Visual control of posture:
the role of motion parallax and cognitive processes

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Thesis submitted for the degree of PhD,
in the Faculty of Science of the University of London.

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ABSTRACT

The thesis investigates visual control of posture in man, in particular the role of visual motion parallax. The moving room paradigm, which simulates self-motion, was used in most experiments. In the first series of experiments the effects of room motion in the presence or absence of a foreground fixation target were investigated. Directionally specific postural responses opposite to background motion were observed when subjects were fixating the foreground target. Neither induced motion, ocular convergence nor binocular vision were sufficient to evoke such responses. It was concluded that such postural response and more generally postural control could be influenced by motion parallax. In experiments carried out in a normal stationary room, it was found that the motion parallax a subject generates during spontaneous body sway is used by the visuo-motor system to control body oscillations. The parallax-based effect was, however, limited to low frequency components of body sway (<0.75 Hz).

The influence of cognitive processes in visuo-postural control was also investigated. It was found that the predictability of the forthcoming displacement of a moving visual scene helped observers distinguish visual flow due to self-motion from that due to object-motion and therefore inhibit postural readjustments induced by object motion.

The visual control of posture in patients with congenital nystagmus, who show involuntary movement of the eyes at a frequency of 3-5 Hz, was also investigated. It was found that, in the moving room paradigm, these patients were able to use motion parallax to control slow reorientation of the body as do control subjects. In contrast, during spontaneous body sway in a 3 dimensional environment they were not able to control rapid oscillations of the body (> 0.5Hz). These findings suggest that in congenital nystagmus, visual control of posture is restricted by low frequency sampling of the visual scene (foveation periods). They also suggest that although motion parallax is a dynamic cue, it can be used to control slow body re-orientation on the basis of solely discrete visual samples.
ACKNOWLEDGMENTS:

I would like to thank everyone who helped me directly or indirectly during my PhD. First, my thank go to my supervisors, Dr Adolfo M. Bronstein and Dr Michael A. Gresty for their constant help and good advice. I would also like to thank everyone who is, or has been in our laboratory over the last three years, for both discussion and distraction from my work. Particularly my gratitude goes to kai, Josephine, Raymond, Nicoll, Brian, Marussa, Konstantin, Kiellen, Dominic, Pierre, Marion, Didier, Théo, Ari, Barri, Brian, Flur, Adrien, Peter, Marry, Bill David, Claire Janet, John, Sven, Katharina, Sam, Richard, and many others.... Special thanks also to all the subjects and patients who kindly took part in the experiments. Finally, I would like to thank my fiancée Ornella and my daughter Elisa for being there for me; this thesis is dedicated to them.
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ABBREVIATION

COP: Centre of foot pressure
LED: Light-emitting diode
EOG: Electro-oculography
CN: Congenital nystagmus
SD: Standard deviation
SwP: Sway path length
ANOVA: Analysis of variance
Chapter 1

General introduction

Posture refers to a complex assemblage of the multiple body segments relative to each other controlled by a neuromuscular system. The orientation of the body and the maintenance of the human erect posture with respect to vertical in both the frontal and sagittal plane is a primary constraint in a world where the effect of gravity must be taken into account. Nashner and Cordo (1981) and later Amblard et al. (1985) and Roll et al. (1988) have suggested that the human postural control system was in charge of two important behavioral goals: postural orientation and equilibrium. Postural orientation was defined by Horak and Macpherson (1996) as the relative positioning of the body segments with respect to each other and to the environment and postural equilibrium as the state in which all the forces acting on the body are balanced so that the body tends to stay in the desired position and orientation (static equilibrium) or to move in a controlled way (dynamic equilibrium). Although human upright stance is considered as being a state of 'static' equilibrium (in contrast to locomotion), the body is constantly moving, and therefore requires a dynamic control. The main frequency of spontaneous body oscillations is below 0.5 Hz, but higher components (up to 10-15 Hz) of sway also exist, particularly important for the lower parts of the body (ankles for instance) as opposed to higher segments such as the trunk and the head (Benda et al. 1994; Amblard et al. 1985).

A. Multi-sensory control of posture

A person locomoting or simply standing upright, can usually sense how he is moving or being moved relative to the world. This 'kinaesthetic' sense, which is essential for controlling stance and locomotion, utilises changes that accompany movement of the body. There are mechanical changes within and at the surface of the body (somatosensory information), head motion information (vestibular input) and optical changes at the eye (optic flow pattern; visual information). The control of
postural orientation and equilibrium involves the integration of these multiple sensory signals that specify information about the position of body segments relative to each other and to the surrounding environment. The main receptors involved in postural control are represented in Figure 1.1.

![Diagram of sensory receptors](image)

**Fig. 1.1: The main sensory receptors involved in the perception of self-motion and postural control: there are vestibular, visual and propriosomesthetic receptors. The later include receptors into the muscles (Golgi receptors and muscular spindles), into the skin (cutaneous receptors, sensitive to pressure and shears) and in the articulations (adapted from Berthoz 1997).**

Somatosensory afferents include cutaneous, musculo-articular and muscular receptors. Since these receptors are distributed throughout the whole body, they are critical for determining body configuration, i.e. the relation of each segment relative to the adjacent ones. In contrast, vestibular and visual receptors are located on the head that can move independently of the trunk. Therefore, in order to contribute to body configuration or orientation, vestibular and visual signals require the integration of the position of the head on the trunk and also specifically for visual
signals, the integration of the position of the eye in the head (Wolsley et al. 1996). Vision must also be distinguished from the vestibular and the propriosomesthetic senses in that visual flow carries information relative both to object-motion and self-motion. Such an ambiguity can however be resolved by reference to information from other sensory systems specifying body movement, therefore indicating body motion instead of self-motion. As we will see in the fifth chapter of this thesis, this ambiguity can also be suppressed by the knowledge or predictability of the spatio-temporal aspect of any displacement of the moving environment. Although the contribution of auditory cues are limited, they can also provide spatial information allowing a reduction of body sway (Easton et al. 1998). Due to the limited implication of the auditory system to postural control in human, this fourth sensory system will not be further considered in the present thesis.

Each sensory modality provides both specific and redundant information about body motion according to their optimum range of frequency and amplitude of body motion in which they operate. The visual and cutaneous systems are considered as primarily effective in the low frequency range of spontaneous body sway (van Asten et al. 1988a; Jeka et al 1997, 1998, 2000). The vestibular and also stretch reflexes are elicited more effectively at higher frequencies, above 1 Hz, relevant to sudden perturbation such as displacement of the support surface (Nashner 1977; Diener et al. 1981; Nashner & Cordo 1981). Due to the redundancies provided by the multiple source of afferent signals, equilibrium can be maintained in certain environment when information from one system is not available. For instance, equilibrium in normal human subjects can be maintained with eyes closed. Similarly, as long as visual and propriosomesthetic information are available, balance in patients without labyrinthine function is reasonably well preserved (Bles et al. 1983). Those redundancies become particularly important for the resolution of perceptual ambiguities. For instance, motion of the visual environment on the retina can be the consequence of both self-motion or motion of the environment. In these circumstances, the ambiguity can be resolved in reference to vestibular information specifying acceleration of the head and indicating self-motion instead of environment motion. Therefore, the use of multiple sensorial information is crucial for the central nervous system to control both body orientation with respect to vertical (either specified by vestibular or visual cues) and body equilibrium or
stabilization against external disturbances. However, in some circumstances, such as when the vestibular system does not specify any head acceleration (as during whole body rotation at a constant velocity), the displacement of the visual environment can be erroneously interpreted as a displacement of the self, giving rise to the illusion of self-motion, also called vection (Held et al. 1975; Dichgans & Brandt 1978; Thilo et al. 1999, 2000) in addition to postural readjustments (see below).

Although the respective influence of visual, vestibular and somatosensory information on postural control has been the subject of extensive research, the way these sensory channels are fused remains poorly understood. As reported recently by Jeka et al. (2000), these sensory channels do not work in a simple additive way. The task of understanding sensory integration becomes particularly difficult when one considers the ability of the nervous system to learn to ignore (to some extent!) some inaccurate information and focus mainly on those which are relevant to the task. This ability can be observed in response to repetitive exposure to disturbances. For instance, the postural strategy adopted in response to an abrupt displacement of the support surface (Maki & Whitelaw 1993) or to a displacement of the visual environment (Bronstein 1986) can be profoundly influenced by prior experience of such a disturbance. Although prior experience prevents from falls or inappropriate postural reactions, it remains that, in normal subjects, false information can still induce postural re-adjustments, well within the limit of stability. A perturbation deployed to any of the sensory systems involved in self-motion perception (visual, vestibular and proprioceptive systems) can induce postural readjustments. These observations indicate that the sensory disturbance is centrally interpreted as due to self-displacement, and requires a compensatory response. In this thesis, we will focus mainly on the role of visual information in the control of postural orientation and equilibrium in standing subjects.

