

Perception of Linear Horizontal Self-Motion Induced by Peripheral Vision (Linearvection) Basic Characteristics and Visual-Vestibular Interactions*

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Received April 24, 1975

Summary. The basic characteristics of the sensation of linear horizontal motion have been studied. Objective linear motion was induced by means of a moving cart. Visually induced linear motion perception (linearvection) was obtained by projection of moving images at the periphery of the visual field. Image velocity and luminance thresholds for the appearance of linearvection have been measured and are in the range of those for image motion detection (without sensation of self motion) by the visual system. Latencies of onset are around 1 sec and short term adaptation has been shown. The dynamic range of the visual analyser as judged by frequency analysis is lower than for the vestibular analyser. Conflicting situations in which visual cues contradict vestibular and other proprioceptive cues show, in the case of linearvection a dominance of vision which supports the idea of an essential although not independent role of vision in self motion perception.

Key words: Visual-vestibular interactions — Linearvection — Otoliths — Motion perception

The role of the periphery of the visual field in self-motion detection has been extensively studied both in man and in animals; the interaction between visual and vestibular cues is now established from psychophysical and electrophysiological data (Brandt *et al.*, 1971; Brandt *et al.*, 1972; Brandt *et al.*, 1973; Dichgans *et al.*, 1972; Dichgans and Brandt, 1973; Dichgans *et al.*, 1973; Gibson, 1954; Maekawa and Simpson, 1972; Mach, 1875; Young and Henn, 1974; Young and Oman, 1974; Young *et al.*, 1975). An essential result is that vision can contribute to the sensation of self-motion during rotation at a constant velocity whereas the labyrinthine receptors, whose specific stimulus is acceleration, can only signal changes of velocity.

* Preliminary reports of this work have been presented in the form of a short communication (Berthoz *et al.*, 1974) and at the European Brain and Behaviour Society Workshop on: "Vestibular function and behaviour" (Pavia, Brain Research, Special issue, p. 17, 1974).

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Most studies thus far have been restricted to circular movements and the corresponding sensation (circularvection). Linear motion sensation, which will be henceforth called "linearvection" (LV), was however investigated by Lee *et al.* (1974), who, because of the strong postural effects produced by small displacements of a moving room, put forward the hypothesis that vision is an "autonomous" and also the "principal" kinaesthetic sense.

The aim of the present work is to establish quantitatively the characteristics of the sensation of linear motion induced by movements of the peripheral visual field in a horizontal direction parallel to the anterior-posterior axis of the human body. A typical instance of such a sensation occurs while sitting in a non-moving train and a neighboring train starts moving. The current experiments were consequently designed to impose controlled movements of either the visual field or the body of the subject, thus allowing a rigorously defined visual-vestibular interaction.

Methods

The experimental apparatus is shown in Fig. 1A. It allows the projection of a moving 35 mm film loop on a screen which was fixed on a mobile cart. The screen was located in the upper part of the visual field of a seated subject at a distance of 0.5 m from his head (Fig. 1C). Two lateral mirrors, inclined by 45° with respect to the vertical, gave two virtual images of the screen which were in a vertical plane parallel to the sagittal plane of the head (Fig. 1B). These images were 0.8 m lateral to each eye of the subject. The projector was equipped with a servo-motor whose angular velocity was measured by a tachometer mounted on the motor-drive itself. The calibration of film velocity was made in m/sec (cf. Appendix for conversion into angular velocity).

Image velocity on the screen (V_i) varied from 0–2 m/sec with an accuracy of 5%. The subject, whose head position was fixed by a chin rest, could view the moving images through a black box equipped with modifiable side windows which limited the visual field between 20° and 70° away from the sagittal plane on each side (Fig. 1B). On the upper part of the black box a variable opening allowed a view of the screen. According to the experimental conditions the subject was instructed either to fix a black cross which was drawn on the upper screen, or a luminous cross inside the black box and in front of the subject.

The cart could roll on wheels guided by rails under the control of two servo-driven torque motors. Cart velocity varied from 0–2 m/sec; it was accurate to 5%, and was recorded by a tachometer attached to the cart. Both the image velocity (V_i) and the cart velocity (V_c) were programmed by a HP 5452 computer and could be controlled independently. In order to eliminate the influence of auditory cues on velocity detection, the subject's ears were covered with earphones delivering a 75 dB broad spectrum noise. Care was taken to limit all vibrations. However, tactile and pressure cues, particularly on the chin, were sometimes reported as used by the subjects and were undoubtedly used increasingly as the stimuli were repeated.

Magnitude Estimation of Subjective Velocity

The sensation of self-motion experienced by the subject was measured by the method of magnitude estimation (Lipetz, 1971). A lever fixed to the cart on the right side of the subject could move forward or backward in the sagittal plane, starting from an upright zero position. Two springs were attached to the beam so that the lever returned to the upright position when no force was exerted. To enable calibration of the velocity magnitude estimation while the subject was looking in the box, two metal reference posts were placed both behind and in front of the zero level position. These posts, which could be sensed by the fingers as the subjects moved the lever forward and backward, were associated with positions corresponding to 50% and 100% of the deflection corresponding to the reference velocity for magnitude estimation. The rotation of the lever was recorded by a potentiometer whose output was fed into the computer, together with the image velocity (V_i) and the cart velocity (V_c).

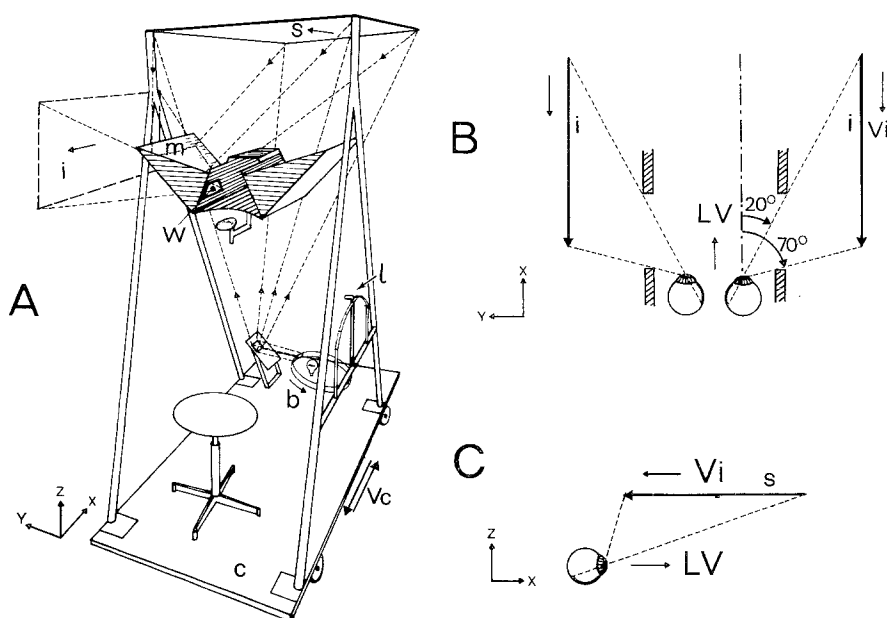


Fig. 1. Experimental apparatus. (A) The subject is seated on a cart (c). A band of film (b), on which are printed randomly distributed signs (letters, points, crosses, etc.), is moved by a projector. The image of this band is projected on a screen (s) (surface 1.6 m², distance to the horizontal plane of the eyes 0.5 m). The subject, whose head is maintained in a normal upright position by a chin rest, looks through three openings in a box: two lateral windows (w), and an opening above the head. Two virtual images (i) of the screen (s) are given by two mirrors (m) tilted at 45° angles. The subject is required to give continuous magnitude estimations of his subjective sensation of linearvection (LV) when the film is in motion at the speed V_i , or when the cart is moving at the speed V_c , by using the hand lever (l) on his right side. This lever is also used to control V_i in the active procedure. (B) Schematic view of image position (i) from above, with respect to the subject's eye (angle of vision: 20° to 70°). LV indicates direction of subjective velocity (forward LV for backward V_i). (C) View from the right indicating the position of the screen (s). Same notations as in A and B

1. For each subject, the film velocity was initially set at 1 m/sec, which was the mean value of V_i to reach maximum LV. The subjects were told that the sensation of LV experienced in this condition was to be taken as the maximum (100%) of the magnitude estimation and should correspond to the maximum forward (or backward) position of the hand lever.

