

J.F. Soechting¹ and A. Berthoz

D6partment de Physiologie Neurosensorielle, Laboratoire de Physiologie du Travail CNRS, F-75005 Paris, France

Summary. The influence of moving visual surround on the maintenance of upright posture has been studied in man during combined motion of a platform (cart) on which subjects were standing. The normal visual surround was either moving together with the cart, or with a velocity equal to cart velocity either in the same or in the opposite direction of cart motion (cart acceleration was either 0.2 m/s² or 0.05 m/s²). The changes in body pitch observed under these three conditions of visual surround motion were in the same direction as those observed when visual surround motion was given in isolation. However, their amplitude was greater, particularly when visual surround motion was in conflict with body motion.

Key words: Vision – Proprioception – Posture – Motor control

Several investigators have recently dealt with visual influences on the perception of self-motion and on the control of posture in man. It was shown that the presentation of a moving visual scene to a stationary observer can produce an illusion of translation (linear vection; Berthoz et al., 1975; Chu, 1976) or of rotation (circular-vection; cf. review in Dichgans and Brandt, 1978). Furthermore, such moving visual environments result in postural readjustments of the observer. For example, a visual surround moving in the antero-posterior direction produces an inclination (pitch) of an erect subject in the direction of surround motion (Lestienne et al., 1977; Lishman and Lee, 1973) (the pitch amplitude can be up to 3° which is approximately 50% of maximum tolerable body pitch compatible with postural stability). Similar effects have also been elicited for subjects viewing a rotating disc (Dichgans et al., 1972; Dichgans et al., 1975). It is now well known that brain stem structures and particularly the vestibular nuclei are involved in the mediation of these effects in primates (Waespe and Henn, 1977).

One question which arises from these observations concerns the capability of visual information about body motion to contribute to, or interfere with, the

¹ Present address: Laboratory of Neurophysiology, University of Minnesota Medical School, Minneapolis, 55455, USA

Offprint requests to: Dr. A. Berthoz (address see above)

Fig. 1. Experimental set-up for the study of postural pertubations during combined visual and body motion. The subject stands erect on a moving platform. The angle Θ of head and body pitch taken as an approximation is measured by a potentiometer fixed to the head by means of a rod and crank attachment. An image moving at velocity Vi is projected on the screen S as described in Lestienne et al. (1977). Lightweight cardboard blinders obliterate the lateral and inferior aspects of the visual field and permit the subject only a view of the screen. This ensemble is placed on a cart which can move at velocity Vc. Schematic description of Vi and Vc waveform generation: (1) A triangular analog signal (Vc) is sent by the computer to the torque motors driving the cart. (2) Due to the inertia of the cart, the actual velocity waveform Vc departs from a perfect triangle. The waveform Vc is consequently stored by the computer before the experiment and used to control the velocity Vi of the image, thus allowing to project visual surround motion precisely equal ($Vi = Vc$) or opposite $(Vi = -Vc)$ to cart motion

dynamic postural readjustments which are necessary in order to keep balance during self-generated motion or suddenly imposed perturbation. Also, how do postural adjustments generated by the activity of vestibular receptors or by proprioceptive inputs from the limbs summate with visually generated postural changes? Is there a more complex logic such as an either/or gating mechanism and what happens when visual and other sensory cues are conflicting?

These questions were addressed in the present work² by measuring the body sway of erect human subjects during linear accelerations in the anteroposterior direction under various conditions of visual input. The dynamic characteristics of the visual and mechanical stimuli used were such as to involve mainly movements in a rather low frequency range. Effects of vision on rapid postural perturbations have been reported elsewhere (Nashner and Berthoz, 1978; Vidal et al., 1978).

Methods

Experimental Set-up

Fifteen healthy male and female subjects participated in this study (age between 20 and 35). The experimental set-up used was a modification of that described in two preceding publications

² A partial presentation of this work was given at the International Symposium On Reflex activity in the Control of Movement and Posture; September 11-14, 1978, Pisa, Italy

(Berthoz et al., 1975; Lestienne et al., 1977). The subjects stood erect on a platform attached to a mobile cart (Fig. 1A). The cart was driven by servo-controlled torque motors and it was enclosed on all sides. The subjects wore lightweight cardboard blinders which blocked the lateral and inferior aspects of their visual field and permitted only a resticted view of the cart's ceiling (1 m square area; height of ceiling above the head: 10 cm). The visual scene, consisting of a black and white checkerboard pattern was projected onto the ceiling using a film projector and mirror. The number of squares per unit of surface was $64/m^2$. The velocity of the checkerboard pattern was generated by another servo-controlled torque motor placed on the film projector. The torque motors driving the cart and the film projector were controlled by a Hewlett Packard 2100/S Fourier Analyzer Computer System, thus permitting accurate synchronized control of cart and film velocity.