B. Role of visual information in postural control

Vision is not necessary for normal balance – one can stand in the dark. Until the early sixties, vision was considered solely as an *exteroceptive* sense, concerned
with obtaining information about the layout of the environment and objects. Proprioception, on the other hand, which is necessary for controlling any activity, has been generally considered the exclusive domain of the mechano-receptors within the body. As early as the works of Travis (1945), Edwards (1946) but also Wapner and Witkin (1950) it appeared however, that body stability was improved by vision. Accordingly, Gibson (1958, 1966, 1979, Gibson et al. 1955) suggested that vision could be integrated in the overall function of proprioception. The visual cues, or ‘propriospecific’ visual information (in Gibson’s terminology) about observer’s own bodily movement, could be obtained through the changing optic array at the eye. Deformation of the retinal image due to ego-motion or transposition of objects in the environment (called optic flow) is then not considered just as a nuisance but actually as a rich source of information concerning the world and the relation of the subject into this world (Gibson et al. 1958).

1. Visual control of spontaneous body sway

A way to understand the nature of the visual basis of postural control consists of modulating the physical visual parameters available and then examine the resultant spontaneous body sway. The most popular protocol is the Romberg test (Dichgans et al. 1976; Black et al. 1982). It involves the comparison of an individual’s spontaneous sway under eyes closed and eyes open. Under these conditions, a reduction of body oscillations with eyes open can be observed in most people, across the different frequency components of body sway (Dichgans et al. 1976; Lestienne et al. 1977).

The degree of postural improvement with eyes open is variable and, among other factors, depends on the stance width, the support surface and the availability of other sensory inputs. For instance, vision reduces body sway more effectively when the feet are close together than with large stand width (Day et al. 1993) and also when the support is unstable or compliant in comparison with a rigid one (Bles et al. 1980; Nougier et al. 1997). Similarly, when either the vestibular (Black & Nashner 1985; Redfern & Furman 1994; Peterka & Benolken 1995) or the somatosensory (Kotaka et al. 1986; Paulus et al. 1987; 1988) systems is impaired, giving rise to a
significant postural instability (or even falls) with eyes closed, then visual stabilization becomes particularly effective.

Modulations of the physical and physiological visual parameters have shown that visual stabilization depends critically upon the characteristics of the visual scene. For instance, both lateral and fore-aft spontaneous body sway and eye-target distance are linearly related such that sway decreases with decreasing eye-object distance (Lee & Lishman 1975; Bles et al. 1980; Paulus et al. 1984, 1989). The explanation of this phenomenon is based on the simple geometric rule that the retinal flow of a viewed scene is greater the nearer the objects are to the eyes. Accordingly, Bles et al. (1980) have shown that the maximum eye-target distance at which vision is still efficient is twice as long when subjects are made unstable by using compliant surfaces (visual stabilization up to 5m) than when subjects are standing still on a rigid support (visual stabilization up to 2.5 m). Other physical and physiological parameters affect spontaneous sway (See Bronstein and Guerraz 1999): we note the object size and localization (Paulus et al. 1984; Nougier et al. 1997), binocular disparity (Fox 1990), visual motion (Amblard et al. 1985) but also visual acuity (Paulus et al. 1984) and spatial frequency (Kunkel et al. 1998).

Further insight into the importance of visual flow on postural control has been gained by manipulating artificial optical flow. The most popular paradigm refers to the moving room paradigm, designed by Lee and collaborators.

2. Visually induced body sway: the moving room paradigm

In their pioneer work, Lee and collaborators (Lishman & Lee 1973; Lee & Aronson 1974; Lee & Lishman 1975) showed elegantly that vision is not a purely exteroceptive sense, but is an integral component of the control system for maintaining stance. In the classical moving room paradigm (Lee & Aronson 1974; Lee & Lishman 1975) the subject assumes a quiet upright stance within a visual environment (room) that can move relative to the fixed frame of reference (floor) on which subjects are standing. The movement of the room creates an optical flow field pattern that is similar to the pattern experienced when translating back and forth through the environment. By measuring the body position in the presence and in the
absence of visual motion, the influence of vision on postural sway can be detected. The result of such experiments showed directionally specific postural response: in response to linear forward and backward motion of the visual environment, subjects sway in the direction of motion (Lee and Lishman 1975; Stoffregen 1985, 1986; Bronstein 1986, Bronstein et al. 1990). Small displacement of the room such as 3 mm for a viewing distance of 30 cm (Lee & Lishman 1975), or 2.5 cm for a viewing distance of 2 m (Stoffregen 1986) are sufficient to induce postural sway. These amplitudes are so small that they are generally not consciously perceived by subjects. Thus the sway induction threshold is lower than that of explicit motion perception.

A drawing of the moving room paradigm is presented in Figure 1.2. In this picture, from Bertenthal et al. (1997), a child is depicted falling backward as a function of the room moving towards him. This response is usually considered to arise from a consequence of a mis-interpretation of the visual flow as due to self-motion instead of object-motion. Unlike in early or pre-walkers (Bertenthal et al. 1997; Lee & Aronson 1974; Stoffregen et al. 1987), in adults the displacement of the room evokes only small body oscillations in phase with the room, instead of falls (Lee & Lishman 1975).

![Fig. 1.2: Schematic drawing of the moving room paradigm. Depicted inside the room is a child falling backward as a function of the room moving towards him (from Bertenthal et al. 1997).](image-url)
In addition to the real moving room, a wide variety of moving visual stimuli have been employed to investigate the phenomenon of visually induced body sway. These include, tilting rooms (Bles et al. 1980), projected displays simulating a moving visual wall, tunnel, floor or ceiling (Lestienne et al. 1977; Fluckiger & Baumberger 1988; van Asten et al. 1988a; Gielen & van Asten 1990; Dijkstra et al. 1994) and visual roll rotations (Dichgans et al. 1972; Clément et al. 1985; Dijkstra et al. 1992). Consistently, it has been reported that in rhythmic motion of the visual scene (sinusoidal motion) with either a linear or a rotational stimulus, the largest effect of vision is observed at fairly low frequencies (~ 0.2 Hz) at which the body is phase locked with the moving scene. At higher frequencies (> 0.3 Hz), this locking is lost and the overall effect of visual motion is reduced (van Asten et al. 1988a,b; Dijkstra et al. 1994; Giese et al. 1996). The amplitude of postural sway, at least in the antero-posterior direction has been shown to be particularly affected by visual properties such as the density of texture (Lestienne et al. 1977; van Asten et al. 1988a) and the velocity of motion (Lestienne et al. 1977; Masson et al. 1995). Lestienne et al. reported that fore-aft sway induced by linear visual motion is linearly related to the logarithm of both the mean spatial frequency in the visual scene and the velocity of motion. However, these results have not been systematically replicated for oscillating motion (see van Asten et al. 1988a).

The directionally specific postural response induced by the 'moving room' demonstrate clearly that the overall changes of the retinal image (retinal flow) due to self-motion or object-motion provide a rich source of information, not only about the environment but also about the orientation of the subject in it. On the basis of these findings, Lee and Lishman (1975) completed Gibson's theory, and added to the exterospecific and propriospecific information, the 'expropriospecific' ones. The function of such visual information is to integrate the interaction between the subject and its environment into the scheme of motor control, or in other words, to integrate the modification of the optic array in relation to self-motion.
Chapter 1: Introduction

C. Physio-geometrical aspects of visuo-postural control

1. Effect of head, trunk and gaze orientation

An important aspect of the visually induced postural response is that its direction does not depend on the orientation of the head on the body nor on the orientation of the body relative to the stimulated motion (Stoffregen 1985; Gielen & van Asten 1990; Wolsley et al. 1996; Thurrell et al. 2000). Wolsley et al. (1996) showed that when subjects were fixating the centre of a rotating disk, the main direction of body sway was always re-orientated to be parallel to the disc, whether both the head and body were parallel to the disc or not. Similar results were previously reported by Gielen et al. (1990) using a visual flow simulating displacements in a tunnel. These observations demonstrate that the signals of eye-in-orbit and head-on-trunk are well integrated in order to redirect visuo-motor commands to the appropriate postural muscles. Also, Gielen et al. (1990) reported that when subjects were looking slightly sideways to the simulated self-motion through a tunnel, their postural responses were re-oriented to be perpendicular to the direction of gaze instead of being parallel to the simulated motion.