2. V_i was subsequently reduced to 0.5 m/sec and the subjects were instructed that the LV they experienced was to be indicated as 50% of the maximum V_s . The position of the hand lever was then to be set at the halfway point between zero and maximum. Although we recognized a non-linear relationship between $V_i V_s$, the choice of 0.5 m/sec for V_i as corresponding to 50% evaluated LV produced a consistent but non-linear scale.

3. V_i was then moved by randomly distributed steps of 0.1 or 0.2 m/sec in repeated sequences. The subjects had to indicate V_s with various positions of the hand lever.

The test was repeated until the subject could successfully return to the 100% and 50% positions whenever V_i reached the initially defined values. In addition, the subjects had to indicate the LV associated with the intermediary values of V_i (in a repeatable manner). Only those subjects (approximately 80%) who could perform this task correctly were subjected to further tests.

Movement Direction Detection

The same lever was also used for a simple all-or-none direction indication for visual-vestibular experiments when the cart was actually moving. A simplified version of this method consisted of a switch which could signal forward-zero-backward motion.

Active Modification of Film Velocity

The lever was also used in some experiments for control of the image velocity by the subject. By varying the position of the lever the subject could vary the image velocity forward or backward from 0–1 m/sec: this procedure was used for active threshold evaluation or for the study of adaptation to a prolonged exposure to a moving visual scene.

Luminance Threshold Measurement

The stimulus for all LV tests was a pattern of randomly distributed black letters (Letraset) moving on a white background (the overhead screen). The mean luminance of the overall screen with patterns was 80% of the background luminance (the ratio of white to black areas). The contrast between letters and background was always approximately 0.9. Velocity was constant in each trial and varied between trials in discrete steps between 0 and 1 m/sec. An active LV estimation was made by the subjects who could continuously adjust the visual stimulus luminance level by a potentiometer regulating the light level of the film projector. The subjects reduced the luminance level until they felt a disappearance of LV. In order to reduce the effects of light adaptation, measures were made at least 5 min after the beginning of each exposure. Luminance was measured on the projecting screen by a SEJ photometer. In the case of low luminance levels, the photometer sensitivity was increased 250 times by reducing the image of the screen optically, thus allowing accurate measurements at a level of 10^{-4} Cd/m².

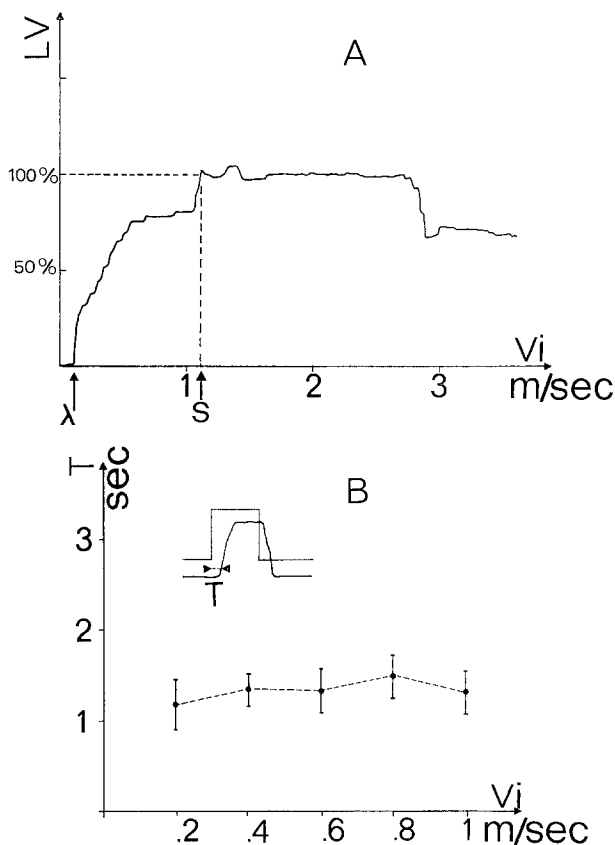


Fig. 2A and B

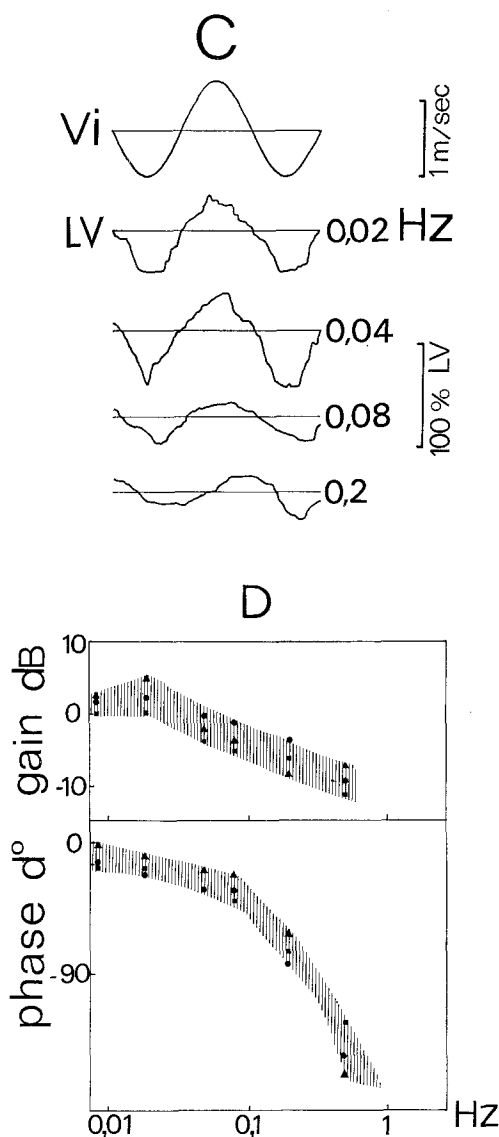


Fig. 2. Typical threshold, saturation, and latency of the subjective sensation of forward linear velocity (forward LV) induced by a backward motion of images at the periphery of the visual field. (A) Typical variation of the magnitude estimation of LV with increasing image velocity for one subject. λ = threshold; S = upper limit of increasing LV (saturation). Notice the drop of LV when V_i exceeds 2.8 m/sec. V_i increased linearly with time (0.01 m/sec^2). (B) Latency T of the onset of forward LV for different steps of image velocity (V_i). Mean and standard error of mean for 10 subjects. (C) Records of LV induced by sinusoidal variations of image velocity (V_i). First trace is reference sine wave for V_i (constant amplitude 0.8 m/sec). From top to bottom: successive samples of magnitude estimation of LV at different frequencies of input V_i . (D) Gain ($\log_{10} = \frac{\text{estimated LV amplitude}}{\text{image velocity (m/sec)}}$) and phase of LV for different frequencies of input V_i

