reflection. Had we had a precise measure of the lamellar angle relative to the wing surface, the incident angle could have been calculated with accuracy by subtraction from the wing angle, and a straight line fit to points based on the data. Calculation of the refractive index and lamellar thickness would have followed (*12*). Instead, we first computed linear functions (sine squared versus wavelength squared) based on assumed lamellar angles varying from 10 to 30 degrees at 0.1-degree increments, and selected the line of best fit, which corresponded to a lamellar slant of 18.1 degrees. The index of refraction and lamellar thickness were inferred from this line (*12*), and provided the basis for construction of the curve in Fig. 4.

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8 August 1972

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Moving Visual Scenes Influence the Apparent Direction of Gravity

Abstract. *When an observer views a wide-angled display rotating around his line of sight, he both feels his body tilted and sees a vertical straight edge tilted opposite to the moving stimulus. Displacement of the perceived vertical increases with stimulus speed to reach a maximum (averaging 15 degrees) at 30 degrees per second.*

The observer's visible surround influences his orientation and localization in space. Most investigators of these phenomena have been concerned with the effects of tilted scenes on the apparent vertical. They have interpreted their findings as the outcome of a conflict between spatial coordinates given on one hand by the dominant orientation of visible contours and, on the other, by the direction of gravity (*1*).

We now report that a visual surround rotating around the observer's line of sight induces tilts of the apparent upright ranging up to 40°. The moving visual displays entailed no cues to visual orientation that could conflict with those of gravity. Consequently, the motion as such caused the tilt. Shortly after initiation of motion, the observer both felt his body rolled laterally and saw a stationary edge turned in the direction opposite to the rotation of the display. Accordingly, the effect of the moving surround was equivalent to displacing the direction of gravity in the direction of rotation. It can be accounted for by assuming that neurally encoded signals of visual motion modulate signals from gravireceptors at some level of the nervous system, an interpretation consistent with neurophysiological results (*2*).

In order to measure the effects of seen motion on visual and postural orientation, we designed two experiments in which our subjects were required to readjust continuously the position of either a visual test edge or the orientation of their own body to the apparent vertical. The corrections made to compensate for perceived tilt were continuously recorded.

In the first experiment, the subject monocularly viewed a display restricting his field of view to 130° of visual angle. At its center, a target disk, subtending 32° of visual angle, carried a central fixation point and a straight edge initially set vertical. The disk was mounted on a shaft whose rotation was controlled by the observer. A potentiometer attached to the shaft allowed continuous recording of the observer's settings. Just behind the target disk, mounted on a concentric shaft driven by a variable speed motor (2° to 130° $\sec^{-1}$), was a much larger disk subtending 130° of visual angle. This disk formed a visible ring around the target and was covered with the random pattern of spots that precludes edge orientation cues.

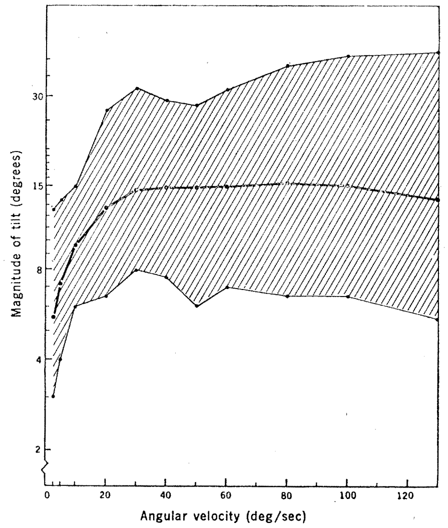

Fig. 1. Magnitude of apparent tilt in relation to stimulus velocity; geometric means on solid line. The shaded region represents the range of single values of the seven subjects. Data for individuals are highly replicable but inter-individual variations are large.

After initiating rotation of the large disk, observers experienced a rapidly increasing tilt of the target edge in the direction opposite to the rotation of the field. The tilt reached its steady state within an average of 18 seconds. When observers were asked to set the target edge to the apparent vertical, the amount of tilt increased with the angular velocity of the ring up to 30° $\sec^{-1}$ and remained approximately constant up to the maximum speed tested of 130° $\sec^{-1}$ (Fig. 1). These settings were obtained in sequence by increasing the angular velocity of the ring every 30 seconds. Among seven subjects the tilt averaged 15° and in one observer, exceeded 40°.