The subjects pitch (angle Θ) in the forward or backward direction was first calculated by measuring the change of foot pressure by means of strain gauges placed under the platform on which the subjects stood. This allows a measure of the vertical projection of the center of gravity when subjects' movements are small. However, when a linear acceleration is applied, it may be contaminated by the component of linear acceleration in the horizontal direction. In the case when a horizontal component of acceleration is present, its value is added vectorially to the gravity vector, and the projection of the resultant forces on the platform may be displaced in the direction of the horizontal acceleration. For this reason, this measurement was replaced in most experiments by simultaneously measuring the linear displacement of the subject's head in the forward-backward direction. For this purpose, an angular potentiometer and a rod and crank mechanism attached to the subject's head be means of a helmet was used. This method gave a measure of angular fore and aft body pitch angle Θ . Because of the low frequency and low amplitude of the acceleration involved, and within the accuracy (0.05°) and time of resolution (100 ms) of our measurements, these two calculations of pitch were found to parallel each other within 5% .

Stimulation Parameters

Cart velocity was measured by means of a tachometer. Acquisition and control of data was also performed by the on-line digital computer which provided the combined visual and cart motion. Two types of motion patterns were generated: (a) triangular waveform of cart velocity with peak velocity 1.1 m/s, maximum cart acceleration 0.2 m/s², and total movement duration 10 s (5 s acceleration and 5 s deceleration); (b) triangular waveform of velocity with peak velocity 0.5 m/s, peak acceleration 0.05 m/s² and total duration 20 s (10 s acceleration and 10 s deceleration).

The low pass filter properties of the cart and its servo-control system smoothed the command signal as indicated in Fig. 1B. To obtain an adequate profile of image velocity identical to the cart motion, the tachometer output from the cart was recorded by the computer and subsequently used to drive the film. The servo-motors driving the film did not introduce any further significant smoothing. Different combinations of image and cart motion were presented to each subject with all conditions appearing three times in a randomized order of presentation.

The precise frequency content of cart acceleration and of film velocity is given in Fig. 2 in which we have plotted the power spectrum (arbitrary units) of these two parameters for the three conditions reported in this paper. This measure shows that the main energy content of the stimulus is for frequencies below 0.2 Hz, which is adequate to test the stabilizing or destabilizing properties of vision.

Results

An initial series of experiments were aimed at providing a rather large cart motion in order to produce a transient perturbation of posture. Cart acceleration was chosen at 0.2 m/s^2 , four times the known thresholds for otolithic detection of linear acceleration (Guedry, 1974), applied for 5 s in each direction. The time to acceleration detection in seated humans from Young and Meiry (1968) at this acceleration level is about 1.4 s.

Fig. 2. Power spectrum of cart acceleration and film velocity. Top: Power spectrum of cart acceleration measured in the three experimental conditions described in the text: (I) high acceleration forward; (II) low acceleration forward; (III) low acceleration backward. The gain is expressed in arbitrary units. Bottom: power spectrum of film velocity in the same three experimental conditions as in top diagram

Influence of Pure Image Motion

The effect of transient movements of visual images on standing subjects without cart motion ($Vc = 0$) was first measured in order to provide a control. The results are given in Fig. 3 where records of body pitch are shown when the images were moving either forward (Fig. 3A) or backward (Fig. 3B). Each of the records is the average of three trials for eight subjects. These records confirm what was already observed in a previous work, namely that a visual motion is sufficient to induce postural readjustments in the direction of the driving visual image. The peak amplitude of the forward pitch induced is about 0.5° which is about 15% of the maximum effect induced by steps of velocity and large field stimulation in our previous experiments (Lestienne et al., 1977).

Effect of Cart Motion Without Visual Information

A second control experiment was made in order to determine what was the effect of partial and total removal of visual information. Body pitch was first measured when image motion with respect to the cart was zero $(Vi = 0)$ with eyes open. In this case the subjects only have visual cues concerning their relative body pitch with respect to the cart and not with respect to the ground. This is equivalent to the situation of a person travelling inside a closed nondark

Fig. 3 A-C. Body pitch during pure visual motion and in two control conditions of cart motion. The traces are the averaged postural responses of eight subjects in pitch (4) obtained under various experimental conditions. In **A** and **B** the cart was stationary ($Vc = 0$). Image velocity (Vi) of a checkerboard pattern projected on the screen above the subject's head was either in a forward (FWD) in **A** or backward (BWD) direction in **B**. The peak velocity was 1.1 m/s. In **C** cart velocity Vc was in the forward direction. The subjects either had their eyes open (EO) viewing a visual scene stationary relative to the cart $(Vi = 0)$, or their eyes closed (EC)

vehicle. The corresponding body pitch is shown in Fig. 3C which gives an average value for eight subjects. The sequence of body movements includes an initial backward pitch (cart motion was forward) followed by an oscillation.