Results

General Features: Latency of Onset and Frequency Analysis of Linearvection

The basic characteristics of the motion sensation induced by linear motion of the visual scene were first investigated. It was observed that linearvection (LV) appeared only above a threshold of film velocity (Fig. 2). When the subjects were asked to estimate the magnitude of LV with the hand lever, the curves obtained with increasing image velocity (V_i) generally had the shape shown in Fig. 2A. This curve was obtained from a single trial with V_i increasing linearly with time at a slow rate (0.01 m/sec^2 acceleration). Above threshold the sensation of motion clearly increased with V_i . When the upper screen was used, a distinct sensation of linear motion generally involved the entire frame surrounding the moving scene. A preliminary set of experiments was designed in order to determine the pattern of visual images which would induce the strongest LV. It was found that the classical optokinetic stimulus made of vertical bars was not as effective as a random pattern. Consequently, the pattern of randomly distributed letters whose characteristics have been described in the methods section was finally used.

It was noted that when naive subjects were submitted to the visual stimulations for the first time, a period of up to 10–20 sec could elapse before they actually reported LV. The current latency for the onset of linearvection was measured by applying a step of velocity and asking the subjects to indicate the onset of LV. This procedure is summarized in the insert of Fig. 2B. The latency T is plotted for forward LV. The delay introduced by the reaction time and manipulation time of the lever has been deducted (approximately 0.4 sec) following a distinct series of experiments in which this time was measured by itself.

The value of V_i which gave saturation of LV (Fig. 2A) was measured by asking 10 subjects to indicate the film velocity above which they did not feel any increase in LV. The mean fell in the range $V_i = 0.8\text{--}1 \text{ m/sec}$ for most subjects. The value $V_i = 1 \text{ m/sec}$ was then taken as 100% for the calibration of LV.

It was expected from previous observations on circularvection that visual detection of linear movement would be more effective in a rather low frequency range. This was studied by a frequency analysis of reported LV measured by the continuous magnitude estimation procedure. (The subject indicates the intensity of LV forward or backward with the lever). Figure 2C and 2D show respectively a sample of records and a Bode plot of the input image velocity — output linearvection, gain and phase data for three subjects. In Fig. 2C it can be observed that the gain shows a rather small drop (less than 10 dB) between 0.01 and 1 Hz. The phase however decreases sharply and at 0.8 Hz, LV is practically in opposite phase with image velocity.

Image Luminance and Velocity Thresholds for the Appearance of Linearvection

The thresholds for the appearance of LV have been measured as a function of image luminance and velocity. The purpose of this set of experiments was to determine if LV thresholds were close to physiological thresholds for the detection of image motion in the periphery.

The influence of luminance was determined by measuring the thresholds of differential luminance levels (ΔL) (see methods) for which LV could be elicited at

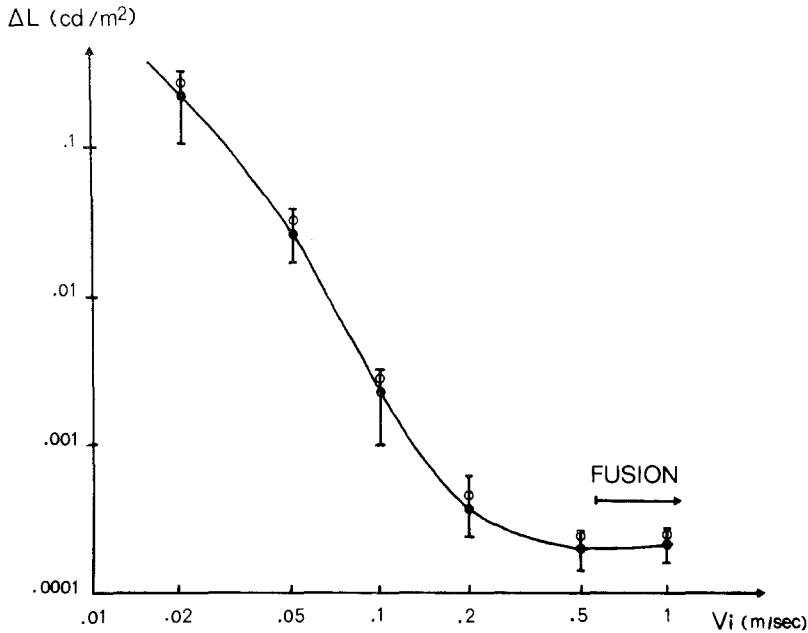


Fig. 3. Differential luminance thresholds for the onset of motion sensation (LV) at different velocities of the visual image (V_i). Differential thresholds of luminance (ΔL) have been determined in the experimental conditions of Fig. 1 (see text). The data points obtained for different magnitudes of V_i (●) indicate mean values and standard deviations. The values obtained by Daniel (1959) with a stationary 1° angular diameter spot, projected at the periphery of the visual field (50° angle) are plotted for comparison (○)

different image velocities (V_i). Figure 3 shows the results for 6 subjects. The values of ΔL which are necessary to elicit linearvection decrease very rapidly with increasing V_i . They reach a minimum for values of V_i where there is a fusion between the black moving pattern and the white background. These data have been compared with results obtained by Daniel (1959). In the experimental conditions used by Daniel the subject was shown a white spot at the periphery of the visual field and was asked to detect the presence of the spot. This spot had a variable angular diameter and was presented on a background of different luminances, at various positions at the periphery. L for which the subject could detect the presence of the spot for all these conditions was measured.

The results of Daniel for 1° angular diameter spot (which is approximately the size of the letters, dots and signs used in our experiments) presented at a 50° lateral angle, show a similarity with the luminance threshold ΔL for LV. Even if the experimental conditions of Daniel and ours were somewhat different, this suggests the luminance thresholds for LV are very close to the absolute luminance thresholds for image detection.

The thresholds (λ) of image velocity which can induce linearvection were measured, as already discussed under methods, using two procedures, passive and active. The results of the passive procedure are shown in Fig. 4A. The insert shows how λ was determined for increasing (λ^+) and decreasing (λ^-) variation

