Exp Brain Res (1985) 61: 21–37

Experimental Brain Research

Lateral orientation and stabilization of human stance: static versus dynamic visual cues

B. Amblard[1], J. Crémieux[1], A.R. Marchand[1], and A. Carblanc[2]

[1] Département de Psychophysiologie Générale, Institut de Neurophysiologie et Psychophysiologie du CNRS, F-13402 Marseille Cedex 9, France
[2] UER d'Education Physique et Sportive, Université d'Aix-Marseille II, Case Postale 910, F-13402 Marseille Cedex 9, France

Summary. The differential contributions of static versus dynamic visual cues to postural control were studied in human subjects. Lateral body oscillations were measured with accelerometers located at head, hips and ankle levels, while subjects righted their balance under various mechanical conditions: i) on either a soft (foam rubber) support or a hard one, and ii) in either the classical or the sharpened Romberg stance. The visual pattern (horizontal or vertical rectangular grating) was illuminated with either a stroboscopic bulb or a normal one, and control measurements were also taken in darkness for each mechanical condition. Acceleration signals were processed into their frequency power spectra, the mean area and shape of which were taken to characterize the postural skills involved and the effects of either the visual suppressions or the mechanical destabilizations. Although dynamic visual cues have already been found to play a major role in the control of lateral body sway (Amblard and Crémieux 1976), we demonstrate here that static visual cues, the only ones available under stroboscopic illumination, also make a clear though minor contribution. Hence we suggest the existence of two modes of visual control of lateral balance in man, which are well separated in terms of the frequency range of body sway: the first mechanism, which operates below 2 Hz and is strobe-resistant, seems to control the orientation of the upper part of the body; the second mechanism, which operates above 4 Hz, centers on about 7 Hz and is strobe-vulnerable, seems to immobilize the body working upwards from the feet. Thus static visual cues may slowly control re-orientation or displacement, whereas dynamic visual cues may contribute to fast stabilization of the body. In between the frequency ranges at which these two visuomotor mechanisms come into play, at about 3 Hz, there is what we call a "blind frequency", a visually neutral sway frequency which may arise from the incompatibility of visual reorientation with visual stabilization, and where vision appears unable to reduce postural sway to any marked extent. Transmission of the destabilization produced by suppression of visual cues or by mechanical methods from one anatomical level to another is also briefly discussed in terms of bio-mechanical constraints, and the correlations between various pairs of levels are considered.

Key words: Posture control – Motion vision – Static vision – Stroboscopic illumination – Accelerometry – Fourier analysis – Man

Introduction

It is now an established fact that vision contributes to the control of the upright stance. Experimental approaches to this topic have mainly focused until recently on techniques that induce postural destabilization either by visual motion cues decorrelated from motor activity (Lee and Aronson 1974; Kapteyn and Bles 1977; Lestienne et al. 1977; Dichgans and Brandt 1978) or experimental stabilization of the visual surround (Vidal et al. 1978) during normal stance or movement of the body. Brandt and Daroff (1980) have suggested, however, that some of these techniques may induce visual vertigo because of a "mismatch between the visual sensation of movement without concomitant vestibular and somatosensory inputs". Arguing along different lines, Nashner and Berthoz (1978) have suggested that "at the time of the rapid selection of an adapted motor pattern, the release of the adequate motor synergies is dependent upon an expected pattern of congruent sensory inputs". The experiments reported here were

Offprint requests to: B. Amblard (address see above) thus designed to preserve normal sensorimotor correlations. The visual control of body balance was therefore mainly studied through experimental manipulations of the visual pattern and illumination.

Classical experiments have often shown that visual stimulation mainly produces a change in body orientation with respect to gravity, both in man (Held et al. 1975; Lestienne et al. 1977) and in animals (Talbott 1980). Low frequency characteristics of such orientational adjustments are suggested by the long latencies of these effects. A more dynamic and rapid contribution of visual information has also been clearly shown in various experimental situations (Nashner and Berthoz 1978; Soechting and Berthoz 1979; Craik et al. 1982), and a selective elimination of dynamic visual cues either by stroboscopic illumination (Amblard and Crémieux 1976) or by an appropriate visual pattern (Amblard and Carblanc 1980) has been shown to produce a drastic destabilization which is almost as severe as that produced by darkness. Similar effects were observed when a natural visual scene was presented five meters away from the subject (Bles et al. 1980), which reduces the apparent visual flow correlated with body sway. These various results suggested the existence of various components of visual postural control which might depend upon experimental conditions. We tried here to find a situation where both slow and rapid visual contribution to body stability could be observed simultaneously.

In addition, the predominant importance of continuous visual information in balance (Amblard and Crémieux 1976) had to be reconciled with the "considerable optic sway" induced by a moving room stroboscopically illuminated (Kapteyn et al. 1979). With strobe frequencies below 6 Hz, the latter described an increasing postural instability as compared to complete darkness; such a "postural destabilization was evident even when no motion was perceived at 0.75 Hz". We suspected a critical difference between these two sets of experiment. Using a tilting room sinusoidally moved with a very low frequency (0.05 Hz), the first one was addressing the slow visual drive of the body orientation. By contrast, we attribute the severe imbalance that we have described under strobe illumination to a lack of motion information subserving the fast postural adjustments required in the sharpened Romberg stance on a soft support. The following set of experiments was therefore undertaken to support this interpretation, and to estimate the respective contributions of static visual cues (the only ones available under stroboscopic illumination) and dynamic visual cues (available only under normal illumination) with respect to the body sway frequency.

The upright posture was studied with special attention paid to the sharpened Romberg situation on a thick foam rubber support, where enhancement of the visual input contribution to posture has been observed (Kapteyn 1972; Amblard and Crémieux 1976; Bles et al. 1980). In the first experiment (first presentation in a symposium: Crémieux et al. 1981), the visual pattern was a vertical grating similar to that previously used (Amblard and Carblanc 1980), and completed with a wide central bar providing the subject with a reference for his lateral body displacements. The same visual pattern could also be presented horizontally. It was assumed that normal illumination of the vertical pattern provided the subject with visual informations about his own movements (dynamic type) or displacements (static type), while stroboscopic illumination of the same pattern would reveal to what extent static visual cues alone could be used. In the case of the horizontal pattern under strobe or normal light both static and dynamic visual information about lateral oscillations would be strongly reduced, with the exception of possible static cues about orientation. Random frequency stroboscopic light was also used, so as to prevent speed from being estimated from the successive images, as already suggested in cat experiments (Amblard and Crémieux 1979). The second experiment (first presentation in a symposium: Amblard et al. 1982) was an attempt to detect some separation of the two kinds of visual contribution (using static or dynamic visual cues) from the frequency range of the lateral body oscillations. We therefore put emphasis on the shape of the power spectra as functions of the component frequencies of the lateral accelerations of the body. The results are tentatively interpreted in terms of two visual mechanisms with different locations in the body sway frequency domain, which seem to be consistent with a recent classification of "movements by function, as either stabilizing or orientational adjustments" (Nashner and Cordo 1981).

Methods

Subjects

Subjects were 12 healthy adults, 6 women and 6 men, either teachers in physical education or research workers, aged from 25 to 45 years. Most of the subjects underwent both experiments 1 and 2.

Testing system and visual environment

The balance support (60 cm long, 30 cm wide) was similar to that previously described (Amblard and Crémieux 1976; Amblard and Carblanc 1980). It was either a thick (15 cm) foam rubber support (soft support SS; experiments 1 and 2) or a flat floor (hard support HS; experiment 2 only).

The balance support was surrounded by an open vertical cylinder – 115 cm in diameter, 190 cm high, covering 4.28 rad. of visual field, i.e. considerably more than the lateral visual field of a subject at the centre of the cylinder facing the middle of the wall. The ceiling of the cylinder consisted of uniformly illuminated white cardboard, and a visual pattern consisting of black and white stripes 1.2 cm wide was placed on the inner wall. This rectangular grating was presented either vertically or horizontally. A wide black bar (6 cm wide) was added to the center of the vertical grating in order to provide the subject with a convenient positional reference for speed calculations and to avoid possible unwanted confusions between identical stripes. A similar bar was also added to the centre of the horizontal grating, with the center at eye level. The contrast of the grating – very close to one – and the spatial frequency – close to 23 cycles per rad – were chosen so as to be sufficiently above threshold, and so that visual sensitivity to movements of the stripes across the retina was good in both central and peripheral vision (Blakemore and Campbell 1969; Blakemore and Nachmias 1971; Campbell and Kulikowski 1966; Sachs et al. 1971; Sharpe and Tolhurst 1973).

Lighting in the cylinder was provided by a stroboscope (flash duration < 0.2 ms; flash energy 0.3 J) or a normal lamp fitted to the centre of the ceiling. Normal dim light was chosen so as to give the same subjective mean brightness as the stroboscopic light. The latter was chosen with either a fixed frequency (3 or 6 flashes/s) or a random frequency (intervals of darkness between flashes being uniformly distributed between 1.0 and 0.143 s, i.e. instantaneous frequency of 1 to 7 flashes/s).

Testing procedure and measurements

Two types of stance were used in which the subjects had bare feet: i) sharpened Romberg, one foot in front of the other, the hindmost foot remaining the same throughout the experiment (narrow base NB, experiments 1 and 2), or ii) classical Romberg (wide base WB, experiment 2 only).

Lateral oscillations of the subject's *head* were measured by an ACB Type J2210 accelerometer fixed to a flying helmet; lateral oscillations of *hips* and *ankles* were measured by two Bruel and Kjaer Type 4333 piezoelectric accelerometers. At the ankle the accelerometer was fixed to the hindmost foot only.

Just before each trial began, the subject leaned back with his right hand on a jointed board fitted with a switch and placed behind him at hand level, which was used to mark the beginning of the trial. In the same way, when the subject placed a foot on either side of the testing support, an electrical contact indicated the end of the trial. The signals from this circuit and from the accelerometers were recorded on an FM tape recorder.