When no visual input is available (eyes closed: EC), although body oscillations tend to increase, no consistent change in the amplitude of postural sway can be measured compared to when the eyes are open. This result is indeed similar to the previous reports concerning the well documented but rather small effect of eye closure on postural control in healthy subjects. The following set of experimental results in which visual and cart motion were combined will show that the contribution of vision under these conditions is much greater than the above results may suggest.

Combined Effect of Image and Cart Motion

The records of Fig. 4 have been obtained in three different experimental conditions which are summarized in Table 1.

When the visual surround moves in the direction opposite to the cart and with equal amplitude ($Vi = -Vc$) the subjects are in a situation equivalent to normal real life conditions. In this case, they have visual information concerning

Fig. 4 A-C. Body pitch during combined cart (forward) and image motion for peak velocity 1.1 m/s. The traces in **A** and **B** show the average pitch θ of 8 subjects in three experimental conditions. In all three conditions the cart moved in the forward (FWD) direction with a peak velocity $Vc =$ 1.1 m/s and peak acceleration $\Gamma c = 0.2$ m/s². The light traces in **A** and **B** were obtained when the image was stationary relative to the cart (Vi = 0). The dark trace in **A** was obtained when image velocity was in a direction opposite to cart velocity ($Vi = -Vc$) and thus stationary relative to the ground, the dark trace in **B**, when image velocity was in the same direction as cart velocity (Vi = Vc). The difference of pitch θ in this last condition and when Vi = 0 is shown in C

Cart motion	Image motion with respect to cart	Condition
V _c forward	$V_i = V_c$	equivalent to normal body to ground visual motion information
	$V_i = 0$	only body to cart visual motion information
	$V_i = V_c$	abnormal conflict condition

Table 1. Experimental conditions for combined image and cart motions

relative motion of the cart with respect to ground (and relative motion of their body with respect to cart). Figure 4 shows average results for eight subjects. The records of Fig. 4A shows that suppressing the cart-to-ground visual information $(Vi = 0)$ but maintaining body-to-cart motion information has a clear but limited influence on postural sway.

Fig. 5 A and B. Body pitch during combined cart (forward) and image motion for peak velocity 0.5 m/s. The traces in **A** and **B** show the average pitch (Θ) of 8 subjects in three experimental conditions. In all conditions the cart was moving in the forward (FWD) direction with a peak velocity Vc = 0.5 m/s and peak acceleration Γ c = 0.05 m/s². The light traces in **A** and **B** were obtained when the image was stationary relative to the cart ($Vi = 0$). The dark trace in A was obtained when image velocity was in a direction opposite to cart velocity $(Vi = -Vc)$ and thus stationary with respect to the ground, the dark trace in **, when image velocity is in the same** direction as cart velocity (Vi = Vc). The difference of pitch Θ for the two conditions of **A** and for the two conditions of B are shown (bottom records)

When the image velocity is of the same direction as cart velocity ($Vi = Vc$) a very clearly abnormal conflict is created in which visual information is in contradiction with other cues concerning cart and body motion. The body angles recorded in this situation are shown in Fig. 4B. The condition $Vi = 0$ which was shown in Fig. 3A is again taken as a control. In this record, the forward body pitch is seen to be greater in the conflicting condition. The difference between the two records shown in Fig. 4C indicates that the forward motion of the visual surround has, indeed, increased the forward body pitch. The time course of the difference is similar, but the amplitude is about twice the forward pitch shown in Fig. 3A when the visual stimulus was given in isolation. This experiment shows therefore that when visual motion is in conflict with cues generated by a postural perturbation, it has a sizeable effect on the motor responses and subsequent body motion.