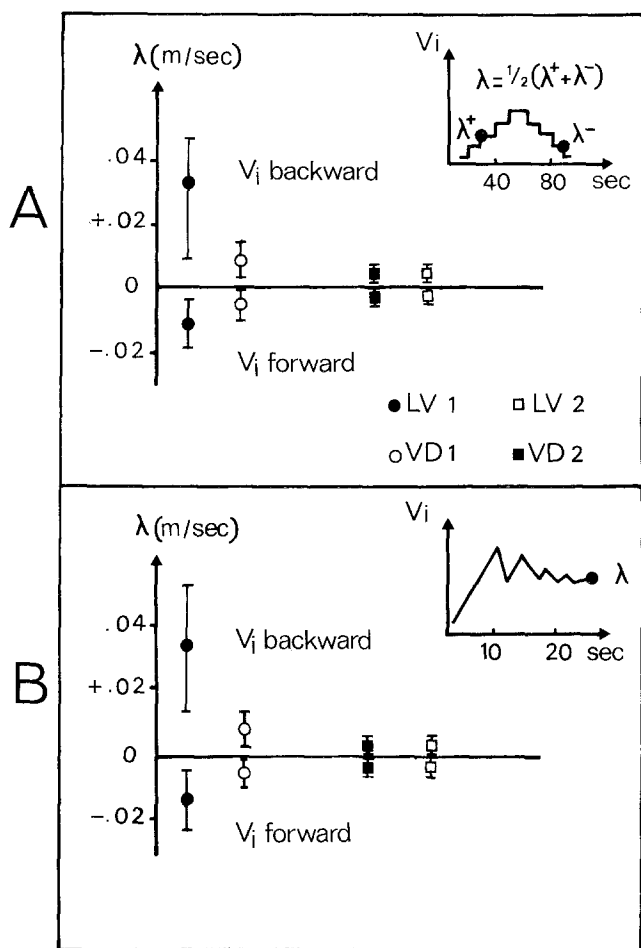


Fig. 4. Thresholds (λ) of image velocity (V_i) for the appearance of linearvection (LV) and for the velocity detection (VD) of image motion. The mean thresholds and standard deviations have been obtained for 10 subjects. The stimulus is presented either peripherally in the side windows alone (circles, LV₁ and VD₁) or simultaneously in the side windows and overhead with a fixation point within the overhead screen (squares, LV₂ and VD₂). Forward V_i induces backward LV and vice-versa. (A) Passive procedure: The stimulus velocity (V_i) is controlled by the experimenter. Thresholds (λ) for forward or backward LV have been determined for increasing (λ^+) and decreasing (λ^-) image velocities (see insert). In the moving field, the linearvection thresholds (LV₂) are as low as the thresholds for detection of stimulus velocity (VD₂). (B) Active procedure: The subject himself adjusts the stimulus velocity (V_i) to the thresholds values for development of LV. λ has been determined asymptotically (see insert). All notations are identical with those in A

(0.002 m/sec steps) of V_i . The values of λ are plotted as positive when forward LV was induced (i.e. backward V_i) and vice-versa. The aim of this experiment was also to compare LV thresholds with image velocity detection (VD) thresholds. Hence, for each subject these thresholds were measured successively in two conditions: 1. with fixation of a point inside the black box, straight ahead of the

subject, but dissociated from the moving visual field; and 2. with fixation of a cross on the upper screen (see methods). These two conditions gave two sets of results, plotted as LV_1 , VD_1 (linearvection and image detection without field centered fixation) and LV_2 , VD_2 (same but with field centered fixation). These results show that thresholds for LV are of the order of 0.03 m/sec in Condition 1, and at the limit of image motion detection (less than 0.01 m/sec) in Condition 2. It can then be concluded that with our experimental device the thresholds for forward linearvection were of the order of magnitude of image velocity detection by the visual system. The thresholds for backward LV were found to be systematically smaller than those for forward LV. The active procedure (Fig. 4B) gave results which were very similar to those obtained with the passive procedure.

Adaptation of Linearvection

It is known from field experiments with vehicle drivers that exposure to a long duration constant velocity leads to underestimation of vehicle velocity (Denton, 1971; Salvatore, 1968; Schmidt and Tiffin, 1969). The effects of prolonged exposure to linearvection¹ were tested by asking the subjects to maintain their LV constant through varying the velocity of the moving field with the hand lever. The results are shown in Fig. 5 for one subject with different initial velocities of the moving film. The subject increased V_1 with time, indicating a slow adaptation to the effect. The magnitude of the increase is dependent upon the initial film velocity. In Condition I (low initial velocity) the increase of V_1 is only from 0.15–0.2 m/sec. It is maximum for Condition III (0.4–0.85 m/sec). The maximum film velocity attained in Condition IV could not be greater than 1.2 m/sec since above this value the saturation effect of LV described in Fig. 2A comes into play and the subjects cannot obtain any increase in LV for higher values of V_1 . The time constant of the adaptation of LV as demonstrated by this experiment is approximately 30–50 sec. It is possible that if experiments had been prolonged up to several hours, other fluctuations would have been noted but long term adaptation has not been investigated here.

Qualitative Investigation of Visual-Vestibular Interactions

In order to determine qualitatively the nature of visual-vestibular interaction in the case of linearvection, horizontal linear movements of the visual field and of the subject himself (cart motion) were combined. In this case the subjects were instructed to indicate the continuous variations of cart velocity (magnitude estimations of cart velocity) under two conditions: 1. with eyes closed (Figs. 6, 7A) and 2. when viewing a visual scene which was moving at constant velocity

1 The term 'adaptation' seems here to be approximate as it is often used when a physiological response decreases with prolonged stimulation. However, this term is also restrictive in the sense that it tends to be used for describing a peripheral event. In the present case no proof can be obtained, with the procedure used, that this decrease of LV with time is due to a central organisation or to an adaptive property of the retina itself.

The alternative term is 'habituation' which is generally attributed to a central process and it is known (Young *et al.*, 1973) that a selective habituation of vestibular nystagmus can be due to visual stimulation. However, habituation is used to designate a decrease in response to repeated (and not prolonged) stimulation. The difference between these two conditions will be dealt with in a subsequent paper.

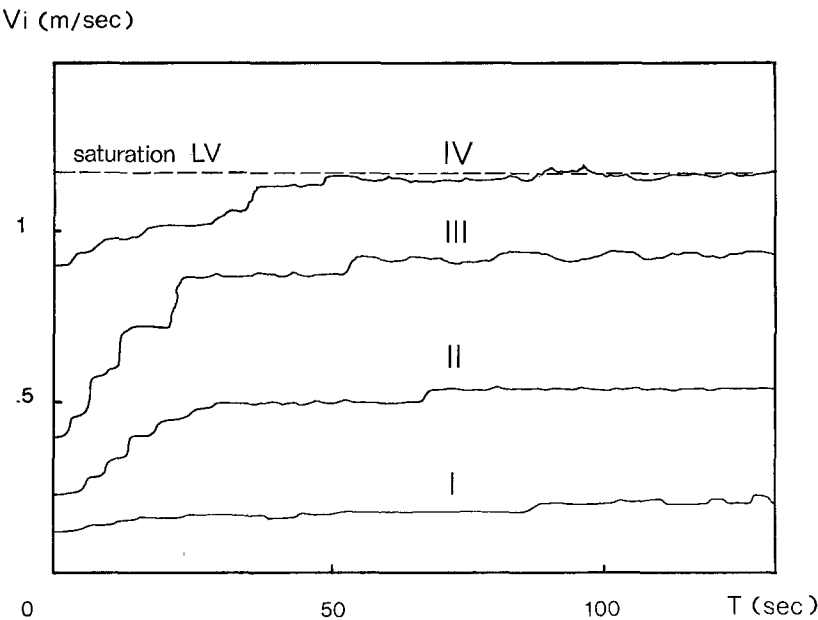


Fig. 5. Adaptation of linearvection during prolonged exposure to a constant velocity moving scene. In this experiment the subject actively controls the velocity of the visual stimulus (V_i) so as to keep his sensation of self-motion (LV) constant. Response curves (I, II, III, IV) are drawn for different initial film velocities. The increase of film velocity (V_i), due to the progressive adaptation of linearvection, is limited in the case of LV by a saturation effect (loss of LV for high film velocities as shown in Fig. 2)

