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Head stabilization during various locomotor tasks in humans

II. Patients with bilateral peripheral vestibular deficits

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Summary. This experiment, which extends a previous investigation (Pozzo et al. 1990), was undertaken to examine how head position is controlled during natural locomotor tasks in both normal subjects (N) and patients with bilateral vestibular deficits (V). 10 normals and 7 patients were asked to perform 4 locomotor tasks: free walking (W), walking in place (WIP), running in place (R) and hopping (H). Head and body movements were recorded with a video system which allowed a computed 3 dimensional reconstruction of selected points in the sagittal plane. In order to determine the respective contribution of visual and vestibular cues in the control of head angular position, the 2 groups of subjects were tested in the light and in darkness. In darkness, the amplitude and velocity of head rotation decreased for N subjects; these parameters increased for V subjects, especially during R and H. In darkness, compared to the light condition, the mean position of a line placed on the Frankfort plane (about 20–30° below the horizontal semi-circular canal plane) was tilted downward in all conditions of movement, except during H, for N subjects. In contrast, this flexion of the head was not systematic in V subjects: the Frankfort plane could be located above or below earth horizontal. In V subjects, head rotation was not found to be compensatory for head translation and the power spectrum analysis shows that head angular displacements in the sagittal plane contain mainly low frequencies (about 0.3–0.8 Hz). The respective contribution of visual and vestibular cues in the control of the orientation and the stabilization of the head in space is discussed.

Key words: Kinematics – Locomotion – Head stabilization – Vision – Peripheral vestibular deficit – Man

Introduction

Impairment of motor functions, in patients with peripheral vestibular lesions, has been mainly studied during postural control after unexpected stance disturbance (Allum et al. 1985; Black et al. 1983) and during head stabilization relative to space in response to passive body rotation in the horizontal plane (Guitton et al. 1986; Gresty 1987; Bronstein 1988). On the other hand, De Waele et al. (1989) have analysed the postural syndromes following unilateral global and selective lesions of the vestibular apparatus in guinea pigs. In contrast, the effects of bilateral vestibular lesions on locomotion in man, to the best of our knowledge, has not been investigated. In a previous study performed with normal subjects (Pozzo et al. 1990), we have shown that during various locomotor tasks, head angular rotation is minimized in the sagittal plane in spite of the vertical head oscillations synchronized with the cyclical locomotor activity. We have hypothesized that such head stabilization during locomotion could provide a stable visual and vestibular reference frame for action. However, in addition to balance impairments, patients with vestibular disorders report frequent oscillopsia during locomotion (Freyss et al. 1988). The inability to perform vestibulo-ocular reflex movements (VOR) is likely to contribute to this effect. Therefore, by minimizing head rotational perturbations these subjects could avoid such distressing illusory movement of the environment. One purpose of the present study is to measure the ability of patients with peripheral vestibular lesions to stabilize their head in space. Our work focuses on rotational perturbations of the head in the sagittal plane induced by head oscillations along vertical axis occurring during locomotion. Previous studies have demonstrated the contribution, in man, of otolith-spinal reflexes to the organization of motor control of the landing phase occurring during free fall (Melvill-Jones and Watt 1971; Greenwood and Hopkins 1974), downward stepping and hopping movements (Melvill-Jones et al. 1973). The latter authors speculate on the possibility that otolith-spinal reflexes may make an active contribution to the overall synthesis of normal locomotion. The present study examines the role of vestibular and visual cues in the control of head posture during several natural locomotor tasks; the implications of our

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Offprint requests to: T. Pozzo (address see above) results in daily practice for patients with vestibular disorders are discussed.

Methods

Subjects

In this experiment we studied head and body kinematics of 10 normal subjects and 7 patients with clinically documented peripheral vestibular deficits. The normal subjects (1 female, 9 males) ranging in age from 20–45 years did not present any previous history of neuromuscular disease. Their heights and weights ranged from 165 to 180 cm and from 65 to 80 kg, respectively.

Seven patients (4 females and 3 males, age span 35 to 70 years), suffering bilateral vestibular disorders were tested. Six of these patients had bilateral caloric areflexia due to gentamycine, and the last one had bilateral section of the eighth nerve after otoneurosurgery for a bilateral acoustic neuroma. Patients were tested at the otolaryngology department of the Hopital Lariboisière with the following procedures: audiometry, caloric test, electrooculography and gaze stabilization in the horizontal plane (Freyss et al. 1989). CT–Scan MRI was also performed in order to rule out patients with lesions of brain and/or posterior fossa; none were found. Oscillopsias were objectively tested with the "DIE" test (Longridge and Mallinson 1987). All the patients had been submitted to vestibular rehabilitation and our experimental tests were carried out after the end of the rehabilitation.

Table 1. Summary of group data of amplitude and acceleration of head translation along the vertical axis, in normals and patients during the 4 experimental conditions, in the light and in darkness

Test condition	Amplitude (cm/s)		Acceleration (g)	
	Light	Darkness	Light	Darkness
Free Walking				
Normal	7 ±2.3	6.7±2	0.50±0.15	0.40±0.16
Patient	4.5±2	2 ±0.8	0.35±0.13	0.22±0.10
Walking (on the spot) in place				
Normal	1.4±0.5	1.5±0.8	0.24±0.04	0.20±0.04
Patient	2.8±1.5	2.5±1.5	0.16±0.04	0.12±0.06
Running				
Normal	12.5±3	12±3.1	1.80±0.60	1.50±0.50
Patient	5.5±1.8	10±3.2	0.60±0.25	1.10±0.65
Hopping				
Normal	18 ±3.1	19 ±2.6	1.60±0.50	1.40±0.40
Patient	7.5±1.5	13.2±1.2 ($n=2$)	1.20±0.45	1.25±0.25 ($n=2$)

The mean values of amplitude and acceleration of head translation are given with their standard deviations. ($g=9.8$ m/s^2)

Testing conditions

The subjects were asked to perform the following locomotor tasks: a) free walking (W), b) slow stepping or walking in place (WIP), c) fast stepping or running in place (R) and d) hopping on one foot (H). These conditions have been chosen because they involve two types of motor activity:

- natural and simulated locomotion (free walking and walking and running in place)
- dynamic equilibrium (hopping).