2. Static versus dynamic visual information.

Although visual flow appears to be a rich source of information for postural control, visually induced body re-orientation has also been reported with purely static displays such as a static tilted room (Bles 1979 reported by Isableu 1999), or a tilted frame (Isableu et al. 1997, 1998, 1999). Sway amplitude caused by static visual disturbances is however of a smaller amplitude (<1° for lateral sway) than sway amplitude caused by dynamic visual disturbances.

The importance of visual flow and particularly motion cues has been evaluated by using stroboscopic illumination. At low frequency, up to 5-6Hz, stroboscopic light only provides position cues, hence offering a degraded spatial reference. Recording of spontaneous postural sway shows that under stroboscopic illumination up to 6-8 Hz, the gain of vision was reduced, leading to postural
performances close to those observed in the absence of visual cues (Amblard & Créminieux 1976; Kapteyn et al. 1979; Amblard & Carblanc 1980; Paulus et al. 1984; Amblard et al. 1985; Isableu et al. 1998). Power spectral analysis of spontaneous sway indicates that the high frequency components of sway (>2Hz), particularly important at the ankle level (and COP), are drastically affected by stroboscopic illumination. In contrast, sway frequency components below 2 Hz, dominants for higher segments of the body (the trunk and the head), are partially preserved (Amblard et al. 1985). Amblard and collaborators concluded that discrete visual information ('static cues') is sufficient to control the upper part of the body, which has predominantly low-frequency dynamics. Visual motion cues ('dynamic cues') control oscillations of the lower part of the body which extend through a higher frequency range. In agreement with the model proposed by Amblard et al. (1985), slow re-orientation of the body induced by either the displacement of a moving scene (Kapteyn et al. 1979) or by a static tilted frame (Isableu et al. 1997, 1998) are preserved under stroboscopic light.

Overall, the experiments with stroboscopic light indicate that an optimal stabilization requires a continuous recording of the visual afferents. In contrast, visual flow may not be necessary for the control of postural orientation; discrete visual sampling, providing only visual displacements instead of visual flow, seems sufficient. However, this statement does not imply that when available, 'motion cues' are not used to control body orientation.

3. Functional specialization of the peripheral retina?

In spatial orientation, two visual systems, a focal one (central vision) and an ambient one (peripheral vision) are usually distinguished. The first one, the central area of the retina, is usually considered as being specialized in object motion perception and object recognition. In contrast, the peripheral region of the visual field is particularly sensitive to moving scenes, and is therefore thought to dominate both perception of self-motion and postural control (Dichgans & Brandt 1978). Such a differential involvement of the central versus the peripheral retina in spatial orientation derives from research on the illusory perception of self-motion (vection). Brandt et al. (1973) were the first to show that circular vection, around the
longitudinal body axis (in yaw) can be elicited with circular visual stimuli (drum) but only if the diameter of the stimuli sustained more than 30° in diameter. Similar results have been observed both with roll vection (Held et al. 1975) and linear vection (Berthoz et al. 1975). However, this dominance of peripheral vision on illusory self-motion has been challenged, and several studies have shown that vection could be elicited in central vision (Andersen & Braunstein 1985; Post 1988). Post (1988) showed that the magnitude of vection was greater with a larger stimulus area, but differences disappeared when an equal area stimulus was presented either centrally or in the periphery of the visual field.

The hypothesis of a dominance of the peripheral vision on postural control has also received an important support (Dickinson 1969; Lestienne et al. 1977; Amblard & Carbland 1980; Delorme & Martin 1986). As for illusory self-motion perception, a central field 30° in diameter reduces spontaneous body lateral and fore-aft sway less effectively than does the peripheral field (~200°) in which the central area is masked (Paulus et al. 1984). However, when the angular size of the visual field is strictly comparable in both the central and the peripheral part of the retina (30°), then the eccentric visual field exhibits a significantly smaller contribution than does the central one. Finally, when the peripheral field size is corrected by the cortical magnification factor of the retina in the primary cortex (V1), spontaneous body sway is stabilized by the peripheral retina to the same extent (Straube et al. 1994). Similarly, postural sway evoked by the displacement or rotation of a visual environment is of smaller amplitude when the stimulus covers only the central visual field rather than the peripheral field. However, when the area is of equal size, visually induced body sway is more potent in the central field than in the periphery (Stoffregen 1985; see above). Therefore, the peripheral dominance often reported in either visual stabilization of spontaneous body sway or visually induced body sway is more likely due to the size of the stimulated field manipulated than to a functional specialization of the peripheral vision for postural control.
4. Structure of the visual flow

An aspect often neglected in investigations based on the dichotomy between peripheral and central vision is that the visual flow generated during self-motion is not uniform throughout the visual field. As shown in Figure 1.3, when a subject is locomoting or simply swaying back and forth in a 3D environment, looking straight at its extremity, a radial flow having a focus of expansion in the direction of motion is projected in the center of the retina. At the peripheral edges of the field of view, the visual flow is nearly parallel to the line of motion. This flow structure at the periphery has been termed lamellar flow. It must be noted that the relationship between the structure of the visual flow and the area of the retina is simply reversed for lateral displacements or when the observer is looking in the direction perpendicular to motion.

![Diagram](image)

Fig. 1.3: Representation of the optical flow field generated by forward displacement through a 3 dimensional environment (a) with the focus of expansion in the direction of sway grading into lamellar flow in the orthogonal direction (b).

The differential effect of radial versus lamellar flow has been investigated in relation to the retinal location. Results of such experiments showed that in central
vision (15-20°), both lamellar and radial flow can induce directionally specific antero-posterior body sway (Stoffregen 1985; Andersen & Dyre 1989). In contrast, in the retinal periphery, only the lamellar flow (horizontal flow) can provoke body sway (Stoffregen 1985). The interaction between the retinal location and the structure of the visual flow was interpreted by Stoffregen as reflecting a differential sensibility of the peripheral and central retina to the different structures of the visual flow.

Irrespective of retinal area, regulation of antero-posterior body sway is commonly considered as being mainly controlled by radial flow (expansion/contraction) when the observer is looking in the direction of self-motion and by lamellar flow (pure translation) when looking in the direction orthogonal to self-motion (Stoffregen 1985; van Asten et al. 1988a). Conversely, when looking in the perpendicular direction of motion, lateral body sway is largely regulated on the basis of lamellar flow. Often neglected, a natural 3D environment provides a pattern of differential horizontal movements between elements in the field related to the displacement of the observer. These relative movements are referred to as motion parallax. Since lateral sway is supposed to be mainly controlled by lamellar cues, motion parallax might be a relevant cue involved in its regulation.

D. Motion parallax and spatial orientation

1. Definition and geometrical aspects of motion parallax

The term motion parallax or relative motion parallax is commonly used to denote the (horizontal) optical motion of a discontinuity produced by a near object against that produced by a far object due to a change in the observer’s position. (Fig. 1.4). It could also refer to change in the projective relations among elements in the visual field in condition of simulated motion while the observer is stationary and the scene moving. Motion parallax contains information about both the direction and the magnitude of depth relative to the fixation point as illustrated in Figure 1.4 and 1.5 respectively.
Figure 1.4: Relative retinal displacements for an observer moving from right to left, fixating an object $F$ at an intermediate distance.

As the observer moves to the left while tracking an object $F$ (fixation point), the direction of motion of the images of other objects in the environment depends on their depth relative to the point of fixation. It is important to note that the retinal projection of the fixation point ($F$) is not displaced on the retina during self-motion; it serves as an anchor. An object in the background (behind the fixation point) appears to move in the direction of self-motion; at time $t_0$, the retinal projection of the tree is on the right of the line of sight, at $t_1$, it is to the left. Relative to the line of gaze, its image has moved to the left (Fig 1.4). An object in the foreground, (in front of the fixation point), appears to move in the opposite direction; at time $t_0$, the image of the rose is on the left of the line of sight, at $t_1$, it is to the right. Relative to the line of gaze, its image has moved to the right. These opposite motions of the background-foreground will be generated as long as the observer does not look in the direction of his self-motion but keeps looking at the fixation point. At some point between $t_0$ and $t_1$, the point of fixation $F$, the near and far objects are aligned on the line of sight, and therefore their retinal projections overlap. This point is called the locus of zero parallax.

