation of the cylinder at 6°/sec generated 30-sec-duration leftward or rightward movement of the LEDs through the horizontal extent of the visual field. A spot of laser light used previously as the fixation stimulus was projected in front of each subject for several trials to confirm that the two moving dot stimuli were capable of inducing apparent motion. The subject was exposed to 10 movements (5 leftward and 5 rightward) of the LEDs for each separation while fixating the laser target. Induced motion was reported to occur for the stationary laser target for each separation on 90% of the trials.

During the subsequent experimental trials without a fixational stimulus, eye movements were assessed with dc electrooculography and displayed on a strip-chart recorder. Electrodes were located at the outer canthus of both eyes with a reference electrode located on the forehead. Records were made at a relatively low gain and only after several minutes had passed with the electrodes in place, in order to insure low levels of drift (between 5 and 10 min of arc/sec during calibration runs). This procedure allowed a resolution of approximately 1.5° saccadic eye movements.

Each of the three subjects underwent 10 trials, consisting of five leftward and five rightward movements of the two LEDs for each of the three separations. The subjects were instructed to maintain gaze straight ahead while attempting to bisect the vertical interval between the two LEDs. Recordings were obtained for the entire time that the moving LEDs were present in the visual field.

The EOG recordings displayed nystagmus for each of the subjects for each of the stimulus separations employed. A typical record is shown in Figure 1 for a 2° separation of stimuli. In this figure it is seen that the frequency and gain of nystagmus appear to be greatest with stimulation near the middle of the record, corresponding to the middle of the subject's visual field. The frequency of beats, or nystagmus fast phases at different eccentricities of the LEDs in the visual field, is presented for all subjects in Figure 2. Because of the relatively low gain of the recording system, fast-phase movements of less than 1.5° are not included in this figure. It is apparent that the frequency of the nystagmus elicited by movements of the dot stimuli depends upon their proximity to the median plane of the subjects, as it reaches a maximum near the middle of the sampling interval. For two of the separations, the maximum frequency appears to occur slightly after the middle of the sampling interval. It is likely, however, that this point in the record actually corresponds to stimulation near the vertical meridian, since the eyes would be expected to be deviated a few degrees in the direction of stimulus motion as a result of the tonic deviation component of nystagmus responses (Jung, 1953b, p. 1325).

The frequencies presented in Figure 2 do not differ markedly as a function of the vertical separation of the two points of light. This finding suggests that the enhanced frequency of nystagmus near the middle of the records depends more on the proximity of stimulation to the vertical meridian than to the fovea.

The finding that nystagmus frequency attains a maximum with stimulation near the vertical meridian is of interest in view of the report of Cheng and Outerbridge (1975) that the gain of OKN elicited by moving point stimuli is also greater with stimulation near the fovea than

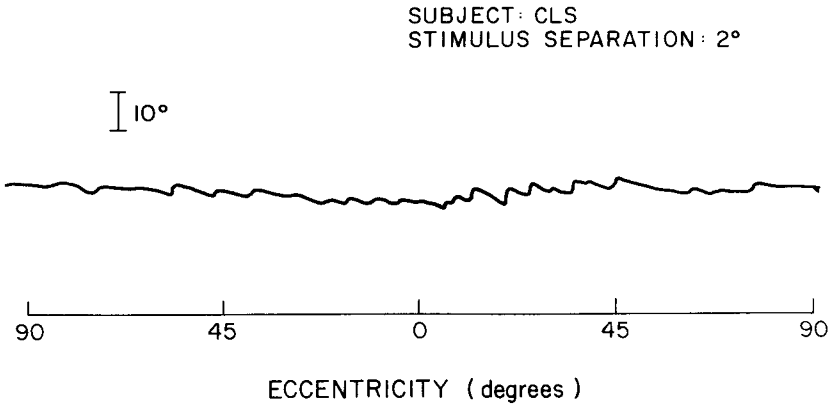

Figure 1. Record showing nystagmus responses for Subject C.L.S. while attempting to maintain gaze straight-ahead during rightward movement to two vertically separated LEDs. Note enhanced gain of slow phases just past the middle of the record. Stimuli entered the edge of the visual field at the left side of the record, crossed the median saggital plane of the subject at zero on the abscissa, and exited the opposite side of the field near the right side of the record.