In the first task (W), the subjects were instructed to walk normally for a distance of approximately 6 m. The computer program was triggered when the subject began to move his head. The WIP, R and H tasks were performed on the ground (without a treadmill or belt) during 5 s each, at the subject's own rate. In each case, performance began immediately before the recording commenced. During the last three conditions of movement (without horizontal displacement) the subjects looked at a wall located 2 m away. Subjects were bare-foot. Following a brief explanation of the tasks, the subjects underwent a training period with a normal visual surround. The experiments were carried out both in the light and in darkness. In the light, no instruction to stare at any specific point was given. The experiment consisted of four trials in each task. Trials were separated by one minute.

Measures

The measurement techniques employed in this study duplicate those described in detail elsewhere (Pozzo et al. 1990). Briefly, the kinematics of the movements were analyzed by means of an optical automatic TV-image processor (E.L.I.T.E. system). Ten hemispherical retroreflective markers (8 mm in diameter), inducing eight links, were placed on:

- the head; two of these markers defined the line between the lower border of the eye-socket and the meatus of the ear called "the Frankfort plane" (F–P) (De Beer 1947);
- the neck, the trunk, the upper and lower limbs.

The following numerical values of several parameters were calculated in the sagittal plane of the body:

1) the angle of the "Frankfort-plane", with respect to the vertical (or direction of gravity) (θ);

2) linear and angular head velocity.

The mean position of the head in the sagittal plane was evaluated for each subject from the mean value of θ averaged over the time of one recording session. During this period, head stability in the sagittal plane was also evaluated by calculating the peak-to-peak amplitude of head angular displacements. This value, averaged over successive trials gave the mean amplitude of head angular displacements and its standard deviation. The mean amplitude was also calculated for the neck and trunk angular displacements. Recordings of head angular position and translation in the sagittal plane were Fourier-analyzed by computer and their power spectral contents were determined with a frequency resolution of 0.2 Hz. The ELITE system use an adaptative filter (D'Amico and Ferrigno 1990). The cut-off frequency is in the range 7 to 20 Hz.

Results

General behavioral characteristics during locomotor tasks

Group data of head translation along the vertical axis from normal and vestibular patients for each test condition are summarized in Table 1. Mean values of the amplitude of vertical head translation in the 4 conditions of movement were not significantly different in the light and in darkness for normal subjects. This shows that translational head movements were similar in the light and in darkness. In addition, during the W condition, the velocity range in which the normal subjects walked was the same in the light and in darkness (1.2–1.7 m/s). The amplitude of trunk rotation under all the movements

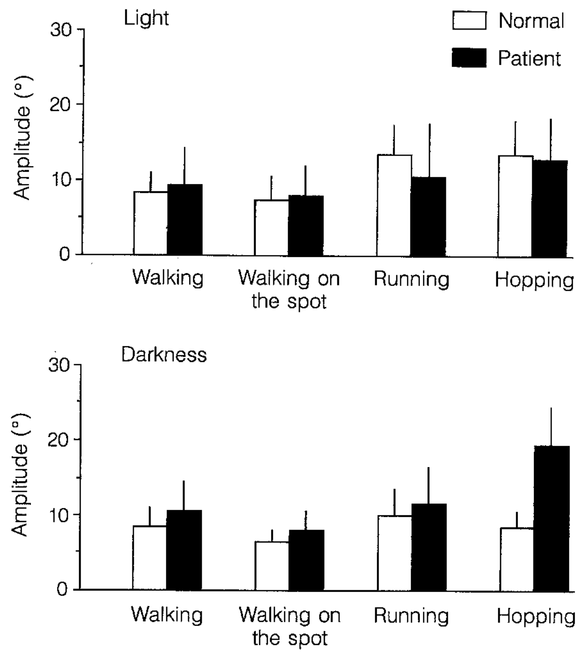

Fig. 1. Histograms of the amplitude of head angular displacements in the sagittal plane, in normal subjects (open bars) and in patients with bilateral vestibular disease (black bars), in the light (upper part) and in darkness (lower part). The mean amplitude of the angle (θ) (ordinate) between the vertical and the Francfort plane has been plotted with the standard deviation during the 4 conditions of movement (abscissa)

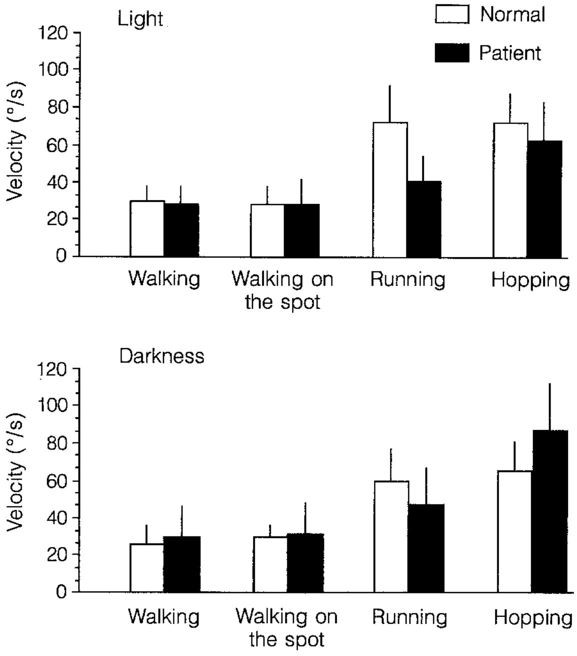

Fig. 2. Histograms of maximal head angular velocities in the sagittal plane of normals (open bars) and patients (black bars) in the light (upper part) and in darkness (lower part). The mean values of the maximal head angular velocities $(\dot{\theta})$ (ordinate) have been plotted with the standard deviation during the 4 conditions of movement (abscissa)

tested and in the 2 viewing conditions, ranges from 6° to 15°.

During the W condition, patients made shorter strides than normal subjects, and had some rigidity in the upper extremities, as manifested by a characteristic stiff arm posture. They also seemed to hold the head stiff in relation to the trunk. In darkness, locomotion became hesitant, with a wide-based gait, the stride length decreases, duration of the stance phase increases, and 3 patients presented a marked out-toeing of the feet. This behavior caused a decrease in the speed range of walking (from 1.1–1.3 m/s in the light to 0.9–1.1 m/s in darkness) and a significant decrease in amplitude of the vertical head translation ($p < 0.001$ with Fisher test).