Thus, when the retinal images of two objects move opposite to each other as a result of the observer’s motion, the observer is fixating at some distance between the two objects. The direction in which the retinal image of an object moves relative to the fixation point therefore indicates whether the object is nearer or farther than the observer’s fixation point.
Further depth information is gained from the magnitude of displacement or relative angular velocity of the retinal image of the objects. Objects of which the retinal images move in the same direction as the line of sight and display large retinal displacements (i.e. higher velocity) are farther from the fixation point than those moving in that direction but displaying smaller displacement (i.e. slower velocity); in this case, both objects would be on the far side of the fixation point (see Fig. 1.5). Objects of which the retinal image moves in the opposite direction to the observer’s line of sight and display large retinal displacements, are closer to the observer than those moving in that direction but displaying smaller displacements; in this case, both objects are on the near side of the observer’s fixation point. Thus, the extent of motion parallax between an object and a second object is proportional to the distance in depth between the two objects. In Figure 1.5 the angles \( \delta_1 \) and \( \delta_2 \) represent the relative displacement of objects \( P_1 \) and \( P_2 \) respectively on the retina when an observer is fixating at point \( F \) while moving from right to left. The distance in depth between the observer and the fixation point is also an important parameter affecting motion parallax. Indeed, motion parallax is proportional to the distance between the different stimuli but inversely proportional to the distance between the fixated object and the observer.

![Figure 1.5: Changes in retinal projections of objects at near (P1) and far (P2) distance from the fixation point F. The further away the object is from the fixation point, the greater its angular displacement (\( \delta \)) on the retina is during lateral displacement of the observer.](image)
Fore-aft displacement of an observer in a 3D environment also generates motion parallax. It is maximum in the perpendicular direction and null in the direction of the displacement (heading). Far and close objects on the side of the heading will move in the same direction, opposite to the that of self-motion, with a velocity that is inversely proportional to the distance from the observer. Thus, the magnitude of motion parallax during fore-aft displacement varies with the sway amplitude. However, as long as the observer is looking in the direction of self-motion, the direction of the retinal displacements of the objects is always in the opposite direction of motion. Thus, unlike lateral sway, fore-aft sway provides only variation in the magnitude of motion parallax, but no differential direction (as shown in Fig. 1.4 for lateral sway). This does not hold true when the subject is looking in the perpendicular direction of motion. For that reason, in this thesis, the role of motion parallax in the control of posture is investigated for lateral body sway instead of for fore-aft body sway.

Motion parallax must be distinguished from binocular disparity, also called binocular parallax. Binocular disparity and motion parallax are very different sorts of information about the 3 dimensional structure of objects and their layout. Lateral image disparity refers to the difference in the relative position of the visual images of objects on the two retina due to lateral separation of the eyes. Thus, binocular disparity is a binocular cue, essentially static whereas motion parallax is a dynamic monocular cue.

2. Motion parallax as a cue for depth perception.

Helmholz (1925) first noted that the relative displacement and angular velocities of objects on the retina were informative about the distance between the observer and the objects and also about the distance between the objects themselves (depth cues). Its use as a potential source of information about the 3 dimensional structure and layout of objects depends in essence upon the ability of the observer to detect the relative angular velocities of objects. Perceptual studies have demonstrated that motion parallax can indeed be a reliable and unambiguous cue to depth when the flow field is created by an observer’s active head movement or when simulated while the observer remains stationary (Rogers & Graham 1979; Howard & Rogers
Chapter 1: Introduction

1995; Braunstein & Tittle 1988; Hayashibe 1993). Perception of the 3D structure of objects is, however, less ambiguous when the visual flow is generated actively, implying that extra-retinal information also provides important cues (Wexler et al. 2001).

3. Motion parallax as a cue for spatial orientation and postural control.

Gibson et al. (1955) pointed out the importance of optic flow patterns, including motion parallax, generated by observer movement as a source of information about the 3 dimensional layout of the environment but also as a rich source of information about the observer’s own movements. Accordingly, motion parallax has been shown to be an important cue in self motion perception and particularly to determine one’s direction of self-motion also called heading perception (Cutting et al. 1992; Frey & Owen 1999). During translation of an observer within a 3 dimensional environment, motion parallax occurs between elements at different distances: to the left of the heading, the images of nearer objects on the retina move to the left relative to those of more distant objects. To the right of the heading, the images of nearer objects move to the right relative to those of more distant objects. The images of objects that are collinear with the motion path remain visually aligned. This locus of zero parallax can therefore specify heading direction.

In contrast to the perception of heading, little is known about the involvement of motion parallax in postural control. As mentioned above, movement of the whole visual surrounding (either 2 or 3 dimensional) induces a postural readjustment in the direction of motion. Recently, postural adjustments in the opposite direction to motion of the surrounding (contra-directional sway) have also been reported. Bronstein and Buckwell (1997) have found lateral postural adjustments in the opposite direction of display motion, when a stationary point of fixation was placed in the foreground. In their experiment, a visual background was moved with a raised cosine trajectory behind a stationary window (foreground) with a velocity profile (peak velocity of 4cm/s) and an amplitude (1.4° of visual angle) that created an optic
flow comparable to what a standing subject would experience during spontaneous quiet lateral sway in a 3 dimensional environment. As shown in Figure 1.4, when an observer moves laterally while fixating a distant object, the images of nearer objects move in the opposite direction of the head. When the observer fixates a nearer object, the images of distant objects move in the same direction as the head. Therefore, postural adjustment in the opposite direction to background motion is consistent with the direction of image movement on the retina that a moving subject would experience in a stationary 3 dimensional environment. Motion parallax, i.e. the relative movement of images across the retina is useful in the determination of depth, perception of heading and during locomotion (Bardy, Warren & Kay 1996; Warren, Kay & Yilmaz 1996). It also appears to be a potential source of information for postural control.

E. Aim of the thesis

In the first experimental chapter (chapter 2), the contra-directional postural response observed by Bronstein and Buckwell (1997) in the foreground-background display was further investigated. Experiment 1 investigated whether this response was only a transient instability or could be a sustained repositioning of the body according to the visual reference. In the following experiments 2-4, alternative explanations to motion parallax were tested. Experiment 5 investigated whether this contra-directional response was sensitive to dynamic characteristics of the relative displacement of the background in relation to the foreground.

The third chapter (Experiment 1-2) reports an investigation on whether motion parallax generated by natural spontaneous body sway in a 3 dimensional environment could be used as a feedback by the postural control system to regulate spontaneous body sway.

The fourth chapter investigated the influence of action and cognition in visually induced body sway because these are essential ecological elements in quotidian behaviour. Action and predictability were investigated by respectively asking subjects to control or trigger the displacement of the visual scene, and by
giving the observer all the spatio-temporal characteristics of the forthcoming visual event (Experiment 1-3).