The magnitude of these effects militates against the notion that small torsional eye movements can account for the effects (*3*). In other experiments, tilt increased with stimulus area and stimulation of the more peripheral parts of the retina exerted a disproportionately strong influence on the apparent tilt of the target (*4*). This result ties in with experiments with stimuli that rotate around the vertical axis of an observer; in this case, stimulation of the periphery also dominates the induction of apparent motion of the body (*5*).

To demonstrate corresponding effects on postural orientation and, therefore, to examine the possibility that the tilt effect might not be an exclusively visual phenomenon, we designed a second experiment. Subjects were seated in a moving-base airplane trainer (Link GAT-1). Using a control stick, they were able to adjust the position of the trainer to subjective upright. Continuous repositioning was required to compensate for a lateral tilt disturbance (sum of 16 input frequencies from 0.05 to 0.3 hz) applied to the drive of the trainer. The resulting small but continuous and unpredictable lateral tilts (roll) of the trainer were introduced to force the observer to reindicate repeatedly his postural vertical and to minimize sequential effects. During the first (control) phase, the subject, fix-

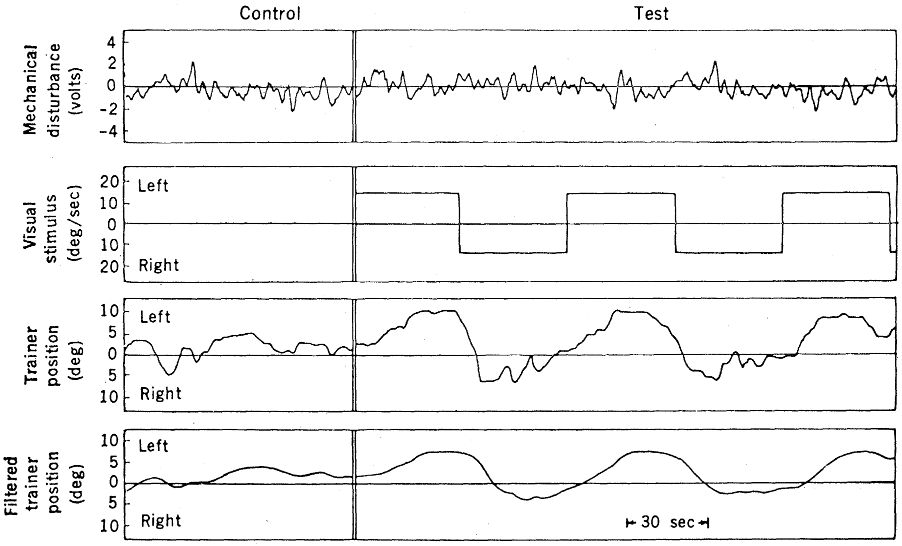

Fig. 2. Settings of one subject to postural upright in the Link trainer. Traces show (top to bottom) the disturbing signal delivered to the drive of the trainer, the velocity of the moving visual display, the roll angle of the trainer (zero represents true vertical), and the position of the trainer recorded through a filter with high-frequency cutoff (10-second time constant). In the control phase (stationary visual stimulus) the subject adjusted the roll angle of the trainer by compensating for its continuous random motion. His subjective postural upright, as indicated by the average trainer position, was slightly displaced to the left. In the test phase (moving visual stimulus), the subject shifted his estimated postural vertical toward the direction of the moving stimulus. The asymmetry in deviation from the true vertical corresponds to the bias of the perceived upright in the control phase.

ating a small spot positioned in the midline of the occluded front window, indicated his average postural upright while a stationary pattern of equally spaced black and white horizontal stripes, 2.3° in width, was projected onto the right and left side windows of the trainer (Fig. 2). The patterns were cast from a single projector, mounted on top of the trainer, by means of an optical system. This arrangement (like that of the first experiment) entailed no cue to orientation in the plane of roll movements. The side windows of the trainer subtended 52° by 52° of visual angle and were centered 68° peripherally. They were covered with translucent screening for light projection. During the second (test) phase, the pattern was set in motion so as to move upward on one side and downward on the other.