During R and H in light, the amplitude of patient's head oscillations along the vertical axis (Zt) decreased significantly relative to normals ($p < 0.005$ during R, and $p < 0.001$ during H with Student's t test). In darkness, this variable increased significantly, as a result of postural imbalances occurring during running without visual input ($p < 0.001$ with Fisher test). Only 2 of the 7 patients performed hopping in darkness. The amplitude of trunk rotation ranged from 10° to 30° during all the movements tested and in the 2 viewing conditions. We have calculated linear head acceleration along the 3 orthogonal axes. The largest values were obtained for head acceleration along the vertical axis (Zt), which in the 4 conditions of movement, ranged from 0.3–2.6 g in normal subjects and from 0.03–2.0 g in patients. Head acceleration ranged from 0.005–0.25 g along lateral axis (Lat) and 0.004–0.15 g along the antero-posterior axis (AP) in normal subjects, and 0.07–0.65 g (Lat) and 0.004–0.3 g (AP) in patients.

Head angular stabilization

In the 2 groups of subjects the best stabilization was obtained during WIP and decreased progressively from W to R and H. The peak values of head angular displacement and velocity during the 4 conditions of movement never exceeded 20° and 140°/s in normal subjects, and 30° and 120°/s in patients.

Figures 1 and 2 show the histograms of the mean values (and their standard deviations) for head angular displacement and head maximum rotational velocities in the light and in darkness for normals and patients. During W and WIP conditions, head stabilization was not significantly different in the 2 groups of subjects, and the maximal amplitude of head angular displacement was roughly the same, while the standard deviation was greater in patients (Fig. 1). Darkness produces no detectible changes in head stabilization during W and WIP in normals and patients.

During R in the light, the mean amplitude of head angular displacement and mean maximal angular velocity were lower in patients (respectively 10.5±7° and 41±13°/s) than in normal subjects (13.5±5° and 72±20°/s) (Figs. 1 and 2): these differences in values between normals and patients are only statistically sig-

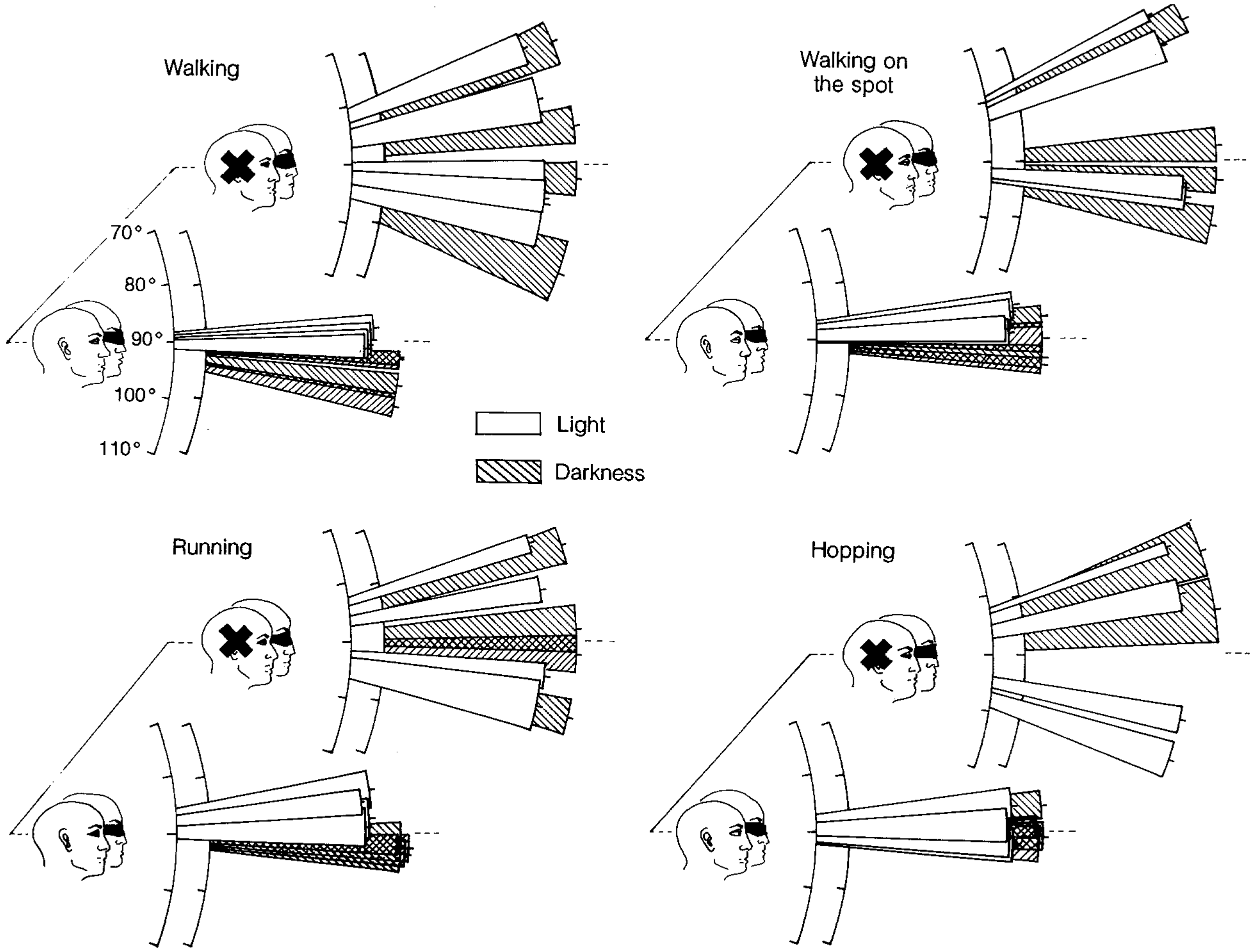

Fig. 3. Effects of darkness on the mean head angular position in 4 normals (foreground) and 4 patients (background, dark cross) during the 4 conditions of movement. Each angular sector corresponds to the mean value of the angle θ and the standard deviation averaged over 3 trials in one normal subject and one patient in the light (open sectors) and in darkness (dotted sectors). The horizontal dotted line indicates the angle for which the Francfort plane is horizontal, i.e., the angle θ is 90°

nificant for head angular velocities ($p<0.02$ with Student's t-test). This result could be partly due to the less effective locomotor performance of the patients, who spontaneously decrease the amplitude of their jumps in order to improve their postural stability.