The fifth chapter explores potential clinical applications of the paradigms developed above. The role of visual information in postural control was investigated in patients with congenital nystagmus who have limited sampling of the visual world. For this purpose, spontaneous body sway with eyes open and eyes closed was analyzed in the frequency domain (Experiment 1). In a second experiment (Experiment 2), visually induced body was evoked in these patients either with displacement of a uniplanar visual background or with relative motion between the foreground and the moving background (motion parallax).
Chapter 2

Motion parallax and visually induced body sway

A. ABSTRACT

Unidirectional motion of an uni-planar background is known to induce in a standing observer a co-directional postural sway. However, Bronstein and Buckwell (1997) showed recently that this postural readjustment could be reversed in direction if subjects were asked to fixate a stationary object placed between themselves and the moving background. The five experiments presented in chapter 2, explore this contra-directional postural re-adjustment and examined whether it does reflect the influence of motion parallax on the control of postural orientation. Centre of foot pressure and head displacements were recorded from normal subjects. They faced a visual background of 2m x 3m, at 1.5 m distance, which could be moved parallel to the interaural axis (58 cm of displacement in 11s). Results showed that when the visual scene consisted solely of a moving background, the conventional co-directional postural response was elicited. In contrast, when subjects were asked to fixate a stationary foreground, a consistent postural response in the opposite direction to background motion was observed (Experiment 1-4). This contra-directional postural response was not transient but was sustained for the 11 sec of background motion. Results of Experiment 2 indicated that this contra-directional response was not the consequence of an induced movement of the stationary foreground by the moving background. In Experiment 3 and 4 respectively, we showed that the contra-directional response could not be elicited if the fixation point in the foreground was fixed to the head instead of earth-fixed and that monocular vision was sufficient. It is concluded that this postural re-orientation, opposite to background motion was determined primarily by motion parallax. Finally, Experiment 5 showed that the velocity of the initial postural response opposite to background was not affected by the acceleration of background motion.
B. INTRODUCTION

The aim of Experiments 1-5 was to explore the contra-directional postural response observed by Bronstein and Buckwell (1997) in the foreground-background condition. In their experiment, these authors used a short duration stimulus of 2 sec with an overall displacement of the visual scene in the background of 1.4° of visual angle. Therefore the peak amplitude of the contra-directional re-adjustment observed in the foreground-background was as small as 1 mm at the level of the head and had a maximum duration of 1-2 sec. The aim of experiment 1 was to determine whether this contra-directional response in the foreground-background condition was only a transient phenomenon or whether it could be sustained for longer than 1-2s. This would parallel findings on the co-directional antero-posterior sway observed with an uni-planar linearly moving visual environment (Lestienne et al. 1977) or a rotating disk (Dichgans et al. 1972).

A perceived movement of the fixated foreground induced by the moving background ('induced movement', see Reinhardt-Rutland 1988 for review) could also be responsible for the contra-directional sway observed by Bronstein & Buckwell (1997). Van Asten et al. (1988 a) investigating visually induced body sway in the antero-posterior direction reported that when the central part of their linearly moving display was masked, body sway was in the opposite direction to background motion (moving forward-backward) in 25 % of the trials. Since the stationary inner part of their display was perceived as moving in the opposite direction of motion (induced movement in depth), the authors interpreted the sway opposite to motion as determined by induced movement of the stationary inner part of the display. Thus, the perceived movement of a target rather than its retinal image movement can be a relevant cue for controlling posture. Analogously, it has been shown that perceived motion can generate nystagmic eye movements with slow-phases in the direction of induced movement both in monkeys (Waespe & Schwarz 1987) and humans (Heywood 1973; Yasui & Young 1975; Collewijn, Curio & Grüßer 1982). Bronstein and Buckwell (1997) did not report whether their subjects had the illusion of an induced movement of the stationary foreground placed in front of the moving background. Therefore, the purpose of Experiments 2 was to investigate whether the
contra-directional sway observed in the foreground-background display could be due to induced movement of the fixated foreground instead of motion parallax.

Experiment 3 investigated whether convergence of the eyes on the foreground target, in front of a moving background *per se*, independently of motion parallax could be responsible of the contra-directional response in the foreground-background display. To test this alternative explanation, we asked our subjects to fixate a close target coupled with head movement instead of earth fixed. As mentioned in introduction, the opposite motion of the foreground against the background is generated as long as the observer does not look in the direction of self-motion but keep looking at the fixation point. When the fixation point is coupled to head movement, subjects fixate in the direction of self-motion and so the opposite motion between foreground-background due to motion parallax does not occur.

In addition, Experiment 4 investigated whether monocular vision was sufficient for the contra-directional postural response to occur as predicted since motion parallax is a monocular cue. Finally, Experiment 5 investigated whether the dynamic characteristics of the displacement of the background in the foreground-background display affected the shape of the postural re-orientation in the opposite direction to motion.
Chapter 2: Motion parallax and visually induced body sway

C. GENERAL METHOD

1. Apparatus

In Experiments 1-5, we recorded head and COP responses in the lateral direction for different visual conditions. Since the main goal of the study was to characterize the direction of visually evoked postural responses, discrete, unidirectional motion of a visual background was the chosen stimulus. The visual background consisted of a 2m x 3m flat board (67° x 90° of visual angle). Photoluminescent yellow-green stripes were used to create the picture of a house with one tree on each side (see Fig. 2.2). Background displacement was achieved by mounting the flat board on a chassis with four pneumatic wheels (bogie) running on a linear track. The bogie was driven by a pair of linear induction motors that generated thrust against a reaction plate situated along the middle of the track. The background was moved at 150 cm from the subject's eyes along an axis parallel to the inter-aural axis, in an otherwise dark room. In Experiments 1-4, the background was moved 58 cm (21°) leftwards or rightwards. A constant velocity of 6 cm/s was reached after approximately 1.25s of acceleration onset and sustained for 8.5s before the deceleration occurred. After each trial, the subjects were asked to close their eyes while the background was moved back to its starting position and re-illuminated with a lamp to keep a constant level of luminance. The experimental set-up can be seen in Figure 2.2. The velocity profile of background displacement was different in Experiment 5 and therefore will be defined in the method section of that experiment.

2. Procedure

In experiments 1-5, subjects were instructed to 'stand still and relaxed' with hands at their side. They stood barefoot on a rigid foot support placed on top of a slab of foam rubber (height 5 cm; specific weight 30g/dm³) resting on the sway platform. The aim was to increase slightly the instability of the subjects so that any effect of visual condition on the subjects' sway could be more easily observed (Lee & Lishman 1975; Bles et al. 1980; Bronstein 1986). Postural sway in the lateral direction was recorded using an AMTI force platform (model BP2436) for centre of pressure (COP) recordings. The X, Y coordinates of force exerted on the platform
are measured by load cells, one located at each of the four corners of the platform. The recording of the movement of the body's point of pressure to the foot support using a force measuring platform is a common method for studying body sway. However, the displacement of the COP is not only caused by a possible shift of the body's point of gravity, but also by the acceleration and deceleration forces related to the movements of the inertial mass of the body. This dynamic component due to body inertia becomes particularly important with increasing body sway frequency (Gurfinkel 1973; Huffsmith et al. 1980). In addition, a shift of the COP can be caused by a movement of the standing subject as such, but also can be caused by a change in the configuration of the parts of the body in which case the measured shift is not representative for the subject sway. Thus, in addition to the COP, head sway was recorded throughout all the experiments presented in this thesis.

Subjects wore a lightweight helmet, on top of which was mounted an infra-red light emitting diode so that head displacements could be measured. Displacements of the light were transduced by imaging a top view of the subject onto a 2-dimensional Schottky barrier photodetector (United Detector Technologies inc) situated 40 cm above the head. Light from the diode was projected onto the detector surface via a Mamiya inc medium format lens, 45 mm focal length, mounted on the front of the photodetector. Use of this technique to record complex human movements has been described previously (Findley et al. 1981). One axis of the detector was oriented in the lateral plane to transduce lateral head sway. The resolution of the detector in the configuration deployed was of 0.1 mm, linear up to +/- 8 cm. Since the distance between the head mounted infra-red light and the Shottky camera was maintained at 40 cm, head sway values were normalized for subjects' heights (signal * mean height of group / individual's height). A computer was used to generate the command signal to the linear motors of the bogie and to acquire the output signals from the sway platform and the Shottky camera at a sampling rate of 125 Hz. The sway signals were also continuously monitored on-line on an oscilloscope. The experimenter familiarized himself with the spontaneous sway amplitude of each subject and delivered the stimuli at points of average or smaller than average sway amplitude.
3. Data analysis

On each trial, calculations were made of: the mean COP/head lateral position over the 4s before stimulus onset (mean baseline position) and the mean lateral position of COP/head over a 8.5s period, from 1.25s to 9.75s after the onset of stimulus motion. The difference between these two means is the 'mean amplitude of the COP/head response or 'mean response'; a measure of how much COP/head deviates in response to the stimulus (Fig. 2.1). The period of 8.5s from 1.25s to 9.75s corresponds to the period of constant velocity of stimulus motion. Since no differential effect between the two directions of motion was expected, responses to leftward and righward stimuli were combined by reversing responses with leftward stimuli. The induced response calculated for each trial was then averaged for each subject and visual condition. Other parameters of body sway, specific to a given experiment, will be presented in the appropriate methods section.