Under the experimental conditions of a trial, at a signal from the experimenter the subject had to let go of the manual support and remain in equilibrium for more than 20 s. During this stage, he would look straight ahead, with his hands behind his back. The instructions were to stand upright keeping optimal balance. In the event of a fall, the attempt was repeated if it had lasted less than 7.5 s (Experiment 1) or less than 20 s (Experiment 2).

Experimental sessions

Experiment 1: upright posture was measured in the sharpened Romberg situation on a soft support. The visual pattern was presented either vertically or horizontally under four lighting conditions: stroboscopic illumination at either 3 or 6 flashes/s; stroboscopic illumination at random frequency; and normal lighting. For each experimental condition and subject, 12 successful trials were run for averaging. There were 4 experimental sessions for each subject, 2 with the horizontal pattern and 2 with the vertical one, in a different order for each subject. During each session, each of the 4 illumination situations was presented in random order.

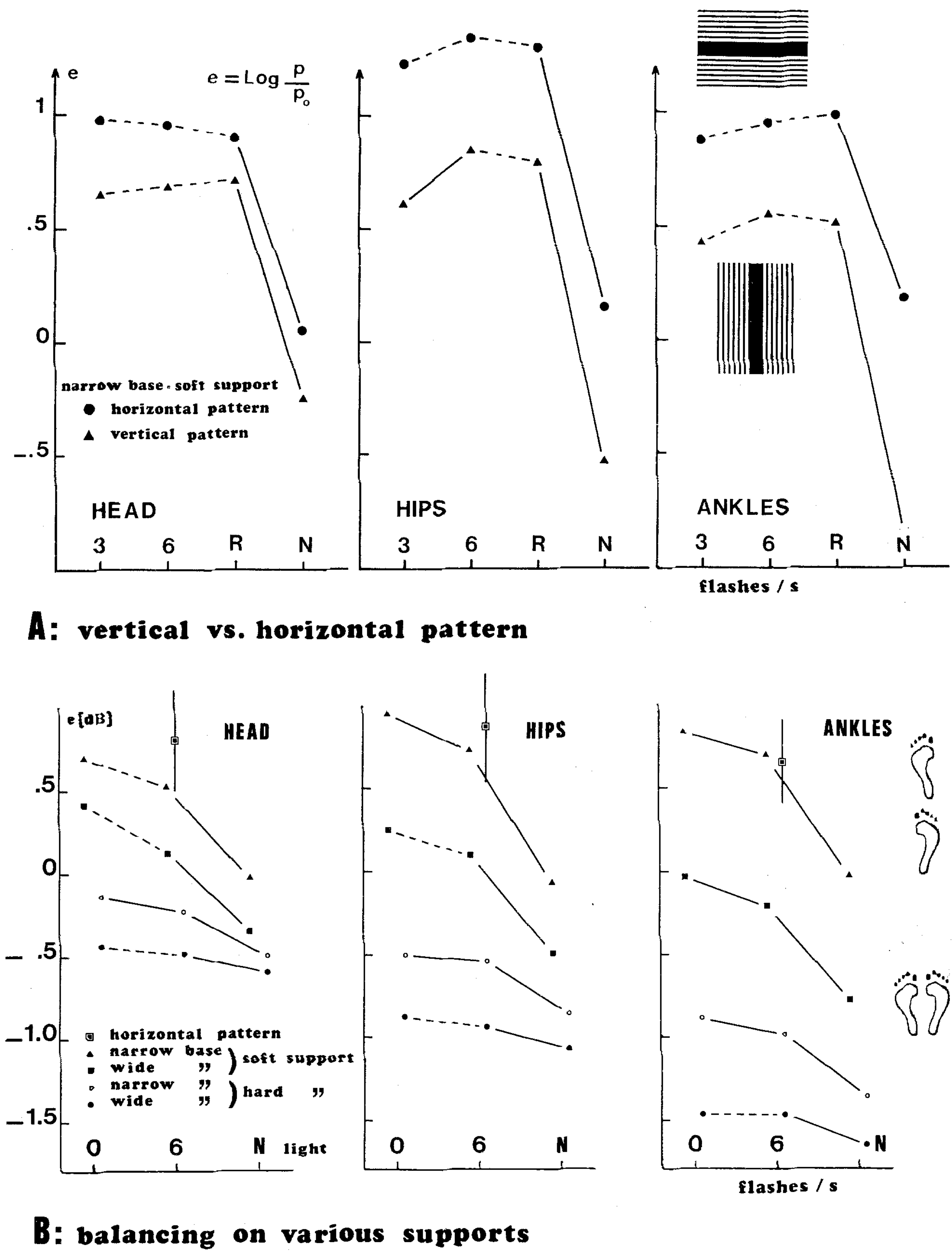
Table 1. Duration of the digitized acceleration signal of each level of measurement and each trial, frequency limits of the spectra, number of trials for each experimental condition and each subject, and total number of trials for the calculation of P

		Exp 1		Exp 2	
Δt	Duration of the digitized acceleration signals	7.5 s		20 s	
		m	M	m	M
Head level	Frequency	0.4	12.0	0.0	20.0
Hips level	limits of the	0.8	12.0	0.8	20.0
Ankles level	spectra (Hz)	0.8	12.0	0.8	20.0
$P = \frac{1}{n}\Sigma P_i$	Number of trials for each experimental condition and each subject	n = 12		n = 8	
	Total number of trials for each experimental conditions and the 12 subjects	144		96	

Experiment 2: the visual pattern was presented mainly vertically, under 3 lighting conditions: darkness (0 flash/s); stroboscopic illumination (6 flashes/s); and normal illumination. The stance was either sharpened Romberg or classical Romberg, on either a soft support or a hard one. Eight trials were performed for each experimental situation and each subject. There were 2 experimental sessions for each subject. At the beginning and the end of each session, 2 successive trials were run with the horizontal pattern under stroboscopic illumination (6 flashes/s) in sharpened Romberg on a soft support. During each session and with the vertical visual pattern, each of the support situations (soft and hard) combined with each of the stances (sharpened or classical Romberg) was presented with each of the 3 illumination situations according to a randomized plan.

Frequency power spectra analysis and statistics

For each successful trial, the first parameter to be considered was the mean power P_i, which was calculated from the power spectrum of the component frequencies of the acceleration signal at each anatomical level (head, hips, ankles). For this, the spectrum – calculated as previously described (Amblard and Crémieux 1976; Amblard and Carblanc 1980) by means of a standard FFT programme – was considered between the frequency limits given in Table 1. P is the average of P_i from n trials (see Table 1) in similar conditions. A standard value P_o was calculated for the 12 subjects at each level of measurement for a reference situation (normal illumination, vertical stripes, narrow base and soft support), thus permitting comparison between the levels. The normalized mea-



e
$e = \mathrm{Log}\,\frac{p}{p_o}$
1
.5
0
–.5
narrow base - soft support
horizontal pattern
vertical pattern
HEAD
HIPS
ANKLES
3 6 R N
flashes / s
A: vertical vs. horizontal pattern
e[dB]
.5
0
– .5
–1.0
–1.5
horizontal pattern
narrow base
wide ,,
soft support
narrow ,,
wide ,,
hard ,,
0 6 N light
flashes / s
B: balancing on various supports

Fig. 1

sure of a subject's overall sway in a single experimental situation was thus:

$$e = \text{Log}\,(P/P_o)$$

In the second experiment, the measured accelerations converted into frequency power spectra were also subjected to a more detailed and elaborate analysis, in order to clarify the meaning of the differences in mean powers of sway between experimental situations. The analysis of the spectra was carried further through successive differences and these were completed by a correlation analysis of the acceleration signals.

It must be stressed that measurements of accelerations rather than positions (as usually in stabilometry) allow a detailed analysis into a higher frequency range (i.e. 2 to 15 Hz) where body sway may still be significant.

Differential spectra. Each average power spectrum being an average of similar stationnary samples had a good signal to noise ratio. These average spectra could thus be used to study differences in sway between two distinct modalities in a single experimental condition (vision, stance or type of support), all other conditions being identical. We call such a difference between two average spectra "effect of a factor", meaning:

a) in connection with the effect of static visual cues, the difference between an average spectrum in darkness and that obtained under stroboscopic illumination;

b) in connection with the effect of dynamic vision, the difference between an average spectrum in strobe light and that obtained under normal vision;

c) in connection with the effect of stance, the difference between an average spectrum in the sharpened Romberg and that obtained in the classical Romberg situation;

d) in connection with the effect of support, the difference between an average spectrum on soft ground and that obtained on a hard support.

At each anatomical level, these differential spectra have a specific shape, which is typical of the effect and the way in which it is transmitted from one level to another. The differential spectra will be shown here as histograms, each bin of which being the mean power over a 2 Hz frequency range. This corresponds to 40 values with a step of 0.05 Hz that have been pooled together. A mean value of zero was used wherever a Student's t-test on the 40 values showed no significance. Plotting the spectra as histograms leaves some details out, especially in the very low frequency range. Mechanisms described, for instance, at head level in the 0–2 Hz bin have therefore not been very accurately located in the frequency domain.

Differential effects or transmission spectra. A differential spectrum for the effect of a factor at a given anatomical level (head, hips or ankles) can be compared to the spectrum obtained simultaneously at another level. This difference between effect spectra at two anatomical levels we will call "transmission spectrum". It reflects the modifications of the effect across anatomical levels.

Correlations. For each successful trial in Experiment 2, the z transform of the absolute value of the correlation coefficient r between the acceleration signals of two anatomical levels was finally calculated:

$$z = \frac{1}{2}\,\text{Log}\,\frac{1+r}{1-r}$$

Acceleration signals were unfortunately not checked for their sign when they were digitized, so that only an absolute value is available for the correlation coefficient r (computed on 1024 samples at 50 Hz). For each subject, the mean value of z is the mean of 8 values corresponding to the number of trials run for each experimental condition.

A standard programme of variance analysis (programme VAR3, University of Paris 6: see also, Rouanet and Lépine 1970) was used to test the degree of significance of the comparisons made between experimental situations, for the overall mean measure of the performance e as well as for the mean z transform.