In contrast, during hopping, the head angular displacement was not statistically different between the 2 groups of subjects, in spite of the smaller amplitude of the vertical head translation in patients. In this condition of movement, 4 of the 7 patients tested reported oscillopsia.

For normal subjects, compared to light condition, head angular stability was improved during R and H in darkness with the mean amplitude of head angular displacement increased by 26% ($p<0.02$ with Student's t test) for R, and 37% ($p<0.008$) for H. This is not the case in patients: compared to normal viewing, the amplitude and velocity of head rotation show some increase during R and H in darkness, but this trend is not statistically significant because of the large standard deviation in the performances of the patients.

Head orientation

For the ten normal subjects in light, head angular position, measured by the mean position of the F–P, was slightly different for each condition of movement, but remained near the horizontal plane: 89 ± 2° (W), 88.5 ± 3° (WIP), 88.5 ± 3° (R) and 89.5 ± 3° (H).

In darkness, during W, WIP and R, mean head angular position was significantly tilted downward (flexion), always below the earth horizontal: 95 ± 2.5° (W) ($p<0.001$ with Student's t test), 94.5 ± 2° (WIP) ($p<0.001$) and 92.5 ± 3.5° (R) ($p<0.03$), ranging from 93° to 105°. This change is not due to the tilting of the whole body because there was no modification of the mean angular position of the trunk with respect to gravity. On the other hand, during H condition, the mean position of the F–P was not significantly modified in darkness. Data for the patients cannot be summarized, because of the extreme variability in head angular position: the F–P can be situated above the earth horizontal plane (extension of the neck) or below it (flexion). The

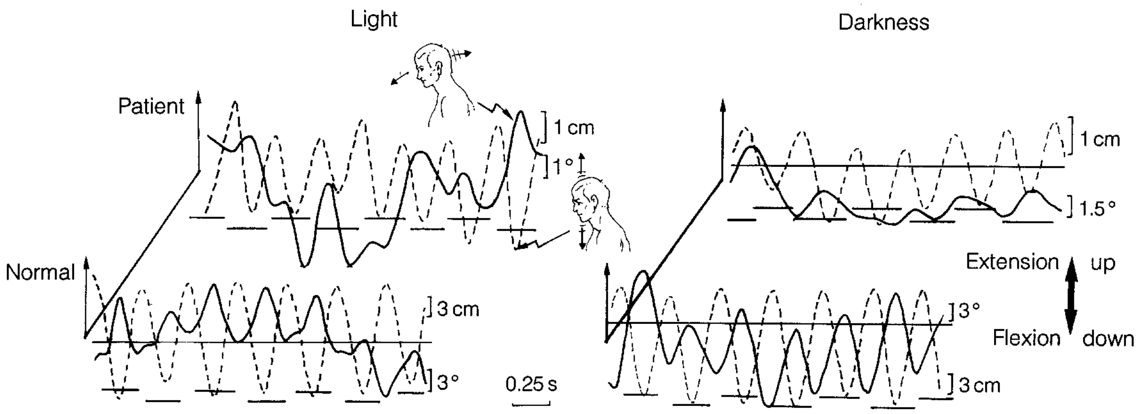

Fig. 4. Typical raw data of head translation along the vertical axis (dotted lines) and rotation in the sagittal plane (solid lines) from one normal subject (foreground) and one patient (background) during running in place in the light (left part) and in darkness (right part). In each graph, rotation and translation curves have been plotted together so as to be synchronized in time (in abscissa) and scaled at the same height (ordinate). Double bars below each graph depict left (upper) and right (lower) stance phases. Horizontal solid lines indicate the angle for which the F–P is in the earth-horizontal

angle between the earth vertical and the FP ranged from 70°–108° during the 4 conditions of movement in the 7 patients tested. Darkness has no statistically significant effect on the patient's mean head angular position. Figure 3 illustrates these results for 4 typical normals and 4 patients. For each subject the mean position of the head and the standard deviation was averaged over 3 trials. However, the bilateral labyrinthectomized patients systematically adopted an exaggerated nose-down position, in each condition of movement in the light and in darkness.

We measured head angular position when the subjects stood quietly before the begining of each condition of movement. The standard deviation was computed separately for the normals and the patients, in order to estimate the precision in orientation of the head before each trial. In normals and patients, this precision was respectively ± 2.5° and ± 3.5°. In darkness, the precision was the same for the normals but decreased significantly for the patients (SD = ± 5°: $p < 0.003$ with Student's t-test).

Relationship between head translation and head rotation

In the 4 conditions, in the light and in darkness, the head rotation of normal subjects always compensated for head translation along the vertical axis (Zt). That is, when the head translates upward, it simultaneously rotates downward (flexion) and vice versa. The peak to peak amplitude of these compensatory angular displacements never exceeded 10°. During R and H, head angular displacement (θ) was sinusoidal and 180° (± 5°) out of phase with respect to head translation along the vertical axis. In patients, such a clear relationship between head translation and rotation was not observed, so that no phase relation can be defined. There is a slight compensatory head rotation in patients compared to values in normal subjects, and a clear phase relationship with respect to head translation could only be defined during short periods of the whole recording session. Head rotation and translation generally showed a random relationship and seem to be generated independently.

In Fig. 4, two movements are simultaneously plotted: the translation of the marker placed on the meatus of the ear, along the vertical axis (dotted line), and the rotation of the head in the sagittal plane (θ) (solid line), for a normal subject (foreground) and a patient (background), during running in the light (left part) and in darkness (right part). The horizontal bars below each curve depict stance phases. Vertical head translations of the normal subject are phase-locked to the movement of the feet: the downwardmost position of the head always occurs during a stance (downward extrema of the dotted line is close to horizontal bars).