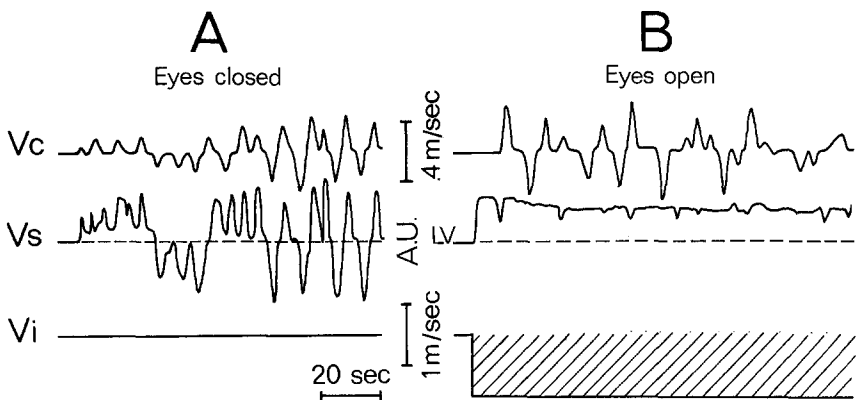


Fig. 6. Interaction of subjective velocity sensation (V_s) induced by conflicting motion of the visual scene and by the translational velocity (V_c) of the cart. (A) Vestibular detection of linear motion with eyes closed. From top to bottom: cart velocity (V_c), subjective velocity (LV) — (arbitrary units) and image velocity (V_i). Note that the subject detects the variations of cart velocity well, with a slight delay. (B) Conflict between a constant velocity visual scene and oscillating cart velocity. From top to bottom: cart velocity, subjective velocity (combination of vestibular induced motion sensation and LV) and image velocity (which is constant, equal to 0.5 m/sec moving backward and inducing a forward LV). Note that the subject indicates a subjective velocity which is always forward, even during periods when the cart is moving backward

backward inducing forward LV ($V_i = -1$ m/sec) (Fig. 6B). V_i was always measured relative to the cart and was purposely chosen at a saturation value for LV in order to induce a maximum forward motion sensation. The cart velocity consisted of pseudo-random slowly varying movements forward and backward as indicated in the upper tracings of Fig. 6. The subjects indicated continuously with the hand lever the magnitude of their subjective velocity (V_s), which here was a combination of visually-induced LV and vestibular sensation of motion. Although the velocity of detection was rather good in the eyes closed condition (Fig. 6A), in the $V_i = \text{constant}$ condition, for which the visual cues were frequently in conflict with vestibular and other kinaesthetic cues, the subjects generally reported the sensation of a constant forward LV (as indicated by the second trace on Fig. 6B). Only transient suppressions of LV were occasionally observed associated with rapid changes of cart velocities either forward or backward.

These results indicate the very powerful central action of visual information from the periphery of the visual field concerning linear self-motion. They also suggest that whenever the visual motion information is presented, it tends to dominate vestibular cues. However, the experimental conditions of Fig. 6 are such that visually induced motion sensation was saturated and vestibular stimulation could have been close to threshold values; this would lead to an underestimation of vestibular motion detection due to these limitations. For this reason another set of experiments was designed, in order to carefully quantify both visual and vestibular stimulation. The necessity for carefully defining the condition of vestibular stimulation led us to perform, in addition, a simple but quantitative prediction of vestibular detection before presenting conflicting visual and vestibular stimulations.

Prediction of Vestibular Linear Detection and Experimental Paradigm for Visual-Vestibular Interaction

Although the purpose of this paper was not to study vestibular detection of linear motion, it was useful to take advantage of some previous experimental work of Young and Meiry (1965) which provided numerical values for linear acceleration thresholds. The curve given by these authors allowed the prediction of the time necessary to detect constant accelerations between 0 and 1 m/sec². Our experimental conditions were designed so as to apply steps of cart accelerations (ramps of velocities) whose duration was at threshold or above threshold for such a detection². The acceleration amplitude was constant (0.4 m/sec²) and the duration varied from 1.6—3 sec. The model, as shown in Fig. 7, predicted the signal provided by the graviceptors during steps of horizontal linear cart acceleration. The corresponding curve, indicated as vestibular response (VR) in the figure, was computed by applying the transfer function shown to the acceleration waveform.

² Absolute vestibular thresholds for linear acceleration are as low as 0.05 m/sec² in man. In our experimental setup (see methods) the maximum available amplitude of acceleration steps (velocity ramps) was 0.4°/sec² because of limitations in the total displacement for the cart (2 m). This in turn led to a detection time of about 2 sec according to the model of Young and Meiry (see Fig. 6).

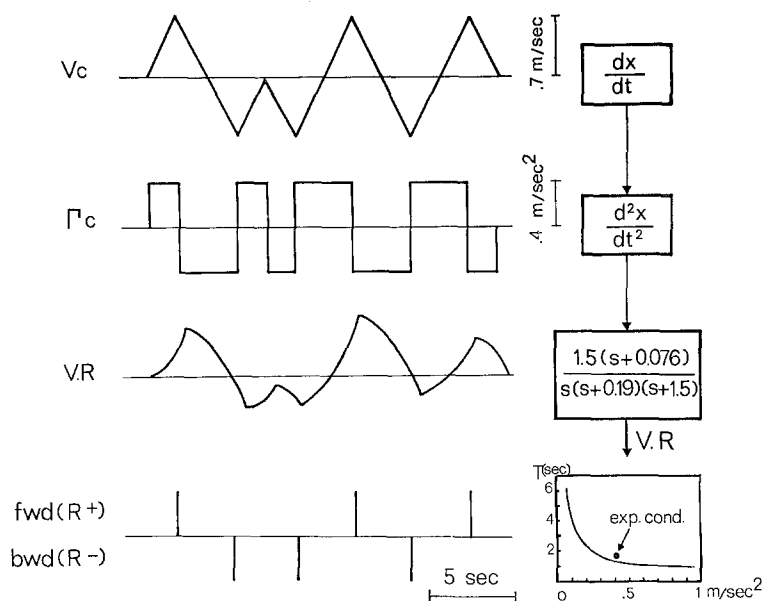


Fig. 7. Experimental paradigm for the study of visual and vestibular detection of linear motion, and use of an otolithic model for the prediction of subject's response. This diagram shows a typical sequence of cart motions. V_c is the velocity of the cart. Triangular wave forms have been chosen because they correspond to steps of constant accelerations (0.4 m/sec^2). Amplitude of velocity is irregular in order to give a pseudo-random movement to the cart.

When such a pattern of acceleration ($\frac{d^2x}{dt^2}$) is sensed by the graviceptors, the model of Young and Meiry (1967) (see block diagram on the right of the third line) allows a calculation of the theoretical output (vestibular response: VR). The model assumed an absolute threshold of approximately 0.006 g for upright subject which placed the 0.4 m/sec^2 latency time for subjective vestibular detection of linear movement at 1.6 sec . R^+ (forward) and R^- (backward) are the predicted all-or-none responses of the subject. VR peaks are above the vestibular threshold

The actual subjective motion detection was measured by an all-or-no procedure (see methods) which is different from the continuous magnitude estimation described in previous sections of these results. The subjects were only required to signal the direction of their linear movement as shown on the last line of Fig. 7. This procedure gave the percentage of correct velocity detection forward (R^+) and backward (R^-).

The experimental paradigm for visual-vestibular interaction was then divided into three successive conditions as shown in Fig. 8. In all three conditions the subject had his eyes open.