Results

I. Experiment 1

Figure 1A shows the postural performances recorded in every experimental situation expressed in mean values of e. Significant differences between two nearby conditions are indicated by a continuous line, whereas non significant differences are represented with a broken line. The higher the mean values, the less successful the performances.

a) Effect of static visual cues. Stroboscopic illumination suppresses most of the visual information, but not the orientation or *successive positions* of the swaying body with the vertical pattern. Position cues are further suppressed under stroboscopic illumination of the horizontal pattern. The differences in the mean performances between horizontal and vertical conditions are significant for every type of strobe light (3 or 6 flashes per second, and random frequency) at the hip and ankle levels (at least $p <$ 0.05), which therefore clearly confirms the contribution of these static visual cues to the control of upright posture.

Fig. 1. A Vertical vs. horizontal patterns: performance in terms of mean area P of the frequency power spectrum for the horizontal (H) or vertical (V) visual pattern and for three anatomical levels. F3, F6: fixed frequencies of stroboscopic light (3 and 6 flashes/s respectively); R: stroboscopic light at random frequency; N: normal dim light. Broken line between two nearby conditions indicates a non significant difference, whereas a continuous line indicates a significant difference. **B** Balancing on various supports: mean performances of the 12 subjects for the mean area of the power spectra at three anatomical levels, under two stance conditions (*wide base* = classical Romberg; *narrow base* = sharpened Romberg) and with two types of support (normal hard support and thick foam rubber). O: darkness; 6: strobe frequency (6 flashes/s); N: normal illumination. Visual pattern is a vertical grating, except for three points obtained with the same grating rotated 90° (horizontal) in the narrow base and soft support condition (mean values with standard deviation in strobe illumination)

None of the differences between strobe conditions is significant with the horizontal pattern. In the case of the vertical pattern, the mean performance is significantly better at 3 flashes/s than at either 6 flashes/s or random frequency ($p < 0.05$) at the hip level. This may point to an overestimation of body displacements with 6 flashes/s (Delorme 1971) associated with unadapted motor responses, while speed calculation from the successive unpredictable visually perceived positions is more difficult with a random frequency. In contrast, the slightly better performance obtained with 3 flashes/s may be partly due to some speed calculation.

b) Effect of dynamic visual cues. At each anatomical level and with the vertical pattern, performances under normal illumination differed very significantly ($p < 0.001$) from those obtained with the 3 kinds of strobe light. These differences, which are at least 3 or 4 times greater (in a Log scale) than those corresponding to the use of static visual cues (differences between horizontal and vertical pattern under strobe illumination), clearly confirm that dynamic visual cues play an important part in the control of upright stance.

At first sight, it seems surprising that better performance is obtained with the horizontal pattern under normal illumination than with a vertical pattern viewed under strobe illumination. But this can perhaps be explained by the fact that dynamic visual cues are minimized with the horizontal grating, but not completely suppressed under normal illumination. A slight vertical component is certainly involved in the lateral body sway at head level, which is peripherally viewed on the retina as a vertical slippage of the more lateral horizontal stripes while under stroboscopic illumination it is poorly informative in terms of change of lateral positions of the body. This residual dynamic visual information under normal illumination is sufficient to explain why a better performance was obtained under normal illumination than in any case under strobe light. This in fact further demonstrates the major role played by peripheral dynamic vision in the control of upright posture.

The differences between vertical and horizontal pattern under normal illumination are statistically significant at every level ($p < 0.05$ for head level; $p < 0.001$ for hips; $p < 0.01$ for ankles). These differences are roughly comparable to those obtained with strobe illumination, both at head level (about 0.25 dB) and at hip level (about 0.5 dB), and can be mainly interpreted in terms of frontal image displacement (static type), or possibly in terms of a superiority of vertical over horizontal orientation cues.

c) General comments. Postural abilities, as revealed by the mean values of e, vary somewhat from one subject to another. However, there is no significant difference between males and females, nor between ordinary subjects and sportsmen, none of the latter subjects being particularly familiar with equilibrium situations.

Under stroboscopic illumination, when their equilibrium was much less stable, subjects usually reported some weariness at ankle level. They sometimes reported a greater difficulty with a vertical pattern under strobe illumination than with the horizontal pattern, although the results were better with the vertical pattern. This indicates that visual assistance to upright posture does not necessarily operate at a perceptual level.

II. Experiment 2

a) Mean performances

Figure 1B shows the mean performances in terms of the mean values of e. This experiment was performed in most cases with the vertical visual pattern. The contribution of static visual cues – visual information about orientation to vertical or lateral position of the head relative to the vertical central band, those cues which are available within a single flash – can be confirmed here by comparing the performances obtained with the vertical pattern under strobe light (6 flashes/s) and those obtained in darkness, while the comparison between horizontal pattern under strobe light and darkness may reveal whether any adequate static visual cues are available outside frontal image positions or displacements (i.e. either lateral image displacements from successive positions or orientation from the horizontal pattern).

The data in fact shows no significant difference – with a soft support and a narrow base – between darkness and horizontal pattern under strobe light, which indicates that under intermittent illumination, a horizontal pattern affords no visual cues relevant for the reduction of lateral body sway. Partly because of the absence of adequate randomization of the corresponding trials, and partly because of the smaller number of these trials, we failed to confirm in experiment 2 the significant difference observed between horizontal and vertical stripes in experiment 1, on soft support and with a narrow base. The design of first experiment was in fact more adequate for this comparison.

Except for the most stable stance (wide base WB and hard support HS), most of the differences between darkness and strobe light are significant: i)

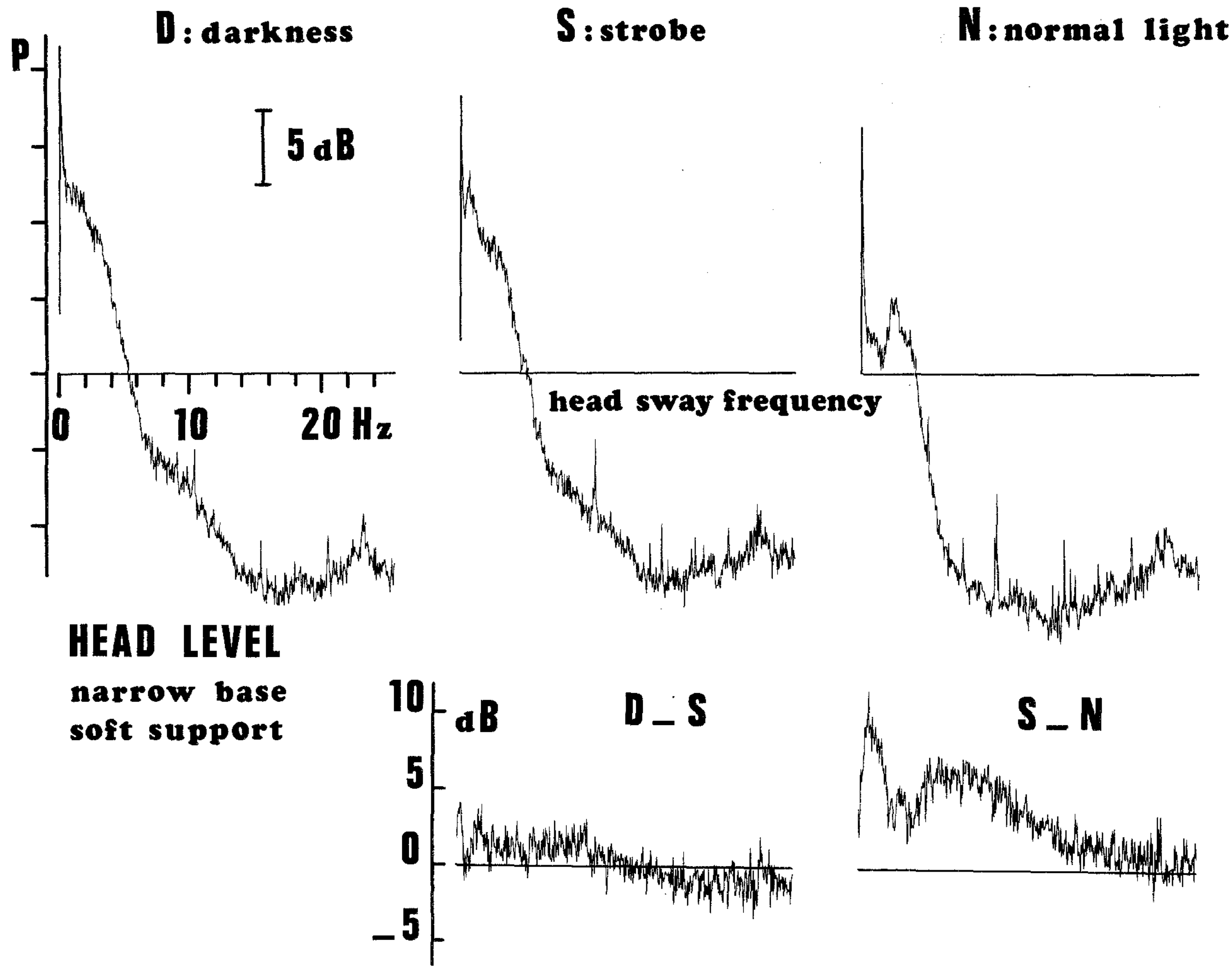


Fig. 2. Mean frequency power spectra for the 12 subjects using semi-logarithmic scale (see text). Head level measurements, in the sharpened Romberg's condition on the thick foam rubber support. Upper traces: power spectra in darkness (D), stroboscopic illumination (S; 6 flashes/s) and normal illumination (N). Lower traces: differential spectra obtained by differences in the upper spectra

under the condition NB-HS, these differences are significant at head ($p < 0.001$), hip ($p < 0.05$) and ankle level ($p < 0.01$); ii) under the condition WB-SS, the difference is significant at ankle level only ($p < 0.05$); iii) under the last condition NB-SS, the differences are significant at the hip and ankle levels ($p < 0.05$). The contribution of static visual cues which was shown to exist in experiment 1 is therefore clearly confirmed in experiment 2, mostly for an unstable equilibrium.

All the differences between strobe light and normal light are highly significant ($p < 0.001$), irrespective of the stance condition, and for the three anatomical levels. This means that dynamic visual cues are always necessary to achieve the best equilibrium.