Figure 5 further clarifies these relationships: head angular position in space (θ), during 5 s of recording in light, is plotted as a function of head position along the vertical axis (Zt), in R condition, for 2 typical subjects. The relationship between Zt and θ is regular in the normal subject, the plot oriented along a positively-sloped diagonal path which indicates synchronous flexion and upward translation or extension and downward translation of the head. In contrast, this sort of orientation in

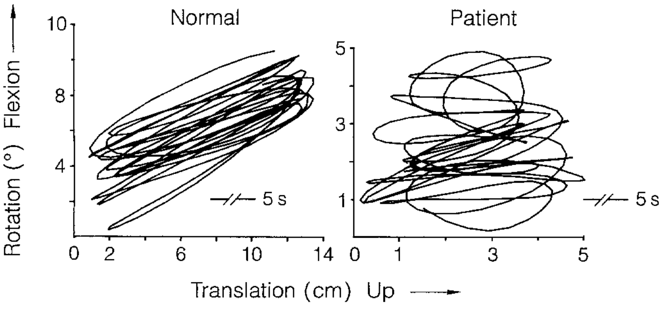

Fig. 5. Relationship between head translation along vertical axis and head rotation in the sagittal plane. Head angular position in space (θ), during 5 s of recording, is plotted as a function of head position along the vertical axis, during running in light, for one typical normal and patient subject

Table 2. Coherence between head rotations in the sagittal plane and head translations along the vertical axis during the 4 conditions, in the light and in darkness

Test condition	Light	Darkness	
Free walking			
normal	0.44 ± 0.09	0.30 ± 0.08	
Patient	0.17 ± 0.10	0.27 ± 0.09	
Walking on the spot			
normal	0.46 ± 0.13	0.37 ± 0.12	
Patient	0.16 ± 0.10	0.18 ± 0.10	
Running			
normal	0.55 ± 0.12	0.48 ± 0.14	
Patient	0.16 ± 0.08	0.23 ± 0.14	
Hopping			
normal	0.70 ± 0.10	0.51 ± 0.10	
Patient	0.22 ± 0.05	0.11 ± 0.04	($n = 2$)

The mean values of the coherence function are given with their standard deviations

Table 3. Frequencies of head oscillations along the vertical axis during the 4 conditions, in the light and in darkness

Test condition	Frequency (Hz)		
	Light	Darkness	
Free walking			
normal	1.40 ± 0.13	1.30 ± 0.25	
Patient	1.65 ± 0.20	1.63 ± 0.14	
Walking on the spot			
normal	1.45 ± 0.16	1.64 ± 0.17	
Patient	1.70 ± 0.23	1.80 ± 0.33	
Running			
normal	2.68 ± 0.15	2.66 ± 0.15	
Patient	2.67 ± 0.35	2.75 ± 0.40	
Hopping			
normal	2 ± 0.10	2.10 ± 0.10	
Patient	2.60 ± 0.20	2.45 ± 0.10	($n = 2$)

The mean values of the frequencies of head oscillations along the vertical axis are given with their standard deviations

the plot cannot be seen in the patient's diagram, indicating the irregular relationship between θ and Zt.

In order to demonstrate the consistance of this observation, we have calculated the coherence function between Zt and θ. The formula of the coefficient of coherence is the following:

$$\mathrm{Co}(\delta) = [(\textstyle\sum_i \mathrm{Z}(\mathrm{i})\theta(\mathrm{i}-\delta)) - \mathrm{E_Z E_\theta}]/[\sigma_\mathrm{Z}\sigma_\theta]$$

where δ is the delay between Zt and θ, σ_Z and σ_θ are the standard deviations of Zt and θ, and $\mathrm{E_Z}$ and $\mathrm{E_\theta}$ are the averages of Zt and θ. The maximum value of this coherence function corresponds to a $\delta_{\max}$ (this value divided by the frequency gives the phase lag between Zt and θ). This value varies from 0 (the 2 signals are totally unrelated) to 1, i.e., the system output (head rotation) is due entirely to the input (head translation). The values of the coherence function between Zt and θ are shown on Table 2. In the light, for normal subjects, at least 40% (during W and WIP) and 60% (during R and H) of the rotation is linearly related to the translation, whereas these values are considerably smaller in patients. Compared to light condition, the values of coherence function are not different in darkness. The slight decrease observed for normal subjects are not statistically significant, while no difference can be seen for patients.

Frequency analysis of head translation and rotation

We have calculated the mean value and standard deviation of the predominant frequency of head oscillations along the vertical axis, averaged over the 10 normal subjects and the 7 patients. The data obtained during the 4 conditions, in the light and in darkness, are presented in the Table 3. These values yield a good representation of the step frequency and the close relationship between the movement of the feet and the vertical head translation shown in the previous section (see Fig. 4) and in other studies (Melvill Jones et al. 1973; Rossignol 1973) which demonstrated that a head accelerometer can be used instead of a force transduction platform as an indicator of mechanical events. Values differ for each condition of movement, ranging from 1.3–3.2 Hz for the 2 populations tested. The mean value of the frequency of head oscillations obtained during W and WIP is slightly greater in patients. This difference is statistically significant only for the values obtained in light ($p < 0.005$ during W, and $p < 0.05$ during WIP, with Student's t test). This result is in agreement with the clinical observations reported above and must be related to the short strides which characterize the patient's gait. In the same way, during H in the patients, the frequency of head oscillations was higher (about 2.6 Hz) than that of the normals (about 2 Hz) ($p < 0.0001$), due to the smaller amplitude of their jumps. During R, the predominant frequency was the same in the 2 groups of subjects (about 2.7 Hz). The standard deviations are significantly greater in the patients than in the normals during R in light ($p < 0.025$ with Fisher test) and in darkness ($p < 0.03$). This result indicates the larger intra and inter-individual variation of the step frequency compared to normal subjects.

Darkness has no statistically significant effect on the frequency of head translation along the vertical axis in the 2 groups of subjects.

The distribution of the frequencies of head angular displacements in the 4 situations in the light and in darkness lay between 0.2–6 Hz in the 2 groups of subjects.