I. Triangular velocities were applied to both the cart (V_c) and the visual scene (V_i) in such a way that at any instant $V_i = V_c$. This is equivalent to a real life situation in which the stationary visual scene has a movement of equal amplitude and opposite direction to the objective movement of the head. In this condition direction detection was expected to be 100% correct.

II. Triangular velocities were applied to the cart while the visual scene was stationary with respect to the subject ($V_i = 0$). In this conflicting situation the

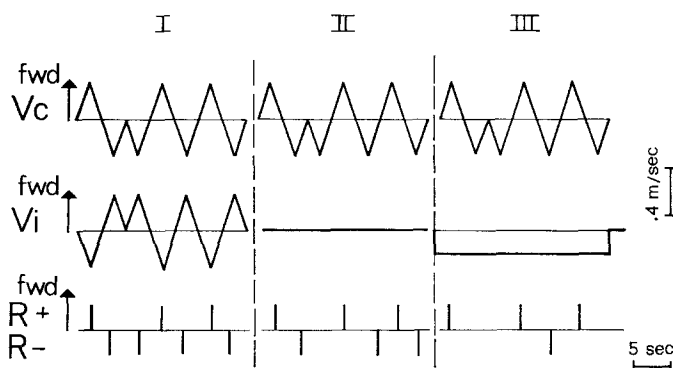


Fig. 8. Experimental paradigm for the analysis of the influence of linearvection on vestibular detection of linear acceleration. From top to bottom: V_c = velocity of the cart; V_i = velocity of visual images; R^+ and R^- have been defined in Fig. 7. The analysis is made for three experimental conditions. (I) $V_i = -V_c$ The velocity of the visual stimulus (V_i) is opposite to the cart velocity. This corresponds to the real-life situation of body movement in a stationary environment. 'fwd' indicates the direction of forward V_c , V_i , or subject's motion detection. (II) $V_i = 0$ The visual world is fixed relative to the cart (moving with the subject). This corresponds to an observer inside a moving closed vehicle. (III) $V_i = \text{constant}$ (0.4 m/sec) A constant forward linearvection (fwd) is induced by a visual field moving backward at constant velocity while the cart is moved fore and aft. Responses have been considered correct if they correspond to the direction of cart velocity at that moment. Subject responses are analyzed as percentages of correct and incorrect detections of forward (R^+) or backward (R^-) motion detection

subject's detection of motion was provided by vestibular and other proprioceptive cues. As stated in methods, it was difficult to isolate pure vestibular cues. Trained subjects learned to use cues other than vestibular ones. This partly explains why the motion detection thresholds, for these subjects, were often much lower than the thresholds predicted by the vestibular model. It is also possible that the threshold values provided by this model are overestimated. However, the present experiments cannot provide an answer to this point.

III. Another conflicting situation consisted of the application of triangular cart velocities (as in I and II), combined with backward V_i (0.4 m/sec) which induced a constant forward LV. According to the direction of cart velocity, the vestibular cue direction then either supported (V_c forward) or conflicted with (V_c backward) the visual cue.

Results of Visual-Vestibular Interaction Experiments

The results obtained from the subject whose motion perception was most influenced by V_i are shown in Fig. 9. Although the movements were delivered in continuous runs of 16 acceleration steps, when the data were analyzed after the experiment, the acceleration steps (ramps of velocity) which gave non-conflicting movements of the cart in the direction of the LV (Fig. 9A) and those which gave conflicting movements in an opposite direction (Fig. 9B) were separated and plotted in distinct diagrams.

The reference conditions I of Fig. 8 ($V_i = -V_c$) gave a 100% correct direction detection for this subject, as plotted on the left side of each diagram. Condition II is plotted as the ordinate of $V_i = 0$ and gave 75% to 80% correct detection.

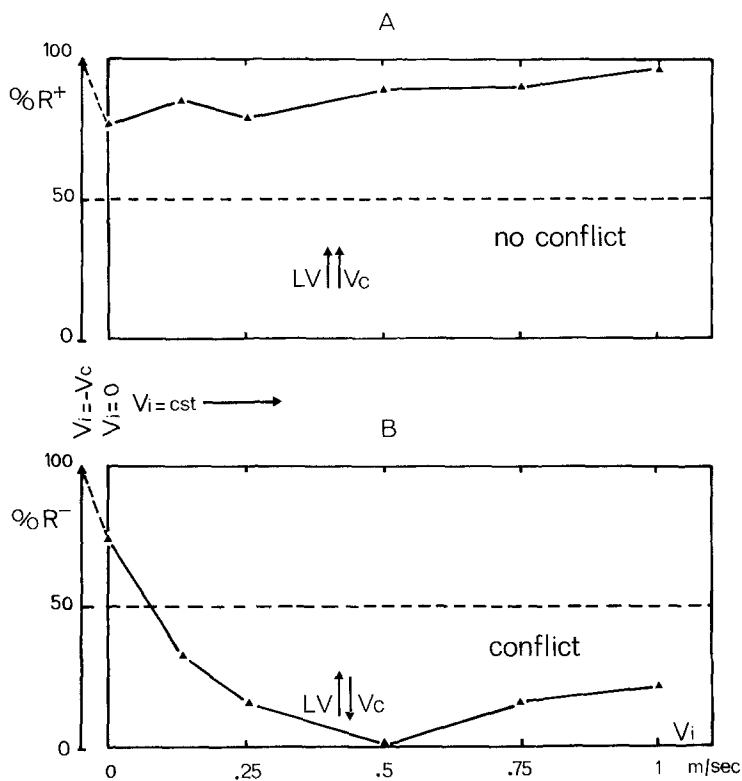


Fig. 9. Perturbation of movement direction detection by conflicting visual and vestibular cues in the case of a very LV-sensitive untrained subject. This diagram shows the percentage of correct detections of cart movements either forward ($\%R^+$) or backward ($\%R^-$) for increasing values of constant image velocities (V_i). Each data point corresponds to the mean value for 30 accelerations repeated in a pseudo-random manner either forward or backward as described in Fig. 8. The three conditions shown in Fig. 8 have been used successively, and the responses have been divided in two groups according to whether the linearvection and cart (V_c) velocities were in the same (A) non-conflicting or in opposite (B) conflicting directions. In both cases the first result plotted on the left vertical scale concerns the condition $V_i = -V_c$ (Condition I of Fig. 8) in which all responses are correct ($R^+ = 100\%$)

When the visual scene is moving (Condition III), the detection remains good and even improves for non-conflicting cues. However, the detection decreases very sharply with increasing V_i in the conflicting situation of an opposite movement between the visual scene and the cart. This degradation is maximum for image velocities much smaller than saturation (0.4–0.6 m/sec). It can be noted that the perturbation decreases when V_i reaches saturation level. This is another indirect evaluation of the range of maximum LV in these experimental conditions.

