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FACTORS CONTRIBUTING TO THE DELAY IN THE PERCEPTION
OF THE OCULOGRAVIC ILLUSION*

Brant Clark and Ashton Graybiel

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THE PROBLEM

The purpose of this study was to observe the effects of factors which contribute to the delay in the change in the perception of the horizontal following a change in the direction of resultant force acting on a subject. Five normal and eight labyrinthine defective men were studied in a Slow Rotation Room. Four separate experiments were conducted with changes in direction of resultant force of 20° or 30° acting on the subjects.

FINDINGS

The results showed very small effects of pre-exposure conditions prior to the change in direction of resultant force. On the other hand, delays in the presentation of a luminous target following a change in the resultant force and before settings to the visual horizontal occurred produced major, systematic effects on the perception of the visual horizontal. The results are discussed in terms of the interaction of visual and gravitational cues in producing the lag effect.
INTRODUCTION

If a subject is seated in a fixed position on a human centrifuge at some distance from the center of rotation, he becomes aware of a change in spatial orientation as the velocity of the rotating platform changes. Thus, if he is accelerated from zero velocity in darkness, he will report that he is being tilted away from the center of rotation, his apparent position assuming roughly the direction of the vector sum of the force of gravity and centripetal force. He will also report that dimly illuminated objects in his visual field will move and assume new positions in space (Figure 1). But during this dynamic phase of these visual effects, which have been called the oculogravic illusion (4), the change in the perceived horizontal does not keep pace with the changes in the force environment acting on the subject unless the change is quite slow (1). For example, in a typical experiment a change in resultant force may take no more than five or six seconds whereas the full visual reorientation may require as much as one or two minutes.

More recently Clark and Graybiel (2) have shown that a similar lag effect will occur simply by manipulating the visual field with the force environment held constant. The subject, rotating in darkness at a constant velocity and having set a luminous line approximately to the gravitoinertial horizontal, is suddenly exposed to the lighted cubicle. The strong vertical and horizontal cues in the visual field cause him to reset the luminous line to a position nearer the gravitational (and visual) horizontal than the gravitoinertial horizontal. If the room lights are subsequently turned out, the luminous line will appear to rotate slowly and resume its former position in space. This lag effect also lasts for about two minutes. It was the purpose of the experiments reported here to investigate further the effects of certain selected conditions which might influence the course of these lag phenomena.

PROCEDURE

APPARATUS

All of the observations were made in the Pensacola Slow Rotation Room which is, in simple terms, a carousel which rotates counterclockwise. The subject was seated in an erect position 5.5 feet from the center of rotation and, in each experimental trial, was accelerated quickly to a velocity to produce a change in the direction of resultant force (phi) of either 20° or 30° (Figure 1). The subject was seated in a lightproof cubicle within the room. He was strapped into position in a chair rigidly to the floor, and a Fiberglas head holder was used to maintain the head firmly in position. A collimator mounted directly in front of him contained a luminous line which could be rotated about its center by either the subject or the experimenter. The experimenter was seated in the room directly behind the subject where he could read the position of the luminous line to the nearest 0.5°.
Diagrammatic representation of subject and the "illusions" he experiences when exposed to a change in gravito inertial force relative to himself (angle $\phi=30^\circ$) in the frontal plane.

Figure 1
Schematic Representation of the Factors in the Oculogravic Illusion
SUBJECTS

Five experienced, normal men were studied, all of whom had normal response thresholds to caloric stimulation (13), normal responses to rotation, and, under proper experimental conditions, had perceived the oculogyral illusion. Eight deaf men with bilateral labyrinthine defects also served as subjects in the first experiment. Detailed clinical findings on this group are described elsewhere (7). All were deaf and had abnormal labyrinthine responses.