Figure 6 displays graphically the typical results of the Fourier-analysis of head translations and rotations. In normal subjects, 2 main peaks can be distinguished: 1)

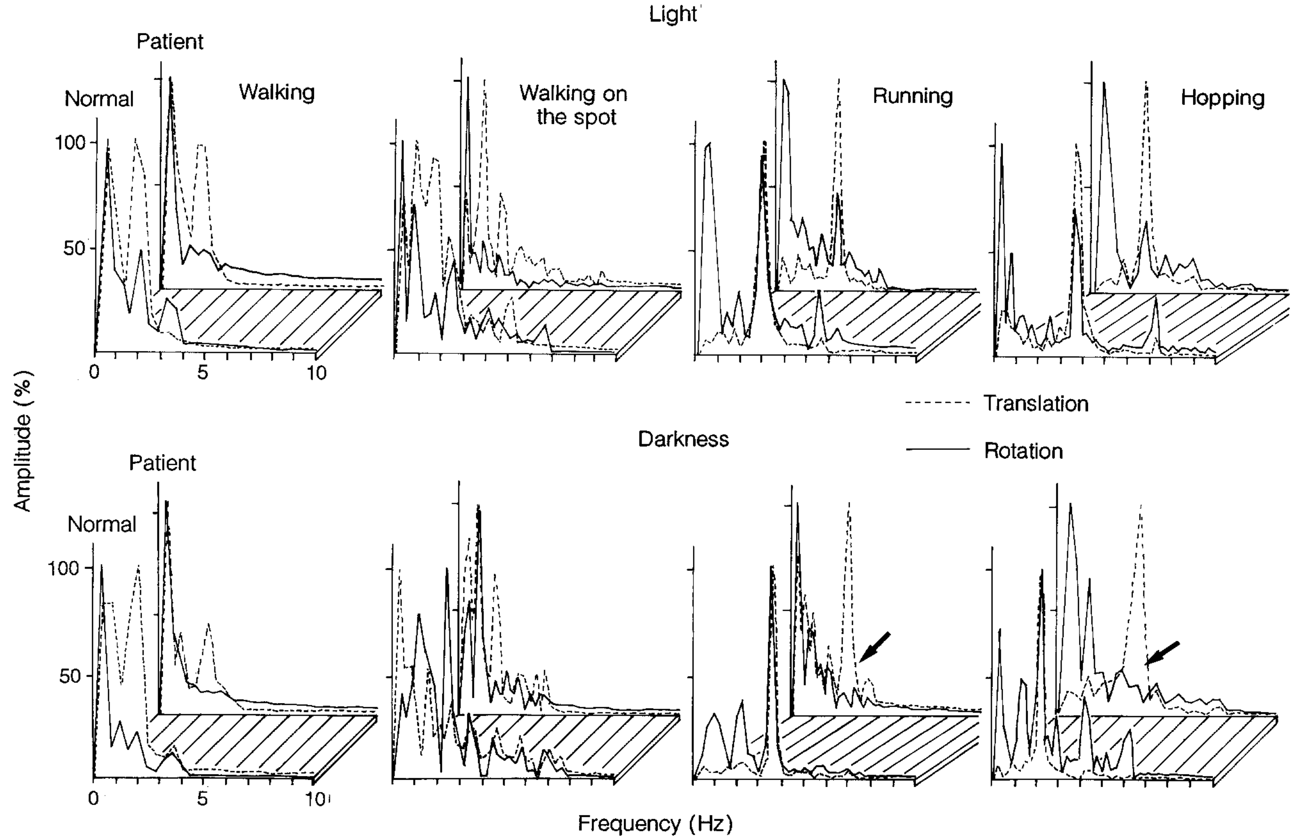

Fig. 6. Fourier power spectra obtained during the 4 conditions of movement (from left to right) in the light (upper part) and in darkness (lower part) for one normal (foreground) and one patient (background). In each of these classes of movements, the power spectra of head angular displacements in the sagittal plane (solid line) and of head translations along the vertical axis (dotted line) are superimposed. The ordinate of the power spectrum is the amplitude of the frequency components. The highest amplitude is assigned a value of 100. The amplitude of the other components are thus percentages of the highest amplitude component. Arrows indicate the lack of rotational component in the same range that the predominant frequency of head translation

the predominant frequency due to the compensatory head angular displacements to up and down movement of the head, ranged from 1.5 Hz to 3 Hz; and 2) a harmonic resulting from the oscillations of the average posture of the head relative to gravity. In addition, during R and H, a subharmonic, produced by the transient component of the self-generated rotation and elicited during the take off and the landing phase, is present (range: 3.5–6 Hz). A general characteristic of the normal subjects' spectra is the good superimposition of the predominant frequencies of head translations and rotations. In contrast, the patients, during the 4 conditions, mainly exhibit predominant rotational frequencies in a low frequency range (0.3–0.8 Hz). In the light (Fig. 6 upper part, background) the amplitude of the rotational components, in the same frequency range as that of the predominant frequencies of head translation, is less than those of the normals and never exceeded 40% of the power of the predominant frequency. In darkness, these components disappear (see arrows in Fig. 6). This emphasizes the previous results obtained in the patients indicating the absence of marked compensatory head rotations to vertical head oscillations (Fig. 4) and the poor correlation between Zt and θ (Fig. 5).

Discussion

The purpose of these studies was to measure the ability of patients with peripheral vestibular deficit to stabilize the head in space, during natural activities performed in the light and in darkness. Although initially we intended to focus only on head rotational perturbations that occur during various locomotor tasks, our experimental technique allowed us to describe the general locomotor behaviour of subjects with deficient vestibular inputs. Even though the patients have adapted very well to the loss of labyrinthine sensation, a more demanding motor control task, such as walking in darkness (experimentally checked) or in half-light (reported by the patients), resulted in a high number of imbalances. We propose that during these imbalance periods, the remaining sensory modalities are transiently unable to compensate for the loss of the vestibulo-spinal reflexes. Supporting this are patients' reports that they tend to walk in such a way as to sweep the ground with the heel, before stopping the heel for a firm stance. This behavior lengthens the contact period, and probably provides more tactile information. We also observe that the heels of their shoes are prematurely worn out.

Contribution of the otolith organs to locomotor control

While, during running and hopping both in light and in darkness, normal subjects maintain their preferred jump frequency with accuracy and consistency, patients show large variations in frequency. Melvill Jones and Watt (1971), and Rossignol and Melvill Jones (1976) previously reported the same striking ability of all normal subjects to set themselves in oscillation during hopping, at the same constant frequency (2.06 Hz). These authors infer that, in rhythmical hopping and perhaps also in running, each landing is effected, as in single steps, by a predetermined pattern of neuromuscular activity occurring in the lower leg, as a result of the downward acceleration. Further studies (Melvill Jones et al. 1973; Watt 1981) suggested, that these periodic vestibulospinal influences might contribute to an integral component in the neuromuscular organization of normal locomotor control. Irregularity of the locomotor cycle, observed in the subjects with bilateral vestibular losses and regardless of visual input, support the above hypothesis.