Concerning the mechanical conditions involved in stance control, first one can note a disjunction in the results between soft (2 upper curves in Fig. 1B) and hard support (2 lower curves in the same Figure). For each category of support firmness, there is a second lesser disjunction between the narrow base and the wide base. The comparisons between those two kinds of mechanical constraints can be studied separately.

At each level of measurement, each category of support firmness, and each visual condition, the difference between narrow base and wide base was highly significant ($p < 0.001$), or just significant in the case of a hard support in normal light.

At each level of measurement, each width of the base and each visual condition, the difference between soft and hard support was highly significant ($p < 0.001$), or significant: wide base with normal light ($p < 0.05$ at head level), narrow base with normal light ($p < 0.01$ at head level) and narrow base in darkness ($p < 0.05$ at head level).

On the other hand, it can be seen from Fig. 1B

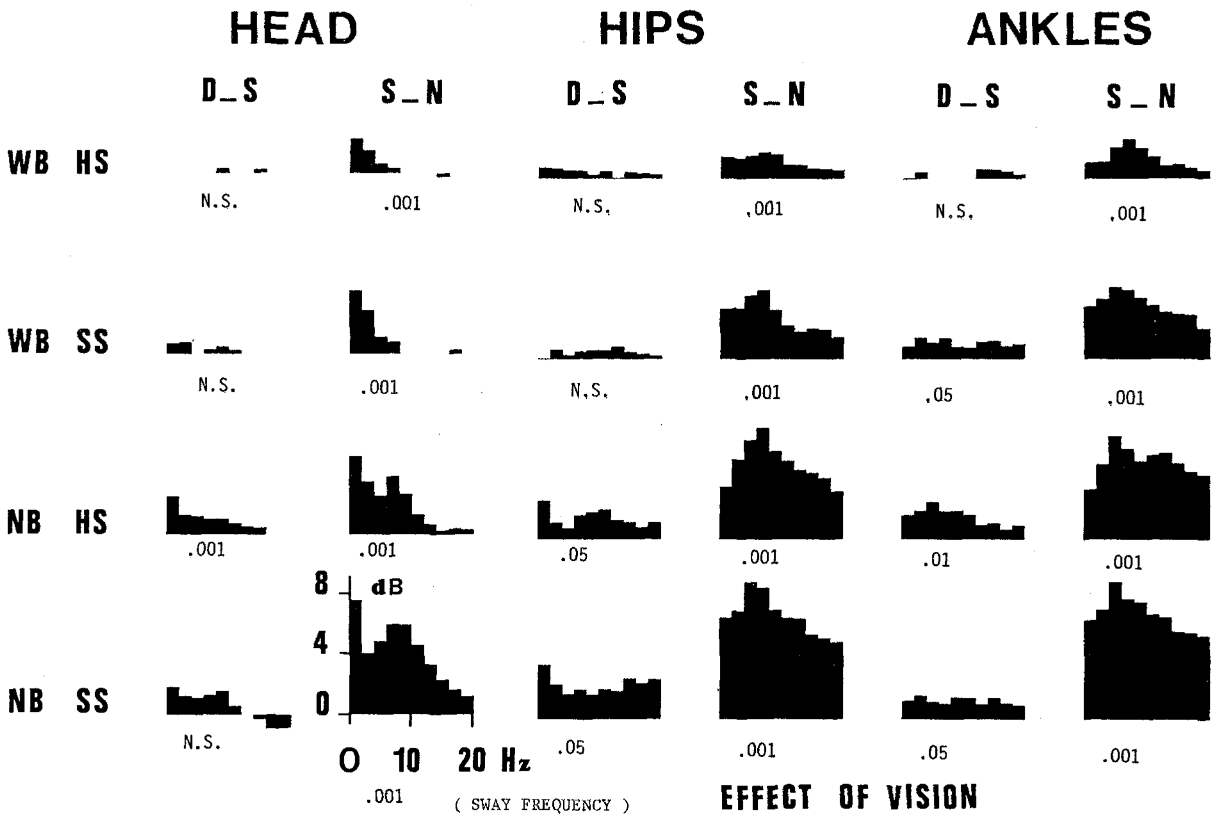


Fig. 3. Mean differential spectra for the 12 subjects and three anatomical levels showing the effect of vision under all the experimental conditions. *WB:* wide base (classical Romberg); *NB:* narrow base (sharpened Romberg). *HS:* hard support; *SS:* soft support (thick foam rubber). The contribution of static vision is the difference between the average spectra in darkness and under stroboscopic illumination (D-S); the contribution of dynamic vision is the difference between average spectra under stroboscopic illumination and under normal vision (S-N). Differences between the mean areas of the original average spectra from which those differential spectra are derived (see methods) may be non significant (N.S.) or significant as indicated under each differential spectrum (see also Fig. 2)

that the gap between two nearby curves decreases from ankles to head, so that the greatest effect of mechanical destabilization occurs at ankle level. Highly significant interactions were found ($p < 0.001$) between the width of the base and the level (with either soft or hard support) as well as between the firmness of the support and the level (with either wide or narrow base).

b) Differential spectra

The above performances as functions of the mean power spectra can now be discussed in detail and studied in terms of the component frequencies of the swaying body. For this purpose, we shall analyse the shapes of various differential spectra (see Methods). Each of the following differential spectra is the difference between two mean spectra, each of which is the average of 96 independent measurements (12 subjects and 8 trials per experimental condition and subject).

1. Effect of vision. Figure 2 shows an example of the mean power spectra P at head level for the condition NB-SS, under various conditions of vision (upper traces); lower traces are the corresponding differential spectra. These first examples of spectra are given with steps of 0.05 Hz. Each bin of all the following spectra is the mean power over a 2 Hz frequency range (see Methods).

For each mechanical condition of the stance (either WB or NB; either HS or SS), and at each anatomical level, the differential spectra corresponding to the effect of vision are shown in Fig. 3, where the first column of a given level represents the contribution of static visual cues (D-S) and the second column the contribution of dynamic visual cues mainly (S-N). Such spectra can be interpreted as follows: for each frequency step, one can read the destabilization (in dB) produced by the suppression of either dynamic vision (column S-N) or static vision (D-S) for the corresponding frequency. In other words, the higher the mean differential power, the higher the contribution of dynamic vision or static

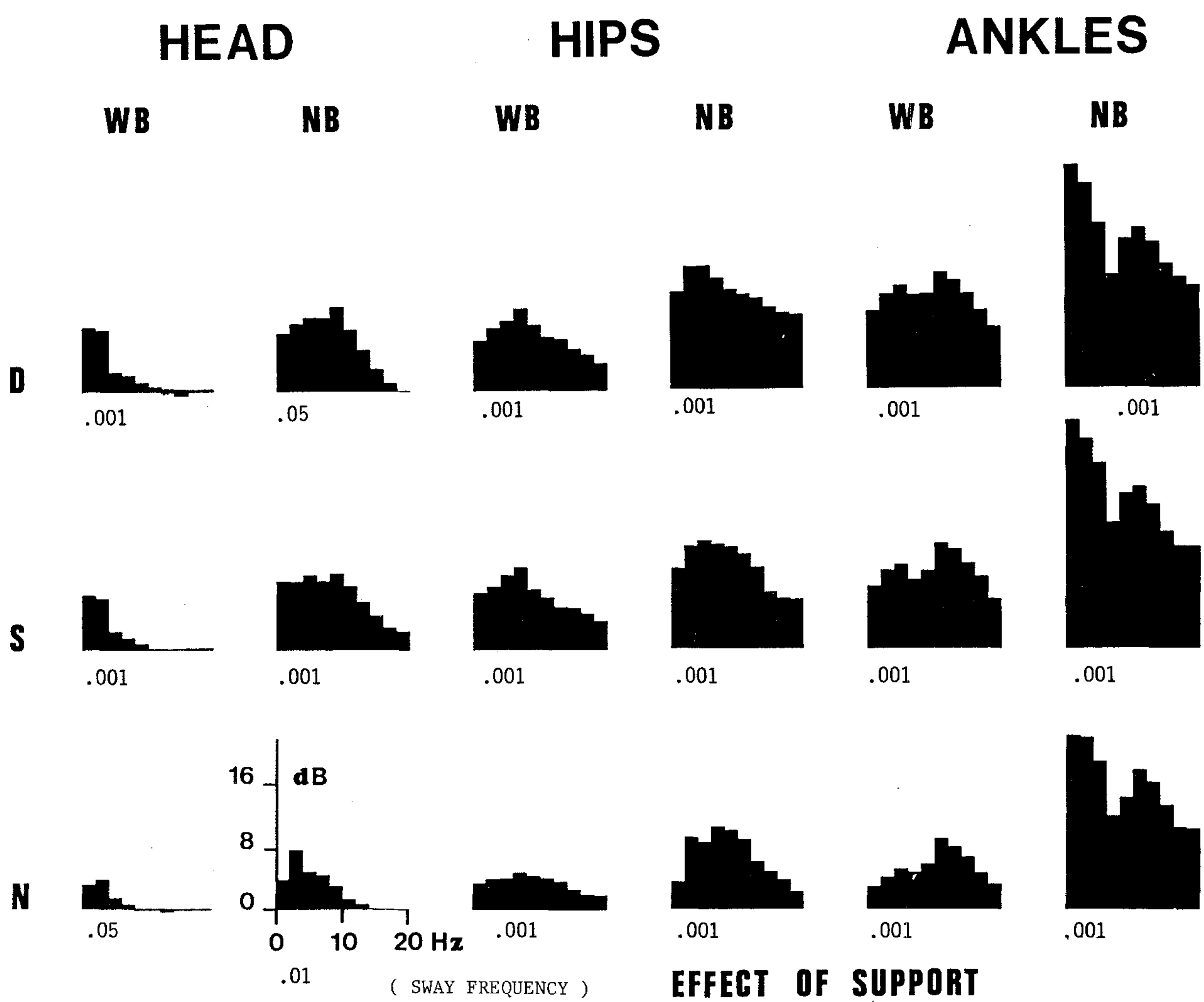


Fig. 4. Mean differential spectra for the 12 subjects and three anatomical levels showing the effects of the firmness of the support. Significance of the symbols as in Fig. 3. The spectra in a given row represent the same visual condition; the spectra in a given column represent the same stance and level of measurement. Each differential spectrum is the average spectrum obtained on soft ground minus that obtained on a hard support

vision, when the appropriate visual cues are available.