METHOD

The same general procedure was used in the four experiments to be reported. Each series of observations began with the room stationary. The line was offset clockwise, and the subject set it to horizontal and maintained it in a horizontal position for fifty seconds. The experimenter made a reading of the position of the line every ten seconds. Following different pre-exposure conditions, the room was accelerated quickly to the desired velocity. The subject's task was merely to maintain the luminous line in a horizontal position throughout the trial. The experimenter again made regular observations of the position of the luminous line every ten seconds throughout the trial. Two-minute rest periods were taken between trials. This procedure produced a record of the subject's perception of the horizontal as a function of time following a change in the magnitude and direction of resultant force acting on him. The measure of the oculogravic illusion at each point in time was the deviation of the absolute setting from the gravitational horizontal corrected for any constant error shown in the preliminary, static settings.

Experiment No. 1

The first experiment was planned to determine whether the nature of the pre-exposure visual field would influence the lag effect. It was predicted that pre-exposure to a lighted room would produce a greater lag effect in the perception of the oculogravic illusion than pre-exposure to darkness. The normal and the labyrinthine defective (L-D) subjects made continuous settings of the line to horizontal for two minutes following a two-minute exposure to a lighted room and then after a two-minute pre-exposure to darkness.

Experiment No. 2

The second experiment was identical with Experiment No. 1 except that only the normal subjects were used and that instead of permitting the subject to set the line freely throughout the trial, the line was offset clockwise every fifteen seconds, and the subject reset it.
RESULTS: EXPERIMENTS NO. 1 and 2

Since the results of the first two experiments were similar, they are considered together. An examination of Figures 2-4 shows the lag effect both in normals and L-D subjects; i.e., the deviation of the settings from the gravitational vertical increased with time. In Figure 2 which shows the mean data for normals with continuous settings, there is a clear tendency for the oculogravic illusion to be greater following pre-exposure to darkness after about thirty seconds of rotation. When the offset method was used (Figure 4), the curves overlap at both velocities. Similar lag effects are shown for the L-D subjects, but the pre-exposure to the lighted cubicle shows a greater effect than pre-exposure to darkness at the slower velocity (Figure 3).

To determine the significance of the differences in the light and dark conditions, the mean performance for each subject for the final thirty seconds of the trials was determined. It was found that only one of the six comparisons was significant at the 0.01 level while for all of the others the p values were greater than 0.10. Thus, the only significant difference was in the predicted direction, but all of the differences were quite small. For example, in the case of the lower velocity for Experiment No. 1 for the normal subjects, it can be said at the 0.05 level of confidence that the difference is between 0.5° and 3.2°.

Experiment No. 3

Some incidental observations following Experiments 1 and 2 suggested that if there was a delay in presenting the luminous line following acceleration to a constant velocity, much of the illusory effect would occur in the absence of the luminous line. This experiment was planned to compare the effects of selected delays in presenting the luminous line following the beginning of rotation with the lag effect when the line was visible continuously throughout the trial.

The procedure was similar to that followed in the second experiment in which only the normal subjects were tested. Immediately after the static observations were completed, the subject was exposed to two minutes of darkness, and then the room was quickly accelerated to produce a change in the direction of resultant force of 20° or 30°. In these trials, however, seven conditions of delay in exposure of the luminous line were used. In the first condition, the luminous line was turned on as soon as the room began to rotate as in the previous experiments. For the second condition, the room rotated with the subject in darkness for ten seconds, and then the luminous line was turned on and readings began ten seconds later at twenty seconds. The seven delay conditions were: 0, 10, 20, 30, 50, 70, and 120 seconds. The room rotated for three minutes during each trial, offsets and settings being made every ten seconds. The order of presentation was randomized, and five trials were taken for each delay period at each of the two velocities of rotation.
EXPERIMENT #1. CONTINUOUS SETTINGS, NORMAL SUBJECTS

Figure 2
Mean Values for the Oculogravic Illusion in Five Normal Subjects: Continuous Settings.
EXPERIMENT #1. CONTINUOUS SETTINGS, LABYRINTHINE DEFECTIVE SUBJECT

Mean Values for the Oculogavic Illusion in Eight L-D Subjects: Continuous Settings.
EXPERIMENT #2. OFFSET METHOD, NORMAL SUBJECTS