Head angular stabilization

The small number of patients tested and the large standard deviation in the performance of each patient did not allow us to estimate rigorously the correlation between the origin of the deficiency (i.e., neuroma or gentamycine) and head stability.

Compared to normal subjects, patients succeed better in stabilizing their heads during R in the light, perhaps partly because their head displacement amplitudes are smaller.

Nevertheless, when the vestibulo-ocular reflex (VOR) is not performing adequately, head rotation may cause disturbances of vision. As the simultaneously triggered optokinetic reflex (OKR) is poor for rapid movements of the visual scene, patients have to reduce their head rotation in order to optimize the pick-up of visual information. In addition, by visually coupling the head to the environment, patients could compensate for the absence of a stable reference frame, which in normal subjects is provided by the vestibular system. Consistently, patients report oscillopsia during hopping on one leg, an exercise which requires fine equilibrium and during which head stabilization is less effective than during running in place. In contrast, normal subjects never complain of any illusory movement of the environment. Grossman et al. (1989), studying the performance of the human VOR during walking in place and running in place, reported that the normal VOR largely preserves stabilized vision during locomotion. However, in the present experiment, the greater amplitude of maximal head translations along the vertical axis (15 cm versus 6 cm in Grossman et al. 1989), which is probably due to our unconstrained testing conditions, and the nearer viewing distance (2 m versus 100 m) probably invoke the compensatory linear vestibuloocular reflex (LVOR). We have not measured eye movements, so that we cannot ascertain whether compensatory eye movements are produced by a LVOR (toward the opposite direction of head translation, as a response to saccular stimulation) or a rotational VOR (toward the same direction of head translation, as a response to the vertical semicircular canal stimulation). A recent study (Paige, 1989) demonstrated the existence of a compensatory LVOR during vertical head translations (frequency 2.7 Hz, peak to peak amplitude 3.2 cm) when subjects alternately fixated targets at 36, 142 and 424 cm. In the present study, according to these findings, either these reflexes, LVOR or VOR, could help to offset the disturbances of the head with respect to the stationary environment.

Vestibulospinal contribution to the control of head posture during locomotion

In normal subjects, frequency analysis allowed us to distinguish, on the one hand *compensatory head rotations,* which are composed of rapid and small head angular oscillations, closely related to head translation along the vertical axis and, on the other hand, slow rotations of the *mean angular position of the head,* which persist for the whole duration of one trial. Then, the question arises as to the contribution of vestibular receptors to the control of these 2 rotational components.

The vertical linear accelerations of the head, found in the present study are of an order of magnitude higher than the corresponding perceptual threshold of the vestibular system (0.005 g; Melvill Jones and Young 1978). Consequently, when the F–P is stabilized around the earth-horizontal, the saccules, which detect early vertical linear head accelerations, could start a vestibulospinal response acting not only on lower limbs, as suggested Melvill Jones et al. (1971), but also on neck muscles. During movements at higher frequencies, such as running and hopping, the subjects could generate these compensatory head rotations by taking advantage of the effects of head inertia, the saccular signals being used only to tune neck muscular stiffness. When the latter signal is absent, as in our labyrinthine subjects, the tuning is degraded, as illustrated by the lack of a clear time relation between head translation along the vertical axis and head rotation. Consequently, the present study demonstrates that, even during movements at frequencies higher than 2 Hz (i.e., where inertia effects are important, Guitton et al. 1986; Rozendal 1986), head stabilization in space is not entirely due to passive mechanical forces as suggested Grossman et al. (1989); head stabilization seems to be part of an active process under vestibular control.

Our results show that normal subjects stabilize their heads accurately, and with consistency from trial to trial. In the light and in darkness, the mean position of the F–P remains near the earth-horizontal, whether subjects stand quietly or perform any locomotor task, even for a long period. It is interesting to compare our results with those of Vidal et al. (1986) obtained in seven species of vertebrates. This radiographic study demontrated that animals at rest adopted a stereotyped posture of the head and the neck: the plane of the horizontal semicircular canals is tilted upwards by about 10° relative to earth horizontal.

Unlike normal subjects, patients are unable to stabilize their head in a position such that the F–P is horizontal. Impairment of head postural orientation with respect to gravity is probably related to the lack of otolithic input which is, in normal subjects, necessary to maintain a normal head attitude relative to gravity. Surgical "plugging" of all six canals leaves alert cats quite able to hold their heads erect, albeit somewhat unsteadily, provided that the otolith organs are intact. In contrast, subsequent total bilateral labyrinthectomy characteristically provokes a wide range of bizarre head attitudes (Money and Scott 1962).

In the present study, many patients relate these abnormal head postures to the necessity of improving the uptake of visual information. For instance, some of them report that head extension is needed to "increase the dimension of the visual field" or that flexion of the head is "necessary to look both to the ground or to the feet". The variety of head postures adopted by each patients, all perceived as facilitating the pick-up of visual information, suggests that their common aim is to anchor the gaze to fixed landmarks located in the surrounding visual space. When vestibular input is lacking, head and gaze stabilization with respect to these landmarks could provide the spatial reference needed to control the balance of the moving body. Otherwise, the exaggerated nose-down position of the head, observed in patients with bilateral acoustic neuroma might reflect the decreased muscle tone as a result of the loss of all vestibular input (Roberts 1967; Watt 1976). In addition, Denise et al. (1989) found a marked downward displacement of the gaze after hemilabyrinthectomy in the cat, particularly when the animal was sleepy. These authors suggest that, in intact animals, the vestibular system (otolith or vertical semi-circular canals) could produce an upward tonic activity on oculomotor system and thus control vertical eye position. These results are in agreement with those of Clément et al. (1986) in human subjects, showing that optokinetic nystagmus beating field is deviated downward in the absence of gravity.