Initiation of pattern motion induced a sensation of slowly increasing lateral tilt of the observer's body counter to the direction of rotation. When the subject adjusted the trainer to regain the perceived upright, he rolled the cabin of the trainer in the direction of the moving stimulus (Fig. 2). Tilt reached steady state after an average of 17 seconds. With stripe velocities of 14° to 26° per second, the lateral tilt of the perceived "upright," indicated by the trainer's position, averaged 8.5° in four subjects. This effect can only be attributed to the motion of the visible pattern.

The fact that the tilt effect during rotation of the visible surround is common to both visual and postural orientation supports the explanation that a shift occurs in the internal representation of the gravity vector. However, the limitation on the amount of shift is puzzling at first glance. One might expect that continuous motion of the surround would lead to a continuous sensation. In fact, the sensation of motion of both the body and the visual target is continuous (*6*), as opposed to the sensation of displacement. What occurs is a paradoxical illusion of continuous motion of the body and the visible target opposite to the display, combined with limited sensed displacement of both in that direction. The limitation of displacement must be ascribed to some constraint. Such a constraint may be provided by veridical graviceptive information given by excitation of the otoliths and pressure receptors (*7*). Since the display itself contains no explicit indication of the vertical, its motion can only alter the subjective vertical by modulation of graviceptive information. Therefore, a simple model represents the perceived vertical (given by vestibular and somatosensory excitation), as subject to displacement of a substantial but limited extent by the visual input (*8*).

If rotation of the scene is equivalent in its effect to shifting the direction of gravity, then a real displacement of the gravitational vector should result in a corresponding change in perceived visual and postural orientations. The human centrifuge accomplishes this shift in the direction of gravity by inertial means, without body movement. The resulting so-called oculogravic illusion, consisting of a slowly increasing tilt of the visual and postural vertical, accompanies the shift in the direction of gravity (*9*). This equivalence also implies that the stability of visual and postural orientation with respect to gravity is in part dependent on the motion occurring within the observer's visual field (*10*).

Among other practical consequences of this equivalence is an explicit recognition that gravitational changes may be simulated by moving visual fields. The uncontrolled consequences can be disorienting, but under proper control the effect may be economically used to simulate flight conditions for research and training purposes.

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References and Notes

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6. An analogous illusion of continuous body rotation occurs when a visual surround rotates around the observer's vertical axis. In this instance graviceptive information is irrelevant, and because there is no other constraint, the subjective displacement is unlimited (*5*).
7. Such considerations may in part explain the difference in the magnitudes of tilt obtained in our two experiments. In the posture experiment, the observer receives changing graviceptive information from pressure receptors and otoliths, which indicate the actual tilt of his body.
8. We include somatosensory information here because we found that a limited tilt was also induced by the moving display in a patient whose vestibular nerves were severed bilaterally because of a neuroma.

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10. As one consequence, large oscillating visual displays increase postural instabilit [S. Wapner and H. A. Witkin, *Amer. J. Psychol.* **63**, 385 (195 H. A. Witkin and S. Wapner, *ibid.*, p. 31.
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Synthetic Rat Scotophobin Induces Dark Avoidance in Mice

Abstract. *Two independent research groups replicate alteration of dark preference to dark avoidance by mice injected with synthetic scotophobin, a pentadecapeptide.*

Several groups of workers have attempted to correlate behavioral changes induced by training rodents or goldfish with the appearance of a new molecular substance in the brain (*1*). One method of detecting this newly formed substance involves a bioassay technique, referred to as the chemical transfer of learned behavior. This method includes preparation of more or less purified brain extracts from trained donors as well as from untrained control or differently trained donors, followed by injection of these brain preparations into naive recipients. The bioassay is considered positive when only the recipients of "trained brain" extracts exhibit behavior resembling that acquired by the trained donors. The problems entailed in experiments of this sort have been pointed out (*2*).