Figure 4

Mean Values for the Oculogravic Illusion in Five Normal Subjects: Offset Method.
RESULTS: EXPERIMENT NO. 3

The changing pattern in the perception of the visual horizontal as a function of the delay in presenting the target is shown by the two sets of curves in Figure 5. It is apparent that with increasing delay, an increasing amount of the illusory effect had already occurred by the time of the first setting. When the time of delay was short, the subsequent pattern was similar to the settings of the zero delay curve. With longer delays, the nonvisual antecedent effects reached the end of their influence before the potential magnitude of the illusion was reached. Nevertheless, with delay times beyond seventy seconds, the illusion may still be quantitatively increased somewhat even after the target has been presented. At $\phi = 20^\circ$ this declining influence of the presentation of the visual target was present for delay times up to the maximum of two minutes. On the other hand, for $\phi = 30^\circ$ delays longer than seventy seconds appeared to have little additional influence on the setting of the line. This suggests that the magnitude of the effects producing the phenomenon are important in influencing the pattern of this lag effect.

An attempt to give a quantitative approximation of the nonvisual constituent of the oculogravic illusion is found in Figure 6. The upper curves of the two sets of curves are identical with the two zero delay curves, one at $\phi = 20^\circ$ and the other at $\phi = 30^\circ$ (Figure 5). The two middle curves are plots of the initial settings of each of the six longer delay conditions. These curves give an approximation of the nonvisual constituent of the phenomenon, but they are overestimations of the amount of the nonvisual constituent because at the time the reading was made, the light had been on for ten seconds. These points, therefore, include the nonvisual influence plus ten seconds of visual influence. A second approximation was then made by extrapolating the six curves backward in time for ten seconds, the time when the light was turned on. These extrapolations are shown in the two lower curves which give an estimate of the nonvisual constituent alone. It is apparent that the two lower curves at each level of $\phi$ are very similar to the zero delay curves for the first thirty seconds. This would appear to indicate the strong influence of the nonvisual constituent during this period. Thereafter, the zero delay curve becomes and remains well above both estimates of the nonvisual effect. For a change in direction of resultant force of $20^\circ$, all of the means of the six delay conditions were significantly less than those for the zero delay condition ($p \leq 0.05$). The differences at the greater velocity were less convincing, but the differences at 50 and 120 seconds were significant ($p \leq 0.05$). Three of the remaining four were in the predicted direction, but none of the differences was statistically significant.
EXPERIMENT #3. DELAY SERIES, CONTINUOUS SETTINGS, NORMAL SUBJECTS

Figure 5
Mean Values for the Oculogravic Illusion in Five Normal Subjects with Progressively Longer Delay Time in Presenting the Target.
The Nonvisual Constituent of the Lag Effect Compared With the Zero Delay Condition.
Experiment No. 4

The fourth experiment involved a comparison of the oculogravic illusion following two minutes of pre-exposure to two visual targets during rotation with the results of a replication of the zero delay condition in the previous experiment. Thus, the oculogravic illusion was determined following two minutes of setting the line to the perceived horizontal after a rapid acceleration to a constant velocity and following two conditions of fixation of a visual target without a determination of the subject's perceived horizontal.

In the first pre-exposure condition, the subject continuously observed a 1/16-inch circular spot of light placed 17 3/4 inches in front of him. Following two minutes of constant rotation, the spot was turned off, the line of light was turned on, and settings of the line to the perceived horizontal were made as in the zero delay condition. During the second fixation condition, the subject viewed the luminous line set to the mean of the preliminary settings made before rotation began. Therefore, the subject observed the oculogravic illusion during the two-minute delay period since the line appeared to be rotated clockwise from the horizontal. At the end of two minutes of continuous observation of the line, the subject began settings to the horizontal as before. The order of the presentation of the three conditions was randomized, and the final setting was made after three minutes of rotation. It should be noted that the first reading of the oculogravic illusion for the two delay conditions was made at 130 seconds following two minutes of continuous fixation of the target. Again, five trials were taken for each subject, for each fixation condition, and for the two velocities of rotation.