Figure 2.1: Sample record of the lateral head translation during background motion. The 'induced response' correspond to the difference between the mean position during the 8.5 sec of constant velocity and the 4 sec baseline with stationary background.
D. EXPERIMENT 1: Transient versus sustained response

1. Method

1.1. Subjects

Twelve normal subjects (25-50 years old) with normal or corrected normal vision (normal visual acuity and stereopsis) gave their informed consent to participate in the experiment in accordance with the local ethics committee. All subjects were healthy without musculoskeletal or neurological disorders.

1.2. Visual Conditions

The three visual conditions to which each subject was exposed were:

1) **Background fixation:** The luminescent background was the only visible display in the otherwise completely dark room (see Fig. 2.2, left panel). The instruction given to subjects was: 'look straight ahead at the background but keep your eyes straight ahead (primary gaze position) and do not deliberately follow any part of the moving scene'\(^1\). This instruction was used throughout the experiments and for brevity is referred to as 'look straight ahead'.

2) **Foreground fixation:** Subjects had to fixate a cross (1 x 1 cm) placed at the centre of a purpose built earth fixed luminescent window frame (30 x 24 cm), 50 cm distant from the subject's eyes. This foreground was placed 100 cm in front of the background (see Fig. 2.2, right panel).

3) **Fixation through the foreground:** Subjects were asked to look straight ahead at the background through the 50 cm distant earth fixed window frame.

Each visual condition consisted of 24 trials, 8 with motion to the right, 8 to the left and 8 with stationary background as a control condition. The 24 trials were equally divided into two blocks of 12 pseudo-randomized stimuli. The first three blocks (one per visual condition), followed by the second three blocks, were presented in a Latin-

\(^1\) The requirement was to prevent substantial gaze deviations by pursuit of the scene. Since the motion would automatically generate nystagmus the instructions were intended to minimise slow and fast phase amplitudes.
square design. A rest of 15 minutes was given to the subjects between the two test sessions.

An analysis of variance (ANOVA) was performed on the three experimental conditions and LSD post hoc test was used for pairwise comparisons. One sample t-tests were used to test whether the head/COP induced response in each visual condition is different from baseline level (zero) both for the group (based on the mean induced response) and for each individual subject (based on the induced response per trial). Finally, Spearman correlation coefficients were used to assess any relation between sway magnitudes for different conditions of visual fixation. A .05 significance level was adopted throughout.

2. Results and discussion

Figure 2.2 shows a typical sample record of head and COP displacements during background and foreground fixation conditions. As can be seen in that figure, head and COP traces evolve in a relatively parallel manner although COP recordings contains higher frequency components of sway as compared to the head.

Background fixation

When subjects were looking straight at the background as shown in the sample record in Fig 2.2 (left panel), there is an initial postural readjustment in the direction of motion with a latency of approximately 800 ms. This initial response was often followed by a resetting which brought the COP and the head towards their initial baseline position. The postural resetting was then followed by a displacement of the COP and the head in the direction of background motion, until the end of the stimulus as shown in the sample record in Fig. 2.2. Finally, when the movement of the visual background stopped, a postural correction brought the COP and the head towards their initial baseline. The tendency to lean in the direction of stimulus motion was observed in 76% of single trials. By synchronizing stimulus onset, the initial postural response can be clearly identified in the mean lateral translation computed for each individual subject (Fig. 2.3) and also in the grand mean in which
all individual averages were combined (Fig. 2.4). The mean slope of the initial postural response (based on the regression line) computed for each individual subject was 6.4 mm/s for the COP and 3.6 mm/s for the head. Three out of the 12 subjects showed no statistically significant postural adjustment (p > .05). Data are presented in Table 2.1.

Figure 2.2: Sample records of both head and COP lateral translation evoked by the displacement of the background while looking straight at the background (background fixation: left panel) or fixating the foreground (right panel). Upward deflections indicate deviation in the direction of stimulus motion while downwards deflections indicate deviation in the opposite direction to motion. As can be seen in these samples, head and COP traces evolve in a relatively parallel manner, whatever the visual condition considered. This indicates that the measured shifts of the head and the COP are representative of body sway. The drawings show the set-up for experiment 1.

<table>
<thead>
<tr>
<th>Background fixation</th>
<th>Foreground fixation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Head</strong></td>
<td></td>
</tr>
<tr>
<td>11 mm</td>
<td></td>
</tr>
<tr>
<td>6 cm/s</td>
<td>Velocity profile</td>
</tr>
<tr>
<td>2 sec</td>
<td>2 sec</td>
</tr>
<tr>
<td>7 mm</td>
<td>COP</td>
</tr>
</tbody>
</table>

Table 2.1
**Foreground fixation**

During fixation of the foreground target, background motion induced a body sway in the opposite direction to motion as represented in the sample recording in Fig. 2.2 (right panel) and in the individual mean head translations in Fig. 2.3. The mean latency of the postural response was of circa 850 ms (Fig. 2.4). The initial postural displacement in the opposite direction to that of the visual stimulus was not followed by a sharp postural correction towards the baseline as in background fixation condition (Fig. 2.2). Instead, subjects continued to lean in the opposite direction to stimulus motion until it stopped. The average peak displacement in the opposite direction of motion was approximately 6 and 8 mm for the COP and the head respectively. 89% of responses in the foreground condition were in the opposite direction to stimulus motion. This postural effect was significant in all subjects except one. One sample t-test analysis confirmed that the displacement of both the COP and the head in the opposite direction to background motion were statistically significant (COP: \( t(11) = 9.4 \ p<.01 \); head: \( t(11) = 6.9 \ p<.01 \)).

The slope of the initial postural response (regression line), measured for 600 ms 1s after stimulus onset was less steep (COP: -3.01 mm/s; head -2.6 mm/s) than in background fixation condition. Mean comparison based on the slope measured for each individual subject in both conditions indicated that the difference did reach significance for the COP (\( t(11) = 2.8 \ p<.05 \)) but not for the head (\( t(11) = 1.5 \ p> .05 \)).

**Background fixation through the foreground**

During background fixation through the foreground window, head/COP induced responses were quite inconsistent. 60% of them were in the opposite direction to stimulus motion and this tendency was significant in only four out of the twelve subjects tested. However, this slight lean in the opposite direction to motion was statistically significant when individual mean induced responses were considered (COP: \( t(11) = 2.2 \ p<.05 \); Head: \( t(11) = 2.7 \ p<.05 \)). See Fig. 2.3 for individual mean lateral head translations and Fig 2.4 for the grand mean combining data from the 12 subjects.
Chapter 2: Motion parallax and visually induced body sway

Figure 2.3: The records show individual mean lateral head translation (in mm) evoked by the displacement of the background in three visual conditions. The time of stimulus onset was used to synchronize the recordings from each trial. Upward deflections indicate deviation in the direction of stimulus motion.
The ANOVA based on the mean induced response indicated that there was a significant effect of the visual condition both for the head (F\(_{2,22}=16.4\) p<.01) and the COP (F\(_{2,22}=24.2\) p<.01). Post hoc mean comparison (LSD) indicated that the three visual conditions differed from each other, both for the head and the COP (p<.05). In addition, the mean response in foreground and background fixation conditions were negatively correlated (Head: r =-0.60 p<.05; COP: r =-0.62 p<.05). Therefore, the more a subject deviated in the direction of motion during background fixation, the more this subject deviated in the opposite direction during foreground fixation. No correlation was observed between the condition of fixation through the foreground and the other two. No postural displacement was observed in the control condition, with stationary visual display (p>.05).

Two subjects reported spontaneously at the end of the experiment that in the foreground fixation condition they experienced the illusion they were moving with the earth-fixed in the opposite direction to background motion (vection). Therefore, both vection and self-displacement were in the same direction, both opposite to background motion. The implication of this anecdotal finding is discussed in the general discussion of the thesis.

Table 2.1: Mean induced head / COP response (average and standard deviation) in mm in the different visual conditions in Experiment 1.