The spectra in Fig. 3 display two types of maxima. The first appears in the low frequency domain (up to 2 Hz), especially at head (columns D-S and S-N) and hip level (column D-S). This first maximum is clearest in the columns D-S (narrow base rows), and represents a low frequency destabilization in darkness corresponding to the lack of static visual informations which are present in strobe illumination. It is not surprising to find this maximum also in the spectra of the head level and column S-N, where it is generally higher than in the column D-S, since static visual cues are naturally more constantly available in normal light than in strobe light: the destabilization observed in strobe light results mainly from the loss of dynamic vision, but also from the fact that static vision is intermittently provided. This is especially clear at head level (column S-N).

There is a second type of maximum, centered at about 6–7 Hz. It only emerges clearly in the spectra of columns S-N, indicating that it is due to the lack of information provided by full illumination. In the most stable stance (WB and HS), there is roughly a pure high frequency maximum at ankle level and a pure low frequency maximum at head level. Although the dynamic visual contribution is mainly obvious at the ankle and hip levels, it is also visible at head level under the narrow base condition.

In the latter case (Head, NB, column S-N), the differential spectra are clearly bimodal: for the least stable equilibrium, at head level and between the two maxima a narrow frequency domain appears (around 3 Hz) where the visual contribution is minimum. This

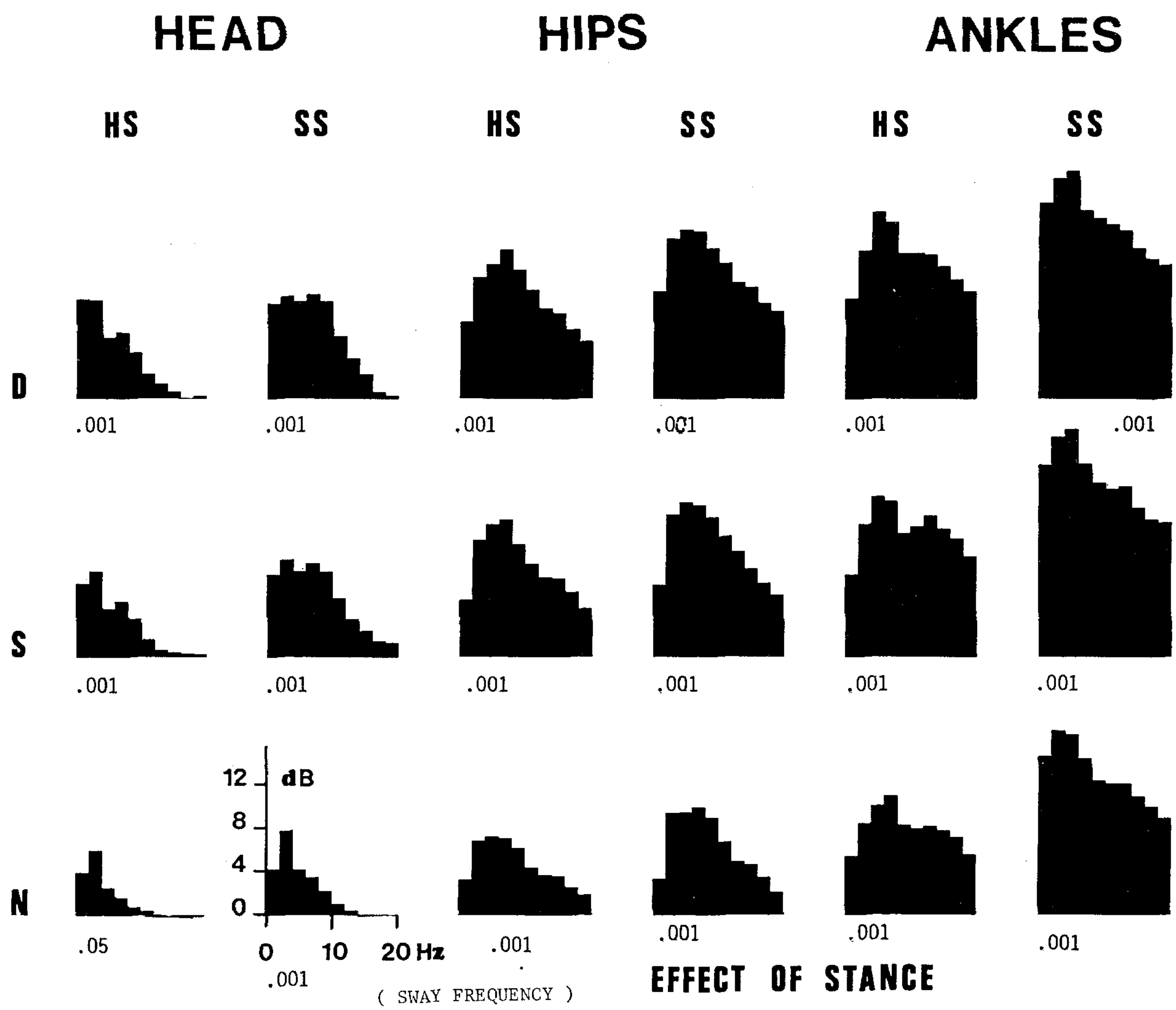


Fig. 5. Mean differential spectra for the 12 subjects and the three anatomical levels showing the effects of stance. Significance of the symbols as in Figs. 3–4. The spectra in a given row refer to the same visual condition: the spectra in a given column refer to the same firmness of support and level of measurement. Each differential spectrum is the difference between the average spectrum obtained in the sharpened Romberg and that in the classical Romberg situation

minimum in the bimodal differential spectrum (see also Fig. 2, lower traces, spectrum S-N) corresponds to a peak in the frequency power spectrum itself, for the same head level under normal illumination (Fig. 2, upper traces, third spectrum): with these unstable mechanical stance conditions, the oscillations of the head show a maximum at 3 Hz, where normal vision has a minimum effect on the control of upright posture.

2. Effect of the firmness of the support. Figure 4 shows the differential spectra corresponding to the differences between soft and hard support for each visual condition, each width of the base and the three levels of measurement. All these mean differences are statistically highly significant (p value under each spectrum). In addition, the consistency of the shape of these spectra (which is particularly striking at the ankles), although all the measurements were conducted quite separately, is a fairly good indication that the main details are significant.

For each type of stance and illumination condition, the effect of the firmness of the support revealed by these spectra decreases from the ankles to the head (see also Fig. 1B), suggesting the presence of active mechanisms controlling the increased sway from the feet level upwards.

The effect is clearly bimodal at ankle level, especially in the NB situation, and might represent the effect of a non-visual mechanism (even in Darkness) limiting within a narrow frequency band (round

7 Hz) the increased ankle sway due to the soft support.

Another result which is particularly interesting is the shape of the effect at head level for the NB stance. The visual contribution can be detected by comparing the effect produced in darkness (upper line) to that obtained under normal illumination (lower line). The residual effect at head level under normal illumination shows a maximum at 3 HZ, where destabilization appears to be irreducible by vision. Visually controlled reductions in destabilization occur at low frequencies (below 2 Hz) and at high frequencies (above 4 Hz), but hardly at all from darkness to normal illumination at 3 Hz.

3. Effect of stance conditions. For each visual condition, each category of support firmness and each anatomical level, the differential spectra corresponding to the differences between narrow and wide base are shown in Fig. 5. As indicated under each differential spectrum, most of these mean differences are highly significant.

For each category of support firmness and each visual condition, the effect of reducing the support width (what we have called "effect of stance") appears to be maximum at ankle level, where this type of mechanical destabilization takes place, suggesting that some active mechanism is responsible for reducing destabilization at head level. Apart from the ankle level, where the body reaction is characteristic of this type of mechanical destabilization, there is a striking likeness between the effect of the firmness of the support and the effect of the stance conditions, particularly at head level.

At head level, particularly in the case of the soft support (the more unstable one), the effect in normal illumination again reaches a maximum at about 3 Hz. In comparison with the effect in darkness, one can observe one visually controlled reduction at frequencies below 2 Hz and another one at frequencies above 4 Hz, visual cues again having a minimal effect on stability between 2 and 4 Hz.

c) Differential effects

Mean differential effects are shown in Fig. 6 either between ankles and hips (column A-Hi), between ankles and head (column A-He), or between hips and head (column Hi-He) for three kinds of destabilization previously described: i) destabilization by dynamic vision deprivation (stroboscopic illumination compared to normal vision, row A); ii) destabilization by sharpening the foot support (row B) irrespective of illumination condition and firmness (the transmission spectra are very similar for soft and hard supports); iii) and destabilization by soft padding of the support (rows C), either with a narrow base or with a wide base, irrespective of the illumination condition.

The mean transmission spectra corresponding to destabilization by elimination of static vision (darkness vs stroboscopic illumination) are very close to zero and not shown in Fig. 6, indicating that no nonlinearity measurable by our method is involved in the transmission of this effect. The same applies roughly to destabilization by elimination of dynamic vision between ankles and hips (Fig. 6A). On the contrary, with the same destabilization source, the transmission spectrum between hips and head may indicate that some active mechanism contributes towards reducing the head oscillations specifically.

The typical mean transmission spectra corresponding to the destabilization accompanying the change of stance from the wide base to the narrow base are not equal to zero, either between ankles and hips or between hips and head (Fig. 6B). Between ankles and hips, the biomechanical constraints obviously differ between the classical Romberg and the sharpened Romberg stances, which may explain why the sharpened Romberg transfer function does damp down the oscillations between ankles and hips better than the classical one. Surprisingly, this is also the case between hips and head, which may suggest some supplementary active mechanism in the case of the sharpened Romberg stance, damping down the oscillations at the head level. However, the linearity of the transmission seems to be preserved at low frequencies (below 2 Hz).