RESULTS: EXPERIMENT NO. 4

The mean oculogravic illusion at 130 seconds following two minutes of setting of the line to horizontal for a phi of 20° was 17.6° and for a phi of 30° it was 30.8° (cf. Figure 5). Following the fixation of the spot, the corresponding means were 15.0° and 23.3°, and following the fixation of the line the means were 15.3° and 26.9°. The following five settings showed a small increase as in Experiment No. 3. The differences in the results at 130 seconds were, however, not statistically significant following the fixation of the spot (p > 0.10 at both velocities). Following the fixation of the line, the difference was not significant for phi equals 20° (p > 0.05), but at a phi of 30°, it was barely significant (p < 0.05). These data when compared with the results of Experiment No. 3, suggest that mere visual fixation during the delay period has a very small influence, if any, on the lag effect of the oculogravic illusion as observed in this experiment.

DISCUSSION

The results of these experiments give additional evidence of a visual and a nonvisual constituent involved in the lag effect in the perception of the oculogravic illusion. They also shed some light on the factors involved and show that in this situation the nonvisual constituent predominates. Graybiel and Brown (5) speculated that the lag effect might
have its genesis either in the end organ or in the time required for the integration of incoming impulses which contribute toward spatial orientation. Regarding the first possibility, de Vries (14) has shown that the time necessary for the stones of the utricle to assume their new position following a change in direction of resultant force is a small fraction of a second. Another possibility at the end organ level would be a prolonged change in the frequency of neural discharge following stimulation. Löwenstein and Roberts (12) have reported such a change in the frequency of discharge of single twigs from the otolith organs of the Thornback ray which terminated within thirty seconds after the cessation of movement of their preparations. But they also reported that when the preparation is held stationary following a tilt "the increased or decreased discharge frequency reverts somewhat toward the initial level remaining, however, significantly above or below it for a matter of minutes." They also point out, "It is clear that the discharge frequency returns in every case to a basic level and that it therefore is unsuitable to furnish a position signal." That is, the change in frequency of discharge of individual fibers per se would not appear to be an adequate cue to produce the lag effect. Consequently, it becomes necessary to look elsewhere for factors contributing to the lag effect, and the time necessary to integrate information from various receptor mechanisms appears to be a likely source. This notion would also be supported by the lag effect at a constant velocity of rotation when passing from a full visual framework to darkness (2).

It has been known for many years that both visual and postural cues interact in the perception of the visual vertical and horizontal (e.g., ref. 3, 4, 15) not only in the case of the oculogravic illusion but also in such effects as the A- and the E-phenomenon. Nevertheless, Experiments No. 1 and 2 show that exposure to a visual framework before rotation begins does not have a substantial influence on the course of the lag effect. On the other hand, it has been shown that when the force environment is held constant and the oculogravic illusion is reduced by exposure to a complex visual framework, a lag effect is again manifested when the visual framework is removed, and the subject observes the luminous line in darkness. That is, the apparent visual horizontal will shift slowly from the visual frame of reference to the gravitational frame of reference (2). It is noteworthy that these two effects have the same general pattern of change over time. This would appear to explain why the pre-exposure to the visual framework did not substantially influence the lag effect.