<table>
<thead>
<tr>
<th></th>
<th>Background fixation</th>
<th>Foreground fixation</th>
<th>Fixation through the foreground</th>
<th>Stationary background</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>SD</td>
<td>M</td>
<td>SD</td>
</tr>
<tr>
<td>Head sway</td>
<td>3.41</td>
<td>4.01</td>
<td>-5.38</td>
<td>2.7</td>
</tr>
<tr>
<td>COP</td>
<td>2.96</td>
<td>2.67</td>
<td>-4.01</td>
<td>1.63</td>
</tr>
</tbody>
</table>

Note - A positive value indicates a deviation in the direction of motion whereas a negative value indicates a deviation in the opposite direction to motion.
Experiment 1

Figure 2.4: Grand mean lateral translation of the head (upper panel) and the COP (lower panel) evoked by the displacement of the background in different visual conditions. Upwards deflections indicate a translation in the direction of stimulus motion while downwards deflections indicate a translation in the opposite direction to motion.
Supplementary analysis: body stability with stationary background

Body stability in the lateral direction was measured with the sway path length during the control trials for each of the 3 conditions with stationary background. The sway path (SwP) is the length of the path described by the head/COP, and is defined as the sum of the distances between sequential points sampled during the analysis period (8.5s).

Equation 1: \[ SwP = \sum_{i=1}^{N} \sqrt{(x_{i+1} - x_i)^2} \]

Data are presented in Figure 2.5. The ANOVA showed that there was significant differences between conditions (n=3) both for the head (F2,22= 7.6 p <.01) and the COP (F2,22= 20.5 p <.01). Mean comparisons indicated that the sway path length was shorter when the foreground was added in front of the background irrespective of the fixation point both for the head and the COP (p<.05). There was no difference between the foreground fixation and background fixation through the foreground. Interestingly, in the background fixation condition, the sway path length with stationary background was significantly correlated (p<.01; Spearmann coefficient) with the slope of the initial postural response following the onset of stimulus motion (head: r=.72; COP: r=.76). Such correlation was not found for the foreground condition.

![Figure 2.5: Sway path length (mm/s) for both the head and the COP measured in the three visual conditions of Experiment 1, when the background was stationary. Error bars are standard deviations.](image)
In summary, Experiment 1 replicated the observation of Bronstein and Buckwell (1997) showing that by fixating a stationary foreground placed between the subject and a moving background, the postural response is reversed in direction. In addition, we showed that 1) this contra-directional postural response was not transient as it was sustained during the 11 s stimulus and 2) the amplitude of the postural responses induced by our visual display was bigger than that reported by Bronstein and Buckwell (1997). Indeed these authors reported a peak displacement of a magnitude of 1mm at the level of the head in both the condition of background and foreground fixation. In Experiment 1, we observed peak displacements in similar visual conditions of a magnitude of 6-8 mm. Two factors could explain this difference. First, the characteristics of the stimulus was rather different in the two studies. The displacement of the background used in Experiment 1 lasted longer, was faster and traveled a longer distance than that used previously by Bronstein and Buckwell (1997). Second, the stimulus in the present research consisted of the displacement of a real object while in the previous studies, the stimulus consisted of the displacement of a checkerboard projected onto a screen.

The absence of visually induced body sway in the condition of background fixation in three out of the twelve subjects, reflects the important inter-individual differences consistently reported in the field of visual control of balance (Lestienne et al. 1977; Cremieux & Mesure 1994; Masson et al. 1995; Lacour et al. 1997; Isableu et al. 1998; Warren et al. 1996; Isableu 1999). For instance, Lestienne et al. (1977) reported that 20% of the subjects tested with linear motion of the visual scene did not show any postural readjustment. Although the reason is not well understood (see Isableu 1998; Isableu et al. 1998), a postural response could be induced in some of these non-responsive subjects when they were asked to do a mental arithmetic task at the same time as the postural task (Lestienne et al. 1977), indicating that attentional mechanisms could affect the postural response. The three above mentioned subjects showing no visually induced body sway in response to background motion in Experiment 1 were not included in subsequent experiments.
E. EXPERIMENT 2: Induced movement

The aim of experiment 2 was to investigate the respective role of motion parallax and induced movement in the contra-directional postural response observed in Experiment 1. While induced movement is most effectively elicited when induced and inducing stimulus are as close as possible in all three dimensions of space (adjacency principle: Gogel & koslow 1972; Gogel & MacCracken 1979; Reinhardt-Ruthland 1988), motion parallax increases with increasing distance between two objects. As a consequence, if the contra-directional sway observed in foreground fixation condition (Experiment 1) was elicited by induced movement of the foreground, it should be even greater and more consistent when the earth fixed foreground is coplanar with the moving background than when the foreground and background are at 100 cm from each other.

1. Method

1.1 Subjects

Eight normal subjects (24-50 years of age) with normal or corrected normal vision gave their informed consent to participate in the experiment. Three out of these eight subjects took part in Experiment 1.

1.2. Visual Conditions

Parameters of background motion were the same as in Experiment 1. Subjects were exposed to three visual conditions:
1) Background fixation: Subject were asked to look straight ahead at the background as in the background fixation condition in Experiment 1.
2) Foreground fixation: Subject had to fixate a laser point projected on a small earth-fixed black dot (1 cm of diameter) taped on a piece of perspex and adjusted at eye level. The fixation point was at 50 cm from the subject’s eyes, and at 100
cm from the background. In that visual environment, motion of the background or motion of the subject generate motion parallax.

3) *Coplanar fixation*: The subjects were asked to fixate an earth-fixed laser point projected directly onto the background. In that condition, motion of the background should induce an apparent movement of the earth fixed point in the opposite direction to background motion, but not motion parallax.

Each condition consisted of 21 trials, 7 with motion of the background to the right, 7 to the left and 7 with stationary background (control), divided in two blocks of 10 or 11 pseudo-randomized stimuli. The first three blocks (one per condition) followed by the second three blocks were presented in a Latin-square design. At the end of each block with the laser spot as a fixation point, subjects were asked to report whether they perceived this point as moving with respect to the background and in what direction. An analysis of variance (ANOVA) based on the mean induced response was performed on the three experimental conditions and LSD post hoc test was used for pairwise comparisons. A .05 significance level was adopted throughout.

### 2. Results and discussion

**Subjective reports**

In the coplanar condition, 7 out of the 8 subjects tested reported to see either systematically or from time to time, the earth-fixed laser point moving in the opposite direction of background motion (induced movement). In the foreground fixation condition, only one subject reported to see the laser point as moving.

**Postural re-adjustments**

When subjects were looking straight at the background (background condition), a lateral displacement of both the head and the COP in the direction of motion was elicited (see Fig. 2.6). In the foreground fixation condition with the fixation point placed 100 cm in front of the moving background, a lateral shift of both the head and the COP in the opposite direction of motion was observed (see Fig. 2.6).
Figure 2.6: Grand mean lateral translation of the head (upper panel) and the COP (lower panel) evoked by the displacement of the background in different visual conditions. Upwards deflections indicate a translation in the direction of motion.
In the coplanar condition, when the fixation point was projected onto the moving scene, no consistent sway was observed; 59% of the readjustments were in the direction of motion while 41% were in the opposite direction. When individual data were combined, a small shift in the direction of motion emerges, (see Fig. 2-6) but was not objectivated statistically (COP: \( t(7)=1.7 \ p = .12 \); Head: \( t(7)= 0.8 \ p = .43 \)). Mean head induced responses in both the coplanar and the foreground fixation are plotted in Fig. 2.7. In 7 out of the 8 subject tested, the lateral displacement of the head (and COP) in the opposite direction to motion was more important than in the coplanar condition. Interestingly, the subject for which this was not true, had already a tendency to lean in the opposite direction to motion in the coplanar condition.

The ANOVA indicated that there was a significant effect of the visual condition both for the head (\( F_{2.14}= 17.2 \ p< .01 \)) and the COP (\( F_{2.14}= 31.2 \ p< .01 \)). Mean comparison (LSD) revealed that the difference between the coplanar condition (induced movement) and the foreground fixation condition (motion parallax) was significant both for head and COP recordings (\( p< .05 \)). Finally, a significant
difference was observed between the condition of background fixation and the coplanar condition, both for the head and the COP (p<.05).

In summary, a consistent postural re-orientation in the opposite direction to background motion was elicited only in the presence of depth between the fixation point and the moving background (foreground condition) and not when the fixation point and the moving background were coplanar. This result suggests that motion parallax is a more relevant cue to elicit a contra-directional sway response than induced motion. In addition, the significant difference between the background and the coplanar conditions indicates that fixating a single stationary point projected onto the moving visual scene, often perceived as moving in the opposite direction of motion, was sufficient to reduce the driving effect of a moving visual surrounds.

Table 2.2 Mean induced head/COP response (average and standard deviation) in mm in the different visual conditions of Experiment 2.