The effects of support firmness differ considerably between ankles and hips in the case of the NB and WB stances (Fig. 6C), which confirms the hypothesis according to which NB and WB are different biomechanical systems. Transmission of the support effect between these two levels appears to be more linear with the WB stance than with the NB one, which may be due to the sharp increase in the leg oscillations recorded on the sharpened Romberg stance. As previously suggested for the stance effect, the sharpened Romberg stance does actively damp down the oscillations up to hip level, especially at low frequencies, by means of these lateral leg movements. On the contrary, the differential effects of the support observed between hips and head are quite similar under both stance conditions, the linearity of the transmission being especially good at very low frequencies (between 0 and 2 Hz).

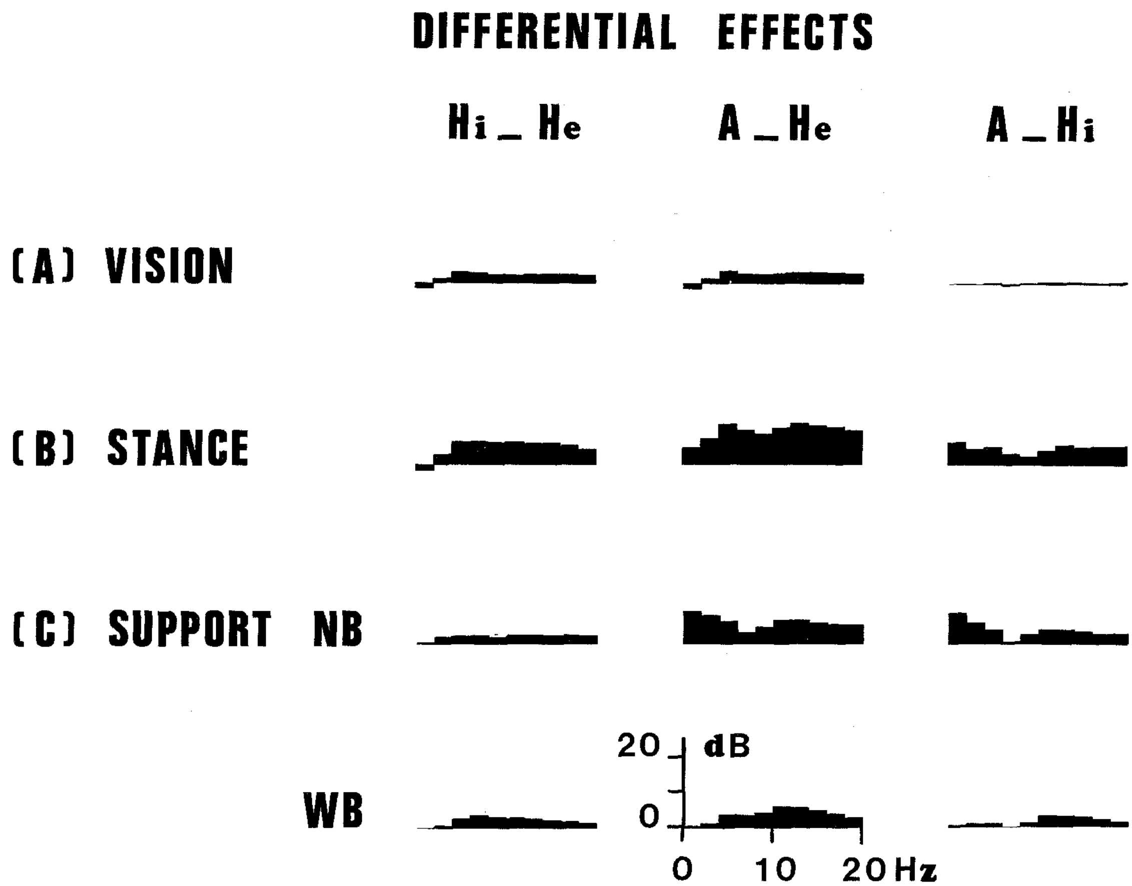


Fig. 6. Mean differential effects or transmission spectra. Column *Hi-He:* difference between the mean differential spectra obtained at hip level and at head level; *A-He:* difference between ankle and head levels; *A-Hi:* difference between ankle and hip levels. Transmission spectra are given for destabilization due to dynamic vision deprivation (row *A*); to narrow support irrespective of its firmness (row *B*); and to soft padding (row C.NB in sharpened Romberg situation; row C.WB in classical Romberg)

d) Correlations

Mean z transforms of the absolute correlation r are shown in Fig. 7 either between head and hips, or between head and ankles, or between hips and ankles, for the various visual conditions (darkness, stroboscopic and normal illumination) and the four mechanical conditions (WB or NB; soft and hard support).

The first major divergence arises between the two stance conditions, especially for the hips – ankles correlations, the various levels being much more closely correlated in the classical Romberg than with the sharpened Romberg stance. This presumably confirms the greater mobility of the body under the sharpened Romberg condition, especially of ankles and hips together, already suggested by transmission spectra. There remain, however, two particular situations in which this rule does not apply: from head to ankles, the correlation appears to be abnormally high in darkness and stroboscopic illumination and with a soft support in the sharpened Romberg situation. The reason is presumably that equilibrium is especially hard to maintain in these mechanical conditions; only continuous illumination (N) can damp the high frequency oscillations from the ankles up to the head. The second peak in the effect of vision at head level, which centered on about 7 Hz (Fig. 3, column S-N, row NB-SS), and which is very similar to the peak in the corresponding spectrum at ankle level, may explain the abnormally high correlations between these two levels in D or S.

Under each stance condition, there is a second divergence between the two degrees of support firmness, the various levels being much more closely correlated with the hard support than with the soft one. In other words, the subjects adapt to a softer support by loosening the link between body segments, especially between ankles and hips, in order to more effectively damp the oscillations up to head level, as already indicated by the transmission spectra analysis.

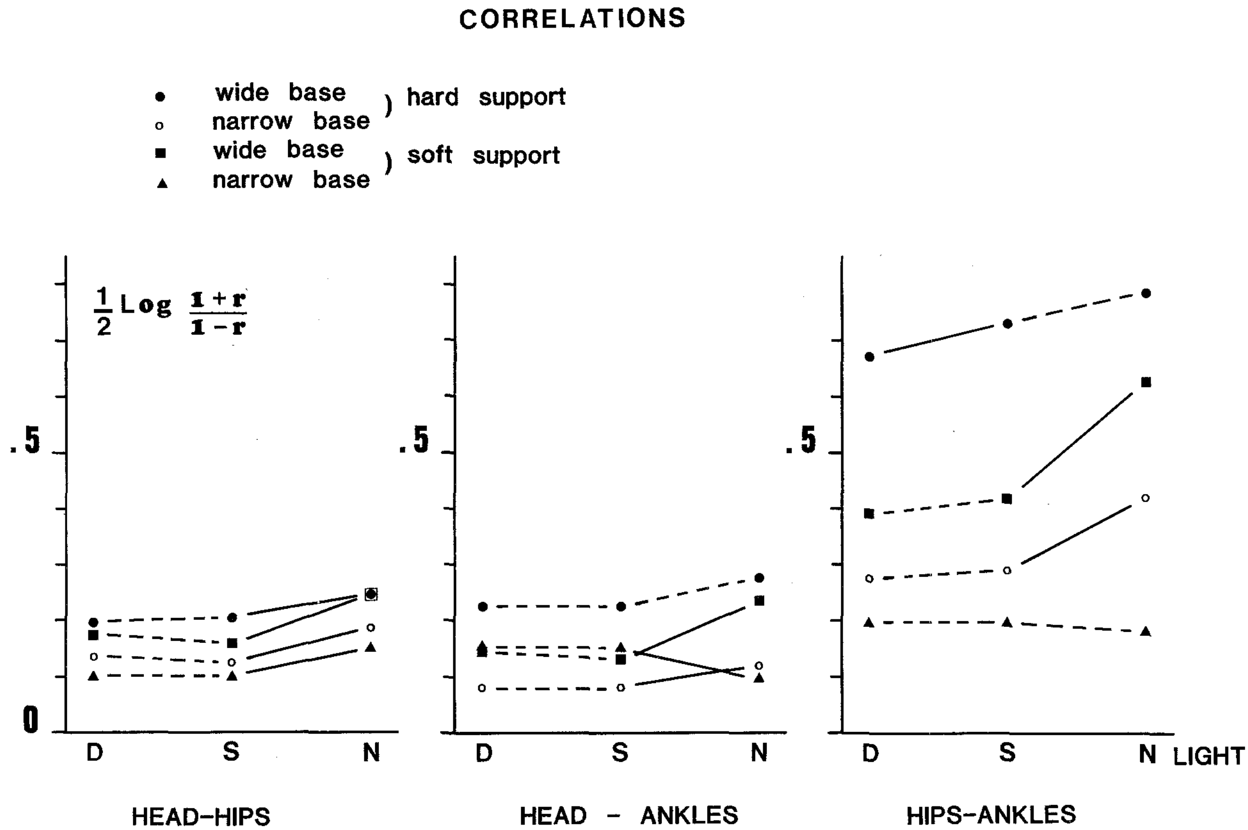


Fig. 7. Mean z transform or the absolute correlation r for the 12 subjects and the 8 trials. Correlations are calculated either between head and hips, or between head and ankles, or between hips and ankles, for the four mechanical situations: i) wide base (classical Romberg) or narrow body-base (sharpened Romberg); ii) and soft support or hard support. For each pair of levels the correlations observed in darkness (D), in stroboscopic illumination (S), and in normal illumination (N) are also given. Broken line between two nearby conditions means non significant difference, whereas a significant difference is indicated by a continuous line

It is interesting to note that, for the mean power of sway, (see Fig. 1B), the main divergence occurs between soft and hard support, irrespective of the type of stance, whereas the secondary divergence occurs between narrow base and wide base. We conclude that the stiffness of the body depends first upon the width of body base and secondly upon the firmness of the support, while the mean frequency power spectra of the lateral oscillations depend first upon the firmness of the support and secondly upon the width of the body base.