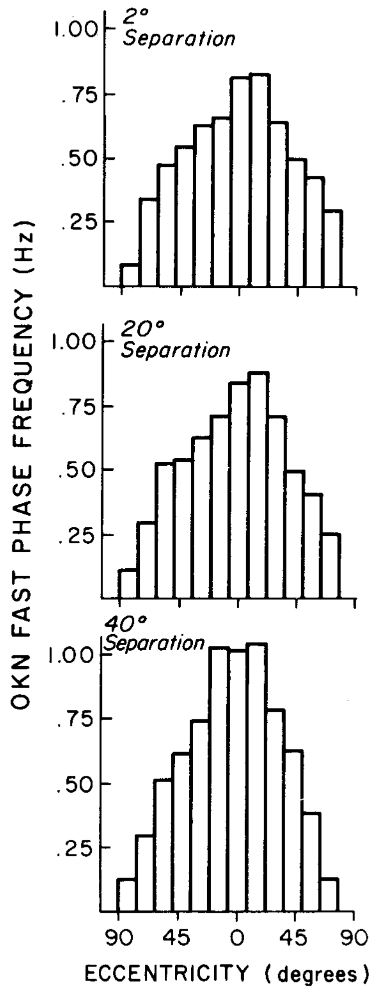

Figure 2. OKN fast-phase frequency as a function of stimulus presentation for each of three stimulus separations. Stimuli entered the edge of the visual field at the left side of the record, crossed the median saggital plane of the subject at zero on the abscissa, and exited the opposite side of the field near the right side of the record. record.

with stimulation of the far periphery. The EOG records were therefore analyzed (using the method of Jung, 1953a) to determine whether the gain of nystagmus varied as a function of distance of stimulation from the median plane in the same manner as frequency. The mean gain of OKN slow-phase responses is presented in Figure 3 as a function of eccentricity of optokinetic stimulation. It is apparent that there is a peak of the gain at a point near or slightly after the middle of the sampling interval, similar to the results for frequency. The peak may be more pronounced at smaller separations of the stimuli, although the differences are small and approach the limits of the recording system.

Discussion

The nystagmus results obtained with moving-point stimuli confirm the previous report of Cheng and Outerbridge (1975) that perifoveal stimulation increases the gain of OKN, and suggests as well that stimulation near the vertical meridian is particularly significant for the frequency of OKN. The implication of this pattern for induced motion within the suggested nystagmus suppression account is that movement of the inducing stimulus in these retinal regions should be particularly effective. This prediction receives empirical support from studies in which separation of the inducing stimulus was varied (Oppenheimer, 1935) and induced motion decreased with increasing separations of the stimuli. Additionally, Wallach (1959) and Gogel and Koslow (1972) report that the movement of relatively close stimuli dominates the path of induced motion when multiple moving stimuli are present.

The present results are apparently consistent with the finding of Wyatt and Pola (1982) that induced motion and tracking are closely related. When these authors presented open-loop induced motion stimuli, tracking resulted for the fixated stimulus.

The present results are also of significance in that they support an account of induced motion that is the same as

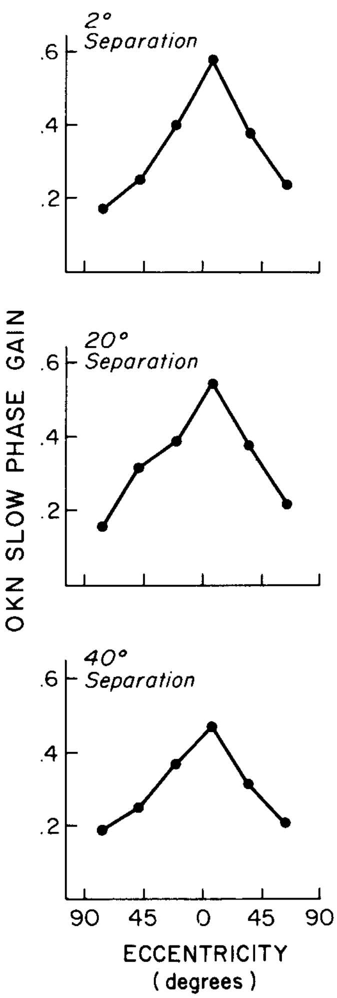

Figure 3. Gain of OKN responses as a function of stimulus presentation for each of three stimulus separations. Stimuli entered the edge of the visual field at the left side of the record, crossed the median saggital plane of the subject at zero on the abscissa, and exited the opposite side of the field near the right side of the record.

that offered for other forms of illusory motion perception, as well as some cases of veridical motion perception. Any pursuit activity, whether to track a moving object, suppress vestibular nystagmus, or in the present instance to suppress OKN, results in apparent movement of the fixated object (Post & Leibowitz, 1982; Whiteside et al., 1965). In the first case, when there is actual target motion, the resulting motion perception is veridical. If vestibular nystagmus is suppressed, the oculogyral illusion results from the required pursuit activity. If the nystagmus being suppressed is elicited through optokinetic stimulation, the phenomenon termed "induced motion" results.[1]

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NOTE

1. The present results do not exclude the contribution of other mechanisms to the induced motion phenomenon. Rather, they suggest that a major component results from the supression of nystagmus by the pursuit system. The results of Nakayama and Tyler (1978), demonstrating simultaneous induced motion in opposite directions, suggest the contribution of other factors, such as relative motion to induced motion, since it is difficult to reconcile such a finding with the nystagmus suppression hypothesis.

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