In normal subjects, the long-term ability to maintain the F–P near the earth-horizontal plane, during sinusoidal vertical accelerations, is likely due to otolithic information (Brindley 1965). As emphasized by Mayne (1974) and recently modelled by Droulez and Darlot (1989), it would be relevant to pass the primary otolithic signal through a "low-pass" filter, to extract the information on orientation with respect to gravity, as with the artificial horizon used in aircraft. Therefore, a good stabilization of mean head angular position relative to gravity provides a stable vestibular reference, in which the otolithic inputs would be mainly devoted to detect linear accelerations, as do accelerometers in inertial guidance systems.

Clinical implications

An important aspect of the experimental technique employed in this study is that vestibular dysfunctions are tested during natural tasks. This avoids the segmentation of behaviour often encountered in laboratory studies, in which each sensor is tested as an isolated subsystem. In contrast, the technique used in the present study could be used to evaluate the motor compensation allowed by a multi-cue interaction following a loss of peripheral vestibular functions. Otherwise, the frequency spectrum of head rotation encountered during the natural locomotor tasks and which characterize normals (high and low frequencies) and patients (low frequencies only), could also be used to detect total or partial (of otolith only) vestibular lesions. Obviously, further studies made on a greater number of patients are necessary to verify the clinical validity of such tests.

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References

Allum JHJ, Mauritz KH (1985) Visual and vestibular contributions to pitch sway stabilization in the ankles muscles of normals and patients with bilateral peripheral vestibular deficits. Exp Brain Res 58:82–94

Black FO, Wall C, Nashner LM (1983) Effect of visual and support surface orientation references upon postural control in vestibular deficient subjects. Acta Otolaryngol 95:199–210

Brindley GS (1965) How does an animal that is dropped in a non-upright posture know the angle through which it must turn in the air so that its feet point to the ground? J Physiol 180:24–44

Bronstein AM (1988) Evidence for a vestibular input contributing to dynamic head stabilization in man. Acta Otolaryngol 105:1–6

Clément G, Vieville T, Lestienne F, Berthoz A (1986) Modification of gain assymetry and beating field of vertical optokinetic nystagmus in microgravity. Neurosci Lett 63:271–274

D'Amico F, Ferrigno G (1990) Technique for the evaluation of derivatives from noisy biomechanical displacement data using a model-based bandwith-selection procedure. Med Biol Cop 24:407–415

De Beer GR (1947) How animals hold their heads. Proc Linn Soc London 159:125–139

Denise P, Corvisier J, Berthoz (1989) Eye movements and neck muscle activity after unilateral labyrinthectomy in the cat. In: Lacour M, Denise P, Toupet M, Christen Y (eds) Vestibular compensation: facts, theories and clinical perspectives. Elsevier, Paris, pp 59–72

De Waele C, Graaf W, Josset P, Vidal PP (1989) A radiological analysis of the postural syndromes following hemilabyrinthectomy and selective canal and otolith lesions in the guinea pig. Exp Brain Res 77:166–18

Droulez J, Darlot C (1989) The geometric and dynamic implications of the coherence constraints in the three dimensional sensorimotor interactions. In: Jeannerod M (ed) Attention and performance, Vol XII, 17. Lawrence Erlbaum, Hillsdale NJ, pp 495–525

Freyss G, Vitte E, Semont A, Tran-Ba-Huy P, Gaillard P (1988) Computation of eye-head movements in oscillopsic patients: modifications induced by reeducation. Adv Oto Rhino Laryng 42:294–300

Freyss G, Vitte E, Semont A, Meligy EL, Gaillard P (1989) An otoligical and physiotherapeutic assessment of vestibular compensation in humans. In: Lacour M, Denise P, Toupet M, Christen Y (eds) Vestibular compensation: facts, theories and clinical perspectives. Elsevier, Paris, pp 261–274

Greenwood R, Hopkins A (1976) Muscle response during sudden falls in man. J Neurophysiol 254:507–518

Gresty M (1987) Stability of the head: studies in normal subjects and in patients with labyrinthine disease, head tremor, and dystonia. Mov Disord 1:165–185

Grossman GE, Leigh RJ, Bruce E, Huebner WP, Lanska DJ (1989) Performance of the human vestibuloocular reflex during locomotion. J Neurophysiol 62:264–272

Guitton D, Kearney RE, Wereley N, Peterson BW (1986) Visual, vestibular and voluntary contribution to human head stabilization. Exp Brain Res 64:59–69

Longridge NS, Mallinson AI (1987) The dynamic illegible e-test. Acta Otolaryngol 103:273–279

Mayne R (1974) A system concept of the vestibular organs. In: Kornhuber HH (ed) Handbook of sensory physiology: vestibular system, Vol VI/2. Springer, New York, pp 493–580

Melvill Jones G, Young LR (1968) Subjective detection of the vertical acceleration: a velocity dependent response. Acta Otolaryngol 85:45–53

Melvill Jones G, Watt DGD (1971) Observations on the control of stepping and hopping movements in man. J Physiol 219:709–727

Melvill Jones G, Watt DGD (1971) Muscular control of landing from unexpected falls in man. J Physiol 219:729–737

Melvill Jones G, Watt DGD, Rossignol S (1973) Eight nerve contributions to the synthesis of locomotor control. In: Stein RB, Pearson KB (eds) Control of posture and locomotion. Plenum, New York, pp 579–597

Money KE, Scott JW (1962) Functions of separate sensory receptors of non-auditory labyrinth of the cat. Am J Physiol 202:1211–1220

Paige GD (1989) The influence of target distance on eye movement responses during vertical linear motion. Exp Brain Res 77:585–593

Pozzo T, Berthoz A, Lefort L (1990) Head stabilization during various locomotor tasks in humans. I. Normal subjects. Exp Brain Res 82:97–106

Roberts TD (1967) Neurophysiology of postural mechanisms. Butterworths, London

Rossignol S, Melvill Jones G (1976) Audio-spinal influence in man studied by the H-reflexe and its possible role on the rythmic movements synchronized to sound. Electroenceph Clin Neurophysiol 41:83–92

Vidal PP, Graf LV, Berthoz A (1986) The orientation of the cervical column in unrestrained awake animals. I. Resting position. Exp Brain Res 61:549–559

Watt DGD (1976) Responses of cats to sudden falls: an otolith-originating reflex assisting landing. J Neurophysiol 39:257–265

Watt DGD (1981) Effects of vertical linear acceleration on H-reflex in decerebrate cat. II. Sinusoidal stimuli. J Neurophysiol 45:656–667