These rather exceptional effects of visual cues on motion sensation can be found, though to a lesser degree, in most untrained subjects as shown in Fig. 10. In general, the total degradation reached 50% of initial detection. Trained subjects, however, showed increasingly good results. This led us to verify the effect of repetition in a separate set of experiments. The same pattern (sequence

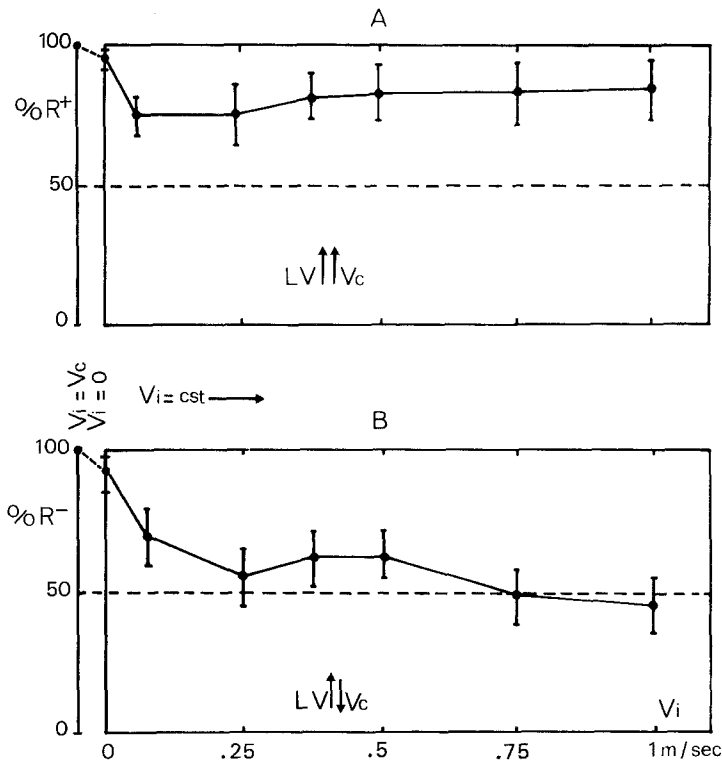


Fig. 10. Perturbation of movement direction detection by conflicting visual and vestibular cues for 10 subjects. Same notations as in Fig. 8. The data points are mean and standard deviations for 10 untrained subjects

of 64 steps of acceleration) of cart velocities, together with a constant velocity movement of the visual scene (Condition III), was presented 10 consecutive times. The perturbation of motion detection decreases with the repetition of the presentation. For the first presentation the percentage of correct detection is about 40% in the case of conflict between V_i and V_c ($V_i = 0.5$ m/sec). It raised up to 90% by the 10th consecutive presentation. Whether this recovery is due to a substitution of tactile cues to vestibular cues, or to a habituation of LV remains to be determined. The possibility of a learning effect restricted to the vestibular detection of the acceleration pattern cannot be excluded, but the use of a pseudo-random distribution of steps of different accelerations and direction, as described above, decreases the probability of this learning occurring.

Discussion

The above results confirm the very powerful character of the sensation of linear motion induced by moving visual fields symmetric to the body. The thresholds of velocity and luminance for self-motion detection are within the same limits as those for detection of the visual images themselves. An interesting result is the clear difference between the thresholds for backward LV which are smaller than those for forward LV.

In normal environment, as man progresses forward, through locomotion or passive movement, he usually observes relative linear movement of his peripheral surroundings backwards, and enlargement of approaching objects in front of him. When moving backward (a less common experience) there are no approaching objects to be seen, but only a diminution of the size of objects in the foreground. Thus, one possible explanation for the relative ease of developing backward LV is that the lack of rearward vision imposes no inhibition, unless the lack of approaching objects for forward LV is a significant missing cue. In addition, the experiments in which conflicting visual and vestibular cues were presented show the great dominance of the visually-induced sensation of motion. These facts are in agreement with the observations of Lee that a very limited translation of a moving room can interfere with the regulation of posture.

However, the latencies of onset (1 sec) are in the lower range for LV compared to those reported by Brandt *et al.* (1973) for circularvection around a vertical axis (1–14 sec). Two hypotheses can be proposed to account for this discrepancy. The simplest and most obvious possibility is that experimental procedures were different. For instance, in the case of CV around a vertical axis (rotating drum), the optokinetic stimulus was made of vertical bars which are, according to our own experiments, less efficient in inducing motion sensation than a random pattern. In the case of a visually-induced tilt around a horizontal axis (rotating disc), the experiments were performed on standing subjects, and proprioception from the legs and feet or the necessity of maintaining an upright posture may have provided conflicting cues delaying the onset of CV.

It is indeed certain that the latency to onset of self-motion sensations, for either circularvection or linearvection, cannot be ascribed to purely visual factors, as the moving field is detected with minimal delay. It was suggested (Young, 1970) that in cases of visual-vestibular conflict, the vestibular signals dominate in the short-term subjective determination of acceleration, but that the visual cues dominate in the long-term sensation of velocity. These views have contributed to the theory of vestibular constraint on visually-induced tilt (Diehgans *et al.*, 1972; Udo de Haes and Schöne, 1970; Young *et al.*, 1973; Young *et al.*, 1975). As applied to the current case, a step change in field velocity, with the cart stationary, implies a visual acceleration impulse which is above the threshold of the otolith system, but is definitely not confirmed by vestibular signals which continue to indicate constant (zero) velocity. Hence, the short term vestibular dominance delays the onset of LV. (The sensation of LV when a neighboring train pulls out of a railroad station is most effective when the *acceleration* of the visual field is low — perhaps below otolith threshold. A step change associated with the sudden passage of a train on the next track does not normally produce LV). With prolonged stimulation, however, LV can develop and dominate, since any constant linear velocity is consistent with the otolith signals at rest.

The detailed differences in latencies between LV and CV may be related to the convergence of visual signals with otolith afferents in the former case and semicircular canal afferents in the latter, recalling their differing dynamic response. The difference may well be equally due to details of the visual field presentation — just as times to onset of CV may vary among different experimental setups.

Another difference between LV and CV is the very small visual after-effect induced by prolonged LV compared to the striking after-effect observed for instance after exposure to a rotating disc in the frontal plane. However, it has been noted (unpublished observations) that a visual after-effect can be observed when the subject associates locomotion with LV. This difference between passively induced LV and the sensation associated with locomotion activity is yet to be studied. At this point it should be remembered that, as shown by the involvement of brain stem structures in visual-vestibular convergence, the mechanisms dealt with here concern fundamental elements of sensori-motor activity which are generally set into work during active motion, and that in addition, the processing of a motor program can alter motion sensation. These considerations do imply that some difference will be found between a passively induced motion, such as the one used in the present experiment, and active locomotion.

Altogether, the view that peripheral vision would provide an "autonomous" kinaesthetic sense, as proposed by Lee, is not convincing. Visual and vestibular information have been shown to converge on vestibular nuclei (Dichgans *et al.*, 1973; Henn *et al.*, 1974), and it is also known that visual CV can habituate vestibular rotatory nystagmus (Young and Henn, 1974). The question would then seem to be to characterize, as we have tried to do above, the complementarity of visual and vestibular cues. Dichgans *et al.* (1973) proposed that vision "improves the speedometer function of the vestibular system". However, whether LV and vestibular linear motion sensation are actually summed algebraically or whether they interact through a switching hierarchical process remains to be determined. The observed reduction in the dominance over conflicting vestibular cues with repeated trials shows that visual-vestibular interaction is modifiable. One occurrence for this modification is when a repeated association of tactile, proprioceptive and vestibular cues opposes visual cues.

Appendix

Relationship between the velocity of visual images projected on the screen and the line-of-sight angle.

The angular velocity $\frac{da}{dt}$ of a point M belonging to these images is a function of:

- a) the velocity of visual images (V_i)
- b) the distance between the eye and the screen (H)
- c) the angle of incidence (a).