This method was used by Ungar to isolate and assay a factor from rats that transferred dark avoidance to mice (*3*). The identification and synthesis of this factor, a pentadecapeptide named scotophobin, have been reported (*4*). The importance of independent replication of the scotophobin studies has been emphasized in a summary on the state of the art by the Psychopharmacology Research Branch of the National Institute of Mental Health (*5*). Transfer of learned dark avoidance by means of crude or partially purified brain extracts has already been reported by six groups of workers (*6*). The groups, however, reported negative results (*7*). One of us has also observed the dark-avoidance inducing effect of synthetic scotophobin in the goldfish (*8*). We now report the results obtained by two independent research groups at Illinois and Michigan on the dark-avoidance inducing effect of synthetic rat scotophobin in mice.

In both laboratories, male albino Webster mice (obtained from different sources) were housed with a light-dark cycle of 12 hours of light followed by 12 hours of darkness.

The mice weighed about 20 g (Illinois) or 30 g (Michigan). The Michigan group housed mice in individual transparent cages and the Illinois group kept six mice in each transparent or metal cage. The Illinois group handled its animals for a week before screening them, while the Michigan group did not give any special handling to its mice.

Both laboratories used exact replicas of Ungar's test apparatus (*6*). In each test, the mouse is allowed to wander freely for 3 minutes between black and white compartments. The score is the total number of seconds spent in the dark box. All mice were screened for initial dark preference, and mice that did not meet the criterion were discarded. About 90 percent of the Illinois mice met a criterion of 85 percent dark-box time in each of four successive screening trials, while only about 50 percent of the Michigan mice met a lower criterion of 50 percent dark time on a single screening trial.

Scotophobin synthesized by W. Parr was supplied by G. Ungar to both laboratories, but the preparations were treated differently, and the degree of hydrolytic degradation was not identical. The Michigan group received its scotophobin as a solution in methanol (1.0 mg scotophobin per milliliter of methanol) that had been transported at room temperature for several days and was subsequently refrigerated for several weeks during the course of experimentation. The Illinois group received scotophobin as a gummy solid, dried from the methanol solution. The material was dissolved in distilled water at the time of use, and any unused remainder was lyophilized. The preparations ranged from 50 to 80 percent purity. Although the precise purity and the number of decomposition products were not determined during these early experiments, the course of decomposition is now routinely followed by the Illinois group by means of the microdansylation method, followed by two-dimensional chromatographic separa-

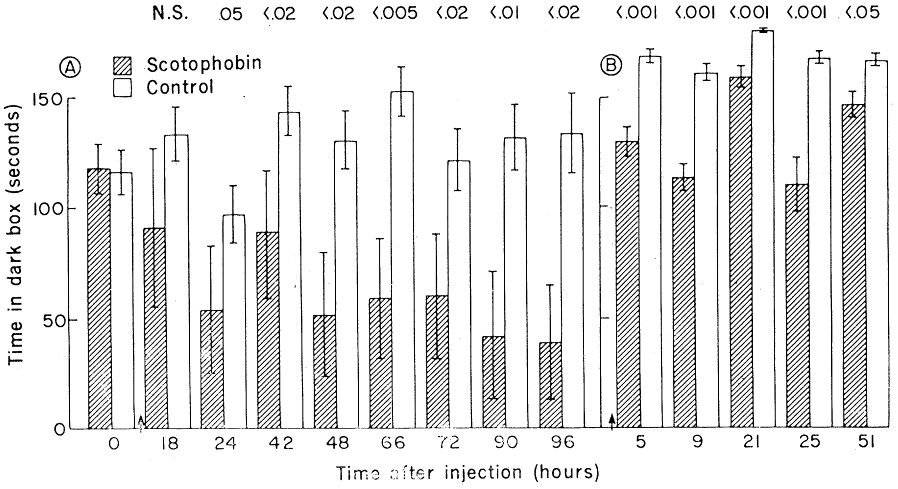

Fig. 1. Dark avoidance induced by synthetic scotophobin. Time of injection is indicated by arrow. Time in the dark box is the number of seconds out of the total time of 180 seconds ± the standard error. Numbers on top indicate P values obtained by the U test. N.S., not significant. (A) Michigan results with 3 μg of scotophobin per mouse, $n = 6$ in experimental groups and 11 in control groups. (B) Illinois results with 0.8 μg of scotophobin per mouse, $n = 20$ in all groups.