There was practically no significant difference between correlations measured in darkness and under stroboscopic illumination (except between ankles and hips under the condition WB-HS), which suggests that static visual cues have no effect on the biomechanical characteristics of the body. On the contrary, in most cases, dynamic visual cues enhanced the correlations observed within each pair of levels, and therefore probably the stiffness of the body.

Discussion

It has already been reported (Amblard and Crémieux 1976) that the visual control of lateral body sway mainly depends upon dynamic visual cues, especially those involving peripheral vision (Amblard and Carblanc 1980; Paulus et al. 1984). The present report confirms the previous results, and shows that a minor but significant contribution is made by static visual cues (Experiment 1), which we failed to establish in the previous report (Amblard and Crémieux 1976) because of the uncontrolled visual pattern. It is also demonstrated here (Experiment 2) that the frequency ranges of the lateral body oscillations corresponding to these two visual contributions are clearly dissociated. Figure 8 summarizes the main results on which we have based a tentative functional interpretation of the visual contribution to upright posture control in man (Paillard and Amblard 1985). This interpretation postulates the co-existence of two separate visual mechanisms reducing the lateral body oscillations (Amblard et al. 1982), the pathways of which would still have to be defined:

– The first, acting below 2 Hz, presumably involves the slow reorientations occurring in the upper part of the body; it is not suppressed by strobe illumination (although less effective in strobe than in full illumination), when static visual cues are available in the visual surroundings;

– The second mechanism, which acts above 4 Hz and centers around 7 Hz, involves the rapid stabilization of the whole body; it relies exclusively upon continuous visual cues arising from body sway – what we would like to call dynamic visual cues, those occurring in the optical images of the surroundings as they move across the retina. We furthermore suggest that these active visuomotor corrections occur mainly at ankle level in a rigidified body, whereas in the absence of continuous visual cues, the body structure loosens.

Between these two separate frequency ranges, there exists at about 3 Hz something like a "blind frequency" or "visually neutral sway frequency", which may reflect the incompatibility between a visual reorientation and a visual immobilization. These results were obtained by comparing various conditions of illumination. Additional comparisons, between soft and hard support on the one hand, and between sharpened Romberg and simple Romberg stance on the other hand, have provided new evidence in favour of this blind frequency range hypothesis. With these two independent causes of destabilization (soft padding or narrow support; see Fig. 8) the effects at head level in normal light are indeed similar, which may be explained by the two visual mechanisms already seen to operate in the case of visual destabilization: vision seems to be capable of reducing the residual effects of such mechanical disturbances both in the low frequency range (below 2 Hz) and in a higher frequency range (above 4 Hz), but seems unable to reduce destabilization of the head to any great extent at about 3 Hz.

This type of model seems to plausibly resolve the apparent contradiction between studies "supporting the general statement of a role of vision in the low frequency range (0–0.2 Hz) which has been suggested both by linear and circular vection experiments" (Berthoz et al. 1979) and those mentioning for instance the contribution of vision to rapid motor reactions during postural perturbations (Nashner and Berthoz 1978) and suggesting that vision also plays an important role in a higher frequency range. Our model assumes that dynamic visual cues contribute to *immobilizing* the body, whereas static visual cues control the re-orientation or *displacement*. This model also seems to fit in fairly well with the functional hypothesis put forward by Nashner and Cordo (1981), classifying the motor aspects of postural control in terms of orientation and stabilization. Our assumption that two separate visual mechanisms exist has led elsewhere to a very convincing interpretation of recovery experiments in the bilabyrinthectomized cat (Marchand and Amblard 1984).

The visual contribution to postural readjustments in a rather low frequency range, which has been found to be the classical frequency domain of a visual moving scene stimulation both in animal (Talbott 1980) and in human experiments (Dichgans et al. 1974), has mainly been described in terms of the subject's pitch. This is in agreement with our hypothesis that a low frequency mechanism is involved in body orientation or positioning. Since such a low frequency mechanism appears to some extent to be strobe resistant, there is no contradiction between our results and those reported by Kapteyn et al. (1979). It is actually not surprising that as much optic sway is elicited under strobe illumination (below 6 flashes/s) as under steady illumination with a tilting room oscillating at a very low frequency (0.05 Hz). These mechanisms are not necessarily related to those responsible for vection (Brandt et al. 1973; Paulus et al. 1984) although vection phenomena have been reported under strobe illumination (Wolfe and Held 1980).

The high frequency mechanism postulated in the present study as feeding on dynamic visual cues and acting at ankle level, is in agreement with Nashner and Berthoz' results (1978), establishing "that visual inputs influence involuntary postural adjustments within 100 ms". We would also suggest in accordance with Nashner and Cordo's teleological hypothesis (1981), that this postural system "seeks to stabilize the body beginning at base of support". We suggest that it is in fact a visual velocity-reducing servomechanism, the efficiency of which would be 1) greatly reduced either by stabilized vision (Vidal et al. 1978), or with increasing eye-object distance up to 5 m (Bles et al. 1980) 2) or totally suppressed under stroboscopic illumination. However, with a foamrubber platform reducing the accuracy of the joint receptors and with the elimination of visual motion cues (more than 5 m between scene and subject), Bles et al. (1980) have assumed that postural destabilization is mainly due to "the increased sensorial weight of the misleading visual signal which is contradicted only by the 'correct' vestibular cues". For these authors, the degree of imbalance might be simply a measure of the magnitude of the mismatch. Our results seem to be in contradiction with such hypothesis: 1) on the one hand, in a situation (strobe illumination) which is similar to Bles', we have

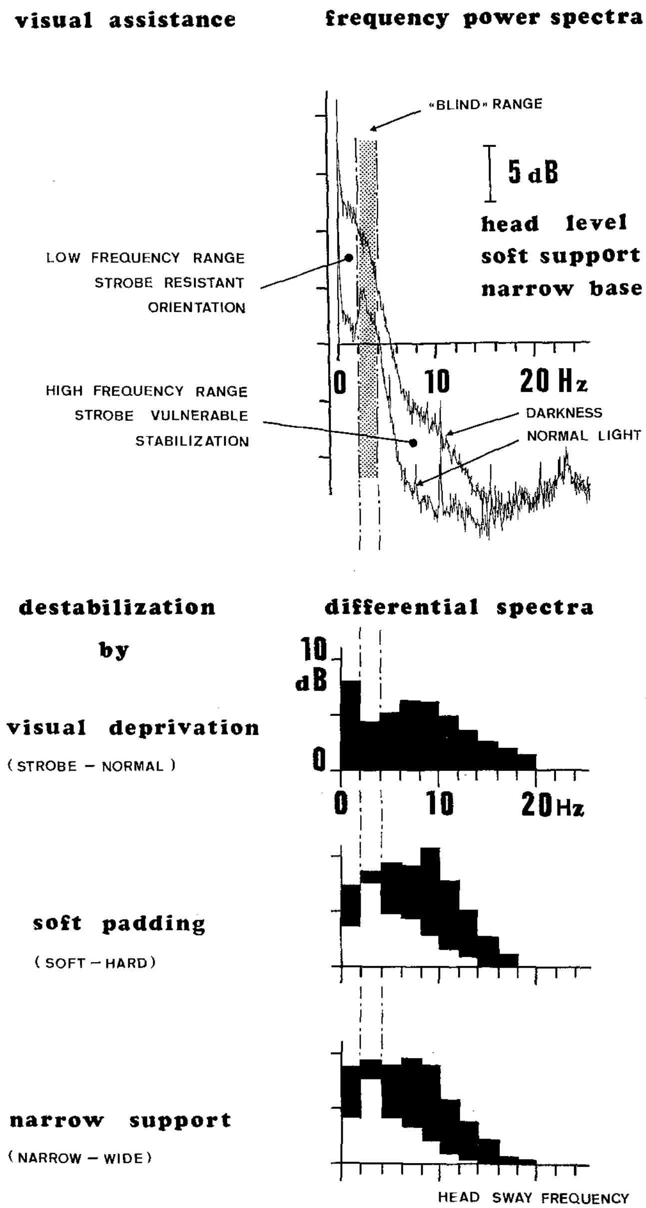


Fig. 8. *Upper part:* Outline of the interpretation proposed here to describe the visual contribution to postural control in man, through either static visual cues (up to 2 Hz) or dynamic visual cues (above 4 Hz). The frequency range (up to about 16 Hz) is that of the lateral oscillations of the head. *Lower part:* Comparison of differential spectra calculated for the head level measurement, showing the destabilization induced either by means of visual deprivation (see Fig. 3 under the narrow body-base and soft support condition; difference between stroboscopic and normal illumination), or softening of the support (see Fig. 4 under the narrow body-base condition) in darkness (black outline) and normal (white) illumination (difference between soft and hard support), or sharpening of the body-base of the upright posture (see Fig. 5 under soft support condition) in darkness and normal illumination (difference between sharpened and classical Romberg). These three independent differential spectra show at about 3 Hz what we call the blind frequency domain of the lateral oscillations of the head as the minimum of the black area representing the effect of vision

demonstrated the existence of a positive visual contribution to posture by means of static visual cues (performances were generally better under strobe illumination than in darkness); 2) on the other hand, the comparison between foamrubber platform and hard one suggests the presence of a non-visual (for instance vestibular or tactile) mechanism reducing the ankle oscillations to the same extent with and without vision and without any particular distortion under strobe illumination. We would then suggest that the degree of imbalance produced by dynamic visual cue elimination does measure the lack of adequate visual cues rather than the magnitude of a mismatch.

We can exclude the possibility that the high frequency peak (around 7 Hz) of the effect of visual deprivation observed at head level (Fig. 8, lower part) might be related to physiological tremor, which is classicaly described in the same frequency domain, since there is no peak around 7 Hz in the original spectrum of the head level under normal illumination (Fig. 8, upper part). As Dymott and Merton (1968) point out, physiological tremor should indeed increase or remain constant when visual cues are present rather than decrease.