Elementary trigonometric considerations give:

$$\frac{da}{dt} = \frac{V_i}{H} \sin^2 a$$

For the upper screen $H: 0.4$ m. Then for an image velocity of 1 m/sec we have:

$$\frac{da}{dt} = 143 \sin^2 a \text{ (deg/sec) Curve I}$$

For the lateral images: $H = 0.5$ m, then

$$\frac{da}{dt} = 115 \sin^2 a \text{ (deg/sec) Curve II}$$

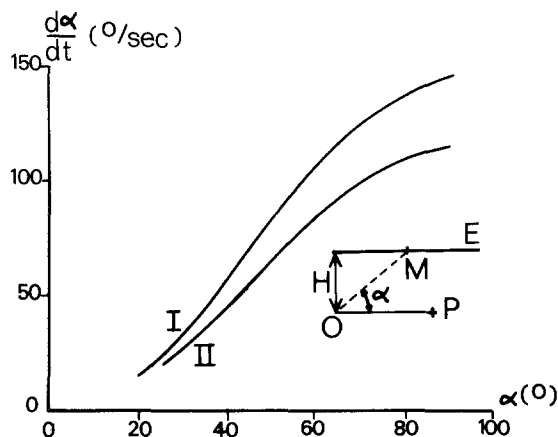


Fig. 11

Acknowledgements. This research was supported by a grant from Organisme National de Sécurité Routière and by C.N.R.S. and C.N.A.M. (France). L.R. Young was supported by NASA Grant NGR-22-009-701(LR4).

References

- Berthoz, A., Pavard, B., Young, L.R.: Rôle de la vision périphérique et interactions visuo-vestibulaires dans la perception exocentrique du mouvement linéaire chez l'homme. *C.R. Acad. Sci. (Paris)* **278**, D, 1605—1608 (1974)
- Brandt, Th., Wist, E., Dichgans, J.: Optisch induzierte Pseudo Coriolis-Effekte und Circularvektion. *Arch. Psychiat. Nervenkr.* **214**, 365—389 (1971)
- Brandt, Th., Dichgans, J., Koenig, E.: Perception of self-rotation induced by optokinetic stimuli. *Pflügers Arch.* **332**, R 98 (1972)
- Brandt, Th., Dichgans, J., Koenig, E.: Differential effects of central and peripheral vision for egocentric and exocentric motion perception. *Exp. Brain Res.* **16**, 476—491 (1973)
- Clark, B.: The oculogravic illusion as a test of otolith function. In: Third Symp. on the role of the vestibular organs in the exploration of space. NASA SP **152**, 331—339 (1968)
- Clark, B., Graybiel, A.: Apparent rotation of a fixed target associated with linear acceleration in flight. *Amer. J. Ophthal.* **32**, 549—557 (1949)
- Daniel, K.: Der Einfluß der Reizmarkengröße auf die Lichtunterschiedsempfindlichkeit der Netzhaut bei verschiedenen Adaptationszuständen. Inaugural dissertation. Tübingen. (1959). In: *Handbook of sensory physiology: visual psychophysics*, p. 126—127. (ed Jameson, D., Hurvich, L.M.). Berlin-Heidelberg-New York: Springer 1972
- Denton, G.C.: The influence of visual pattern on perceived speed, p. 409—420. Crowthorne, G.B.L.R.: Road Research Laboratory Report 1971
- Dichgans, J., Brandt, Th.: The psychophysics of visually induced perception of self-motion and tilt. In: *The Neurosciences III*, p. 123—129. MIT Press 1974
- Dichgans, J., Held, R., Young, L., Brandt, Th.: Moving visual scenes influence the apparent direction of gravity. *Science* **178**, 1217—1219 (1972)
- Dichgans, J., Schmidt, C.L., Graf, W.: Visual input improves the speedometer function of the vestibular nuclei of the goldfish. *Exp. Brain Res.* **18**, 319—322 (1973)
- Fischer, M.H., Kornmüller, A.E.: Optokinetisch ausgelöste Bewegungswahrnehmungen und optokinetischer Nystagmus. *J. Psychol. Neurol. (Lpz.)* **41**, 383—420 (1930)
- Gibson, J.: The visual perception of objective motion and subjective movement. *Psychol. Rev.* **61**, 304—314 (1954)
- Graybiel, A.: Oculogravic Illusion. *Arch. Ophthal.* **48**, 605—615 (1952)
- Henn, V., Young, R.L., Finley, C.: Vestibular units in alert monkeys are also influenced by moving visual fields. *Brain Res.* **71**, 144—149 (1974)

- Jongkees, L.B.W.: On the otoliths: their function and the way to test them. In: Third Symposium on the role of vestibular organs in space exploration. 1967. NASA SP **152**, 307—331 (1968)
- Lee, D.N., Aronson, E.: Visual proprioceptive control of standing in human infants. *Perception and psychophysics* **15**, 529—532 (1974)
- Lishman, J.R., Lee, D.N.: The autonomy of visual kinaesthesia. *Perception* **2**, 287—294 (1973)
- Lipetz, L.E.: The Creation of physiological and psychological aspects of sensory intensity. In: *Handbook of Sensory Physiology*, Vol. I, p. 191—225. (ed. Loewenstein, W.). Berlin-Heidelberg-New York: Springer 1971
- Mach, E.: *Grundlinien der Lehre von den Bewegungsempfindungen*, 129 pp. Leipzig: Engelmann 1875
- Maekawa, A., Simpson, J.: Climbing fiber activation of Purkinje cells in the flocculus by impulses transferred through the visual pathways. *Brain Res.* **39**, 245—251 (1972)
- Salvatore, S.: Velocity sensing. *Highway Res. Record* **282**, 79—90 (1968)
- Schmidt, F., Tiffin, J.: Distortion of drivers' estimates of automobile speed as a function of speed adaptation. *J. appl. Psychol.* **53**, 536—539 (1969)
- Schöne, H., Mortag, H.G.: Variation of the subjective vertical on the parallel swing at different body positions. *Psychol. Forsch.* **32**, 124—134 (1968)
- Sharpe, C.R., Tolhurst, D.J.: Orientation and spatial frequency channels in peripheral vision. *Vision Res.* **13**, 2103—2112 (1973)
- Udo de Haes, H.A., Schöne, H.: The effectiveness of the statolith organs in human spatial orientation. *Acta oto-laryng. (Stockh.)* **69**, 25—31 (1970)
- Young, L.R.: On visual-vestibular interaction. In: 5th Symposium: The role of the vestibular organs in space exploration (Pensacola). NASA SP **314**, 205—210 (1970)
- Young, L.R., Meiry, J.L.: A revised dynamic otolith model. *Aerospace Med.* **39**, 606 (1965)
- Young, L.R., Dichgans, J., Murphy, R., Brandt, Th.: Interaction of optokinetic and vestibular stimuli in motion perception. *Acta oto-laryng. (Stockh.)* **76**, 24—31 (1973)
- Young, L.R., Henn, V.S.: Selective habituation of vestibular nystagmus by visual stimulation. *Acta oto-laryng. (Stockh.)* **77**, 159—166 (1974)
- Young, L.R., Oman, C.: Influence of head position and field on visually induced motion effects in three axes of rotation. In: *Proc. of 10th Annual Conference in Manual Control* Wright Patterson AFB, (Ohio) (1974)
- Young, L.R., Oman, C., Dichgans, J.: Influence of head orientation on visually induced pitch and roll sensation. *Aviation and Environmental Medicine* **46**, 264—268 (1975)

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