Combined Effects of Image and Cart Motion with Weaker Accelerations

Another experimental series whose results are shown in Figs. 5 and 6 (average of eight subjects) was undertaken with weaker acceleration stimuli in order to increase the effect of vision. The amplitude of linear acceleration given in the previous series exceeded largely the vestibular threshold of perception of linear

motion. In this second series, the cart's acceleration was purposely set to about 0.05 m/s^2 which is roughly the threshold of perception as measured by several authors (Guedry, 1974; Young and Meiry, 1968). The case when the visual scene was stationary with respect to the cart $(Vi = 0)$ was taken here again as a control. It was observed that in this condition the subject would still, as in the case of higher acceleration, reliably detect the direction of motion, very probably through somesthetic or cutaneous cues. However, when the visual scene was moving, the subjects were strongly disoriented despite the significant amplitude of postural sway produced by cart motion. This observation is coherent with previous observations made on the influence of linear vection on vestibular detection of motion (Berthoz et al., 1975).

The light traces in Figs. 5A and B show the average pitch for eight subjects in the Vi = 0 condition. In this case, pitch angle Θ follows closely the acceleration of the cart. When the visual surround is also in motion $(Vi = -Vc)$ with a direction opposite to cart velocity (Fig. 5A), there is a change of pitch in the direction of image velocity, namely backward, and the reverse is true (Fig. 5B) when Vi = Vc. The difference $\Theta_{\text{Vi}} = -v_c - \Theta_{\text{Vi}} = 0$ of the body pitch for the two conditions in A and the equivalent difference for the two conditions shown in B have been computed in order to show the amount of pitch due to changes in visual surround motion. The conclusion from this calculation is that in all cases the body is pitching in the direction of image velocity whether this has a stabilizing consequence or not. When $Vi = Vc$, i.e., image velocity is in the same direction as cart velocity, the difference is both greater than when $Vi = -Vc$ and than when image motion is given in isolation (Fig. 3A). This observation is consistent with the result described in the case of a larger acceleration (Fig. 4). We can conclude from this experiment that visual cues about body motion are indeed influencing the postural readjustments following a dynamic perturbation in a direction-specific manner during cart motion.

In order to show that this result is not dependent upon the direction of cart motion the same experiment was repeated on eight subjects for backward cart motion. The records of Fig. 6 demonstrate the same direction specific influence of visual surround motion and the same asymmetry in the effect with a greater difference when the cart and visual motion are in conflict.

Test of Statistical Significance of the Results

In order to test the statistical significance of the results, a simple measure was used to characterize the postural response, namely the maximum body pitch during cart acceleration. The effect of eye closure was first tested and compared with the control visual condition $Vi = 0$. The ratio of maximum amplitude of body pitch (eyes closed/eyes open) based on averages obtained from 3 trials for 7 subjects, and two values of acceleration and direction of cart motion was calculated. The numerical results are summarized below in Table 2. This confirms that closing the eyes during a low acceleration has a destabilizing effect as mean body pitch is, for low accelerations, about 40% and 20% greater when eyes are closed. However, note that the opposite result was obtained for high accelerations.

Fig. 6 A and B. Body pitch during combined cart (backward) and image motion for peak velocity 0.5 m/s. The traces in **A** and **B** show the average pitch (Θ) of 8 subjects in three experimental conditions. In all conditions, the cart was moving in the backward (BWD) direction with a peak velocity Vc = 0.5 m/s and peak acceleration Γ c = 0.05 m/s². The light traces in **A** and **B** were obtained when the image was stationary relative to the cart (Vi = O). The dark trace in **A** was obtained when image velocity was in a direction opposite to cart velocity $(Vi = -Vc)$ and thus stationary with respect to the ground, and the dark trace in \bf{B} when image velocity is in the same direction as cart velocity (Vi = Vc). The difference of pitch Θ for the conditions of **A** and for the two conditions of B are shown (bottom records)

The mean value of body pitch was also calculated for either congruent (no conflict) or conflicting visual surround motion for the same group of subjects. The motion of the visual surround does not produce a simple scaling of the body pitch (see Figs. 5 and 6). Instead, the observed difference seems to reflect the dynamics of purely visual effects on posture (Fig. 3). Therefore, the influence of visual surround motion was tested by comparing the ratio between maximum values of the differences shown in Figs. 5 and 6 and the control value when $Vi =$ 0. These differences can be expressed by the two formulas:

(1)
$$
\frac{(\Theta_{\text{Vi}} = -v_c - \Theta_{\text{Vi}} = 0)_{\text{max}}}{(\Theta_{\text{Vi}} = 0)_{\text{max}}} \text{ for the no conflict situation.}
$$

and $\frac{(\Theta_{\text{Vi}} = \text{v}e^{-\Theta_{\text{Vi}}})_{\text{nu}}}{(\Theta_{\text{Vi}} - \Omega)_{\text{max}}}$ for conflict situation.