A comparison of Figures 2 and 3 shows that the L-D subjects have a smaller oculogravic illusion and less lag effect than the normal subjects. This gives further support to the well-established relationship between the oculogravic illusion and the vestibular mechanism (6). Furthermore, the L-D subjects exhibited a much greater variability of response. An examination of the individual curves (not shown) of the L-D subjects showed much variability throughout the two-minute trials for some subjects while others showed a lag effect similar to that of the normal subjects. These results correspond to the variability of the same group of L-D subjects on a parallel swing (8).
The data from Experiment No. 3 support the principle of interaction of visual and gravitational factors in producing the oculogravic illusion. It is also clear that in the absence of vision, certain nonvisual processes produce the major part of the effects which result in a modification of the perceived visual horizontal producing the oculogravic illusion. These nonvisual processes show their influence immediately upon the presentation of the luminous line (Figure 5). It is equally evident that the nonvisual constituent increases for sixty to eighty seconds and then remains relatively constant at least up to three minutes. Following the presentation of the line, the illusionary effect again increases somewhat for sixty seconds or more until it approximates the level of the zero delay condition with the exception of the two-minute delay in which case it remains two or three degrees less than that during the zero-delay condition for the final minute of the observations. Whether the curves for the prolonged delay periods would continue to rise after three minutes is not clear from these data, but it is reasonable to expect that they would not in the light of the fact that the major portion of the lag effects is completed in sixty seconds. The data suggest that the visual constituent of the lag effect would also be found for more prolonged periods of delay because these two curves also level off after about one minute (Figure 5).

The basic neurophysiological mechanisms underlying the lag effect are not known, but many studies have shown visual-vestibular coordination, and it is well known that certain neurons in the visual cortex respond to vestibular stimulation (11). Two experimental findings appear clear from this and other studies. First, if a normal subject observes a luminous line in darkness following an abrupt change in the direction and magnitude of resultant force acting on him, there is a gradual reorientation of the visual horizontal (lag effect), the end result of which is roughly in accord with the gravito-inertial horizontal. Second, if the judgments of the horizontal are delayed, the lag effect is even greater. These experimental results may be understood in terms of what Helson (10) has called pooling, or in this case "cross modality interactions," in processing information from various sense organs. Helson argues, within the framework of his adaptation level theory, that stimuli are not equally weighted in perception, and this would appear to apply directly to the oculogravic illusion in general and to the lag effect in particular. He states that, although some investigators believe that the pooling of cues can involve only present and immediately preceding stimuli, the experimental evidence indicates that these interactions may operate over extended periods.

Helson's notion of differential weighting of cues over time would appear to apply to the lag effect. It would assume that there would be a decrease in the weighting of visual factors and a corresponding increase in the weighting of gravitational factors over time, producing a shift in the perceptual norm. In the static situation, the retinal lines of the horizontal are in accord with the gravitational cues, and there is no conflict in information and hence no problem of differential weighting of cues. On the other hand, when there is a sudden change in the direction of the resultant force, the gravitational cues become disparate with respect to the retinal horizontal. At the outset, the visual cues may be said to have the heaviest weighting in the perception of the horizontal. This is supported by the fact that there is no measurable lag effect when a luminous line is
viewed in darkness during constant rotation and a visual framework is then presented (2). The shift to the visual framework is immediate. Studies by Witkin (e.g. ref. 16) also support the notion of the heavy weighting of visual factors, and recently Hammer (9) has found that there are relatively small constant errors in setting a luminous line to vertical in darkness under zero gravity conditions. Subjects set a luminous line very close to vertical as represented by the position of the retinal receptors, but Hammer did find significantly greater average errors. In the case of the lag effect, this heavy weighting of visual cues decreases with time, and the apparent visual horizontal changes in a series of steps over time (2) as the weighting is shifted to the gravitational cues until the visual horizontal is perceived to be very close to the gravitational horizontal. It would appear, therefore, that these results are an example of the pooling of information from different sensory processes and of changes in weighting over time as suggested by Helson (10).
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Factors Contributing to the Delay in the Perception of the Oculogravic Illusion

Clark, Brant and Graybiel, Ashton

Five normal and eight labyrinthine defective men were studied in a Slow Rotation Room to observe the effects of factors which contribute to delay in change in perception of the horizontal following a change in direction of resultant force acting on a subject. Results showed very small effects of pre-exposure conditions prior to change in direction of resultant force. Delays in presentation of a luminous target following a change in resultant force and before settings to the visual horizontal occurred, however, produced major, systematic effects on the perception of the visual horizontal. Results are discussed in terms of the interaction of visual and gravitational cues in producing the lag effect.
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