The intermediate frequency band which seems to separate the two different visual mechanisms around 3 Hz has been shown here to be a frequency domain where visual assistance to lateral body sway control is minimal. The maximum destabilization centered on 3 Hz which was elicited either by diminishing the firmness of the support or by narrowing its width leads one to expect that a brief visual perturbation during normal vision could also produce a maximum of destabilization around 3 Hz. Such a peak in the lateral oscillations of a subject standing on one foot has indeed been reported (White et al. 1980) with a visual pattern changing briefly from stationary to a saccadelike motion at irregular intervals. Surprisingly, it has been reported elsewhere (Diener et al. 1984a) that patients with cerebellar diseases (anterior lobe atrophy) show a predominant antero-posterior sway, with a spontaneous body tremor around 3 Hz which disappears with vision. This discrepancy with our results may be due either to some difference between mechanisms controlling antero-posterior and lateral oscillations, or to the cerebellar disease itself. The latter authors suggested in fact that the visual stabilization of posture depends upon the functional integrity of some vestibulo-cerebellum projections and possibly other connections to the cerebellum hemispheres.

Obviously, the organization of the elementary units of postural action as postulated by Nashner et al. (1979) should be different for the sharpened and the classic Romberg stance. These two types of stance clearly correspond to two different biomechanical-systems, implying two different sensorimotor strategies. In the classical Romberg, the subject corrects his lateral sway by applying a different push with the right and the left limb. The same motor strategy can be maintained for the antero-posterior sway in the sharpened Romberg situation. In that situation, however, the lateral sway, which is considered here, can be controlled only by changing the pattern of pressure under the sole of each foot (similar strategy for anterio-posterior sway in the classical Romberg). This amounts to a change of postural strategy such as Nashner et al. (1979), Nashner (1983) reported. Furthermore, although we did not measure the EMG activities in the present work, we suspect the organization of synergies during stance postural adjustments to be not only stance-specific but also dependent upon the availability of visual inputs. Within a given stance condition indeed, most of the correlations between sways at two anatomical levels significantly change from strobe to normal lighting condition (see Fig. 7), probably indicating a central switching (visual specific) between different strategies of equilibrium control. Dynamic visual cues seem to be the only visual cues to participate to such a choice of strategy, since there is no significant change in the observed correlations between anatomical levels from darkness to stroboscopic illumination conditions.

In addition within a given stance condition, the clear dissociation between the correlation measurements corresponding to hard and soft support (Fig. 7) may correspond either to a change of the motor strategy of equilibrium control, or to the expected change in pressure distribution from a support to another. Unfortunately, the use of a soft support does not only remove some exteroceptive cues – which are ordinarly "provided by ankle joint rotation and by changes in the distribution of pressures within the foot and lower leg" (Nashner 1970) – but also it considerably increases the difficulty of the task. We may notice in the present work (Fig. 4) that the imbalance produced by foam rubber support not only peaks in the low frequency domain but also extends steadily into the higher frequency range. Using a moving supporting platform and a removal of proprioceptive input from skin, pressure and joint receptors of the foot by ischemia at the ankle, Diener et al. (1984b) reported that these proprioceptive inputs act mainly for low frequency body sway movements (around 0.3 Hz). Nothing was known about the possible contribution of these proprioceptive cues at higher frequencies. However, we have come to suspect the existence of a non-visual mechanism acting at ankle level (Fig. 4) and reducing ankle oscillations in the same frequency range as dynamic visual cues. This hypothetical and unidentified mechanism would specifically minimize around 7 Hz the increase in lateral body sway produced by foamrubber support in the frequency domain in which there is a peak on the original spectra of the ankle level corresponding to the hard support condition (not shown here). It may be attributable to some vestibular contribution, the high-frequency behaviour of which has still largely escaped investigation, but also to reflexes of muscular or tactile origin.

References

Amblard B, Carblanc A (1980) Role of foveal and peripheral vision information in the maintenance of postural equilibrium in man. Percept Motor Skills 51: 903–912

Amblard B, Carblanc A, Crémieux J, Marchand A (1982) Two modes of visual control of balance in man according to frequency range of body sway. Neurosci Lett Suppl 10: S42

Amblard B, Crémieux J (1976) Rôle de l'information visuelle du mouvement dans le maintien de l'équilibre postural chez l'homme. Agressologie 17: 25–36

Amblard B, Crémieux J (1979) Visually guided reaching in the cat reared in fixed or random frequency stroboscopic light. Neurosci Lett 15: 9–14

Berthoz A, Lacour M, Soechting JF, Vidal PP (1979) The role of vision in the control of posture during linear motion. In: Granit R, Pompeiano O (eds) Reflex control of posture and movement. Prog Brain Res 50: 197–209

Blakemore C, Campbell FW (1969) On the existence in the human visual system of neurons selectively sensitive to the orientation and size of retinal images. J Physiol (Lond) 203: 237–260

Blakemore C, Nachmias J (1971) The orientation specificity of two visual aftereffects. J Physiol (Lond) 213: 157–174

Bles W, Kapteyn TS, Brandt T, Arnold F (1980) The mechanism of physiological height vertigo. II Posturography. Acta Otolaryngol 89: 534–540

Brandt T, Daroff RB (1980) The multisensory physiological and pathological vertigo syndromes. Ann Neurol 7: 195–203

Brandt T, Dichgans J, Koenig E (1973) Differential effects of central versus peripheral vision on egocentric and exocentric motion perception. Exp Brain Res 16: 476–491

Campbell FW, Kulikowski JJ (1966) Orientational selectivity of the human visual system. J Physiol (Lond) 187: 437–445

Craik RL, Cozzens BA, Freedman W (1982) The role of sensory conflict on stair descent performance in humans. Exp Brain Res 45: 399–409

Crémieux J, Amblard B, Carblanc A (1981) Visual information on self-motion and control of upright posture in man under stroboscopic illumination. Behav Brain Res 2/2: 252–253

Delorme A (1971) La perception de la vitesse en éclairage intermittent. Rev Can Psychol 25: 213–221

Dichgans J, Diener HC, Brandt T (1974) Optokinetic-graviceptive interaction in different head positions. Acta Otolaryngol 78: 391–398

Dichgans J, Brandt T (1978) Visual-vestibular interactions: effects on self-motion perception and postural control. In: Teuber HL, Held R, Leibowitz H (eds) Handbook of sensory physiology, Vol 8: Perception. Springer, Berlin Heidelberg New York, pp 753–804

Diener HC, Dichgans J, Bacher M, Gompf B (1984a) Quantification of postural sway in normals and patients with cerebellar diseases. Electroenceph Clin Neurophysiol 57: 134–142
Diener HC, Dichgans J, Guschlbauer B, Mau H (1984b) The significance of proprioception on postural stabilization as assessed by ischemia. Brain Res 296: 103–109
Dymott ER, Merton PA (1968) Visually and non-visually determined peaks in the human tremor spectrum. J Physiol (Lond) 196: 62P–64P
Held R, Dichgans J, Bauer J (1975) Characteristics of moving visual scenes influencing spatial orientation. Vision Res 15: 357–365
Kapteyn TS (1972) Data processing of posturographic curves. Agressologie 13: 29–34
Kapteyn TS, Bles W (1977) Circular vection and human posture. Relation between the reactions to various stimuli. Agressologie 18: 335–339
Kapteyn TS, Bles W, Brandt T, Wist ER (1979) Visual stabilization of posture: effect of light intensity and stroboscopic surround illumination. Agressologie 20C: 191–192
Lee DN, Aronson E (1974) Visual proprioceptive control of standing in human infants. Percept Psychophys 15: 529–532
Lestienne F, Soechting J, Berthoz A (1977) Postural readjustments induced by linear motion of visual scenes. Exp Brain Res 28: 363–384
Marchand AR, Amblard B (1984) Locomotion in adult cats with early vestibular deprivation: visual cue substitution. Exp Brain Res 54: 395–405
Nashner LM (1970) Sensory feedback in human posture control. Thesis MIT Center for space research. Ed. Cambridge, 198p
Nashner LM (1983) Analysis of movement control in man using the movable platform. In: Desmedt JE (ed) Motor control mechanisms in health and disease. Raven Press, New York, pp 607–619
Nashner LM, Berthoz A (1978) Visual contribution to rapid motor responses during postural control. Brain Res 150: 403–407
Nashner LM, Cordo PJ (1981) Relation of automatic postural responses and reaction-time voluntary movements of human leg muscles. Exp Brain Res 43: 395–405
Nashner LM, Woollacott M, Tuma G (1979) Organization of rapid responses to postural and locomotor-like perturbations of standing man. Exp Brain Res 36: 463–476
Paillard J, Amblard B (1985) Static versus kinetic visual cues for the processing of spatial relationships. In: Ingle DJ, Jeannerod M, Lee DN (eds) Brain mechanisms of spatial vision. Martinus Nijhof, La Haye, pp 299–330
Paulus WM, Straube A, Brandt Th (1984) Visual stabilization of posture. Physiological stimulus characteristics and clinical aspects. Brain 107: 1143–1163
Rouanet H, Lépine D (1970) Comparisons between treatments in a repeated-measurement design; ANOVA and multivariac methods. Br J Math Stat Psychol 23: 147—163
Sachs MB, Nachmias J, Robson JG (1971) Spatial-frequency channels in human vision. J Opt Soc Am 61: 1176–1186
Sharpe CR, Tolhurst DJ (1973) Orientation and spatial frequency channels in peripheral vision. Vision Res 13: 2103–2112
Soechting JF, Berthoz A (1979) Dynamic role of vision in the control of posture in man. Exp Brain Res 36: 551–561
Talbott RE (1980) Postural reactions of dogs to sinusoidal motion in the peripheral visual field. Am J Physiol 239: R71–R79
Vidal PP, Gouny M, Berthoz A (1978) Rôle de la vision dans le déclenchement de réactions posturales rapides. Arch Ital Biol 116: 281–291
White KD, Post RB, Leibowitz HW (1980) Saccadic eye movements and body sway. Science 208: 621–623
Wolfe JM, Held R (1980) Cyclopean stimulation can influence sensations of self-motion in normal and stereoblind subjects. Percept Psychophys 28: 139–142

Received July 17, 1984 / Accepted July 25, 1985