The numerical values of these two expressions are shown on Table 3 for the same three protocols as those of Table 2. When there is no conflict, visual surround motion induces a change in body pitch which is, 70% , 56% , and 19% . respectively, of the total maximum body pitch during the control condition (no visual surround motion). When there is a conflict ($Vi = Vc$), the effect is more pronounced and the additional body pitch produced in this situation is equivalent to that elicited when $Vi = 0$.

Discussion

These results indicate clearly that vision plays an important, direction specific, role in the control of postural reactions during sudden perturbation of stance. When the linear acceleration is of short duration (less than 10 s), visual influences become apparent only when the visual information conflicts with other sensory inputs. By contrast, when the accelerations are of longer duration and smaller amplitude, the effects observed are more complex but very clear.

The main conclusions stemming from the present results are the following: firstly, it is clear that motion of the visual environment produces a greater effect when tested in the dynamic condition of postural change than when tested in isolation in static posture maintenance condition as in the work by Lestienne et al. (1977). Consequently, the role of a sensory system in the control of movement or posture is itself dependent upon the state of the ensemble of central neuronal networks and erroneous generalizations may be induced by studies which are done during static laboratory conditions. It can also be inferred from this conclusion that the role of vision may be even greater when subjects are tested in the performance of rapid movements, as suggested by Nashner and Berthoz (1978) and Vidal et al. (1978). The recent results of Talbott and Brookhart (1976, 1978) who, in similar experiments in the dog, propose a concept of "variable gain of visual influence depending on the environmental context" is in the line of this "state dependent" role of vision. We would, however, stress the idea that the variable gain is dependent not only upon the environmental context defined as a whole, but upon the particular cues from the environmental context which are relevant for a given motor performance. This statement must, of course, be supported by further experiments, but it is in line with the theory which assumes that posture is only

Table 3

one particular kind of movement and, in general, is always preparatory to or part of a movement. It must also be remembered that the original results of Reynolds et al. (1972) had emphasized the role of cutaneous cues in postural control by selective supression with anesthesia. The powerful influence of vision shown in the present experiments should not consequently preclude any further study on the role of other sensory cues in the control of posture.

References

- Berthoz, A., Pavard, B., Young, L.R.: Perception of linear horizontal selfmotion induced by peripheral vision (linear vection). Basic characteristics and visual-vestibular interactions. Exp. Brain Res. 23, 471-489 (1975)
- Chu, H. N.W.: Dynamic response of human linear vection. M.S. Thesis, 100 pp. MIT 1976
- Dichgans, J., Held, R., Young, L., Brandt, T.: Moving visual scenes influence the apparent direction of gravity. Science 178, 1217-1219 (1972)
- Dichgans, J., Mauritz, K. H., Allum, J. H.J., Brandt, T.: Postural sway in normal and ataxic patients: Analysis of the stabilizing and destabilizing effects of vision. Aggressologie 17, 15-24 (1975)
- Guedry, F.E.: Psychophysics of vestibular sensation. In: Kornhuber, H.H. (ed.), Handbook of sensory physiology, V.1/2, Vestibular Systems, p. 3-154. 1974
- Lestienne, F., Soechting, J.F., Berthoz, A.: Postural readjustments induced by linear motion of visual scenes. Exp. Brain Res. 28, 363-384 (1977)
- Lishman, J. R., Lee, D.N.: The autonomy of visual kinaesthesis. Perception 2, 287-294 (1973)
- Nashner, L., Berthoz, A.: Visual contribution to rapid motor responses during postural control. Brain Res. 150, 403-407 (1978)
- Reynolds, P. J., Talbott, R.E., Brookhart, J. M.: Control of postural reactions in the dog: The role of the dorsal column feedback pathway. Brain Res. 40, 159-164 (1972)
- Talbott, R.E., Brookhart, J.M.: Variable postural response of the dog to visual stimuli depending upon the environmental context. Neurosci. Abstr. 2, 762 (1976)
- Talbott, R. E., Brookhart, J. M.: Predicted characteristics of the intact dog's postural control system based on a perturbation analysis of response during blind folding and optokinetic stimulation. J. Neurophysiol. (submitted) (1978)
- Vidal, P.P., Gouny, M., Berthoz, A.: Role de la vision dans le déclenchement des réactions posturales rapides. Arch. Ital. Biol. 116, 281-291 (1978)
- Waespe, W., Henn, V.: Neuronal activity in the vestibular nuclei of the alert monkey during vestibular and optokinetic stimulation. Exp. Brain Res. 27, 523-538 (1977)
- Young, L.R., Meiry, J.L.: A revised dynamic otolith model. Aerosp. Med. 39, 606-608 (1968)

Received November 30, 1978