<table>
<thead>
<tr>
<th></th>
<th>Background fixation</th>
<th>Foreground fixation</th>
<th>Coplanar fixation</th>
<th>Stationary background</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>SD</td>
<td>M</td>
<td>SD</td>
</tr>
<tr>
<td>Head sway</td>
<td>3.52</td>
<td>3.03</td>
<td>-3.68</td>
<td>2.27</td>
</tr>
<tr>
<td>COP</td>
<td>3.1</td>
<td>1.7</td>
<td>-2.8</td>
<td>1.53</td>
</tr>
</tbody>
</table>

Note - A positive value indicates a deviation in the direction of motion whereas a negative value indicates a deviation in the opposite direction to motion.
F. EXPERIMENT 3: Ocular convergence

The aim of this experiment was to examine the possibility that the contra-directional postural response described in Experiments 1-2 was due solely to ocular convergence in front of the background rather than to motion parallax. Convergence on a fixation point in the foreground produces a defocused double image of the visual background behind. The defocusing reduces spatial frequency corresponding to a reduction in visual acuity which has been found to play a significant role in the regulation of spontaneous body sway in a stable environment (Paulus et al. 1984). In order to test this alternative hypothesis, the fixation point in Experiment 3 was either earth-fixed or head-fixed. In these two conditions, convergence and accommodation remained the same while the background remained out of focus. With an earth-fixed fixated target, body sway causes a retinal displacement of the background in the direction of motion (Fig 2.8 left panel). So, if the background moves in one direction, the subjects assumes he has swayed in that direction and therefore compensates with a postural correction in the opposite direction. In contrast, with the head-fixed target, any postural sway causes a retinal displacement of the background in the opposite direction of motion (Fig 2.8 right panel). If the background moves in one direction, the subjects assumes he has swayed in the opposite direction and would compensate with a postural correction in the same direction of the background.

![Diagram](image)

Figure 2.8: Changes in retinal projections of the background when the fixated foreground is either earth-fixed (left panel) or head-fixed (right panel). The red arrows indicate the retinal displacement of the background during self-motion.
1. Method

1.1. Subjects

Seven subjects with normal or corrected normal vision gave their informed consent to participate in this experiment (21-52 years of age). Three out of the seven subjects tested took part either in experiment 1 or 2. One subject had to stop in the middle of the experiment because of nausea. Since this subject performed one block per visual condition, his data were included in the analysis.

1.2. Visual conditions

Subjects were exposed to three visual conditions:

1) Background fixation: Looking straight ahead at the background as in Experiments 1 and 2.

2) Earth-fixed foreground fixation: Fixating a LED mounted on a piece of perspex adjusted to eye level. The fixation point was at 40 cm from the subject’s eyes, and at 110 cm from the background.

3) Head-fixed foreground fixation: Fixating a LED at 40 cm from the subject’s eyes, attached to the helmet with a rod (like the lure of an angler fish).

Parameters of background motion were the same as in Experiment 1. Each condition consisted of 12 stimuli, 4 to the right, 4 to the left and 4 shams (no motion), divided in two blocks of 6 pseudo-randomized stimuli. The first three blocks (one per condition) followed by the second three blocks were counterbalanced. Observation of the different visual scenes was binocular as in Experiments 1 and 2. A rest of 15 minutes was given to the subjects between the two test sessions.

2. Results and discussion

Figure 2.9 shows the mean head and COP displacement obtained from the seven subjects for each visual condition. The mean induced head response for each subject with both head and earth-fixed fixation is plotted in Fig. 2.10.
Figure 2.9: Grand mean lateral translation of the head (upper panel) and the COP (lower panel) evoked by the displacement of the background in different visual conditions. Upwards deflections indicate a translation in the direction of stimulus motion.
When the fixation point was coupled with head movements (head-fixed foreground), the displacement of the visual scene evoked a body tilt in the direction of motion in the seven subjects tested as in the condition of background fixation. In contrast, when the fixation point was earth-fixed, the displacement of the visual scene induced consistent body sway in the opposite direction to motion.

The ANOVA indicated that there was a significant effect of the visual conditions both for the head ($F_{2,14}= 11.8 \ p<.01$) and the COP ($F_{2,14}= 13.5 \ p<.01$). Mean comparison analysis (LSD) revealed that the three visual conditions differ from each other for the COP. For the head, the earth-fixed foreground fixation condition was different from the other two ($p<.05$), and the difference between the head-fixed foreground fixation and background fixation condition was at the level of significance ($p=.05$). As can be seen in Fig. 2.10, the mean induced head response (but also COP response) in the condition of head-fixed foreground was systematically in the direction of motion as expected. In contrast, in all subjects but one, the mean response was in the opposite direction of motion when the foreground was earth fixed (see also table 2.3).

![Figure 2.10](image.png)

Figure 2.10: Mean head induced response in both the condition of earth-fixed and head-fixed foreground. Positive values indicate a displacement in the direction of background motion while negative values indicate a displacement in the opposite direction.
Chapter 2: Motion parallax and visually induced body sway

As indicated by the mean comparisons, the amplitude of the visually induced body sway in the head-fixed foreground condition was in the same direction as that observed when subjects were looking straight at the background and of even greater amplitude. This difference might stem from the difference of retinal slippage between these two conditions. Indeed, although in the background condition subjects were asked to keep looking straight in primary gaze, the optokinetic nystagmus elicited in such a situation does reduce, if not completely suppress, the retinal slippage. This explanation is however not supported by recent reports. Indeed, it was found that similar visually induced body sway was observed whether subjects were allowed to pursue a moving scene or had their eyes fixed in space (Severac-Cauquil et al. 1998).

In summary, it was found that when the fixated foreground was coupled with head movement, a sway co-directional to background motion was elicited. Then, fixating a near foreground, or in other words, convergence in front of the moving visual surround, is not sufficient to elicit a contra-directional postural response.

Table 2.3: Mean head/COP induced response (average and standard deviation) in mm in the different visual conditions of Experiment 3.

<table>
<thead>
<tr>
<th></th>
<th>Background condition</th>
<th>Head-fixed foreground fixation</th>
<th>Earth fixed foreground fixation</th>
<th>Stationary background</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>SD</td>
<td>M</td>
<td>SD</td>
</tr>
<tr>
<td>Head sway</td>
<td>3.64</td>
<td>4.02</td>
<td>5.96</td>
<td>2.2</td>
</tr>
<tr>
<td>COP</td>
<td>2.66</td>
<td>2.5</td>
<td>4.49</td>
<td>1.9</td>
</tr>
</tbody>
</table>

Note - A positive value indicates a deviation in the direction of motion whereas a negative value indicates a deviation in the opposite direction to motion.
G. EXPERIMENT 4: Monocular versus binocular fixation

The aim of the fourth experiment was to compare the sway responses during foreground fixation when viewed monocularly and binocularly. Since motion parallax is primarily monocular, a contra-directional postural response should be observed both with monocular and binocular vision.

1. Method

1.1. Subjects

Nine subjects with normal or corrected normal vision gave their informed consent to participate in this experiment (15-52 years of age). Four out of the nine subjects tested took part in one of the first three experiments. As the purpose of this experiment was to compare the effect of binocular versus monocular viewing on the postural re-orientation opposite to background motion, one subject who exhibited a systematic co-directional sway both with monocular and binocular vision was excluded from data analysis.

1.2. Visual conditions

The displacement of the background was the same as that used in Experiment 1-3. 100cm in front of the moving background was placed the earth fixed foreground used in Experiment 1. Subjects were fixating the foreground binocularly or monocularly with their dominant eye, the second eye being covered by a patch. Three subjects had a left dominant eye and five had a right dominant eye. Each condition consisted of 15 stimuli, 5 to the right, 5 to the left and 5 shams (no motion), divided into two blocks of 8 or 7 pseudo-randomized stimuli. The first two blocks (one per condition) followed by the second two blocks, were counterbalanced. A rest of 15 minutes was given to the subjects between the two test sessions.
Chapter 2: Motion parallax and visually induced body sway

2. Results and discussion

For both viewing conditions, the displacement of the background evoked a postural re-adjustment in the direction opposite to motion, as in Experiment 1-3 (see table 2.4). The mean COP induced response in the opposite direction to background motion was slightly but significantly larger during binocular than monocular fixation ($t(8)=3.4\ p<.05$). Similar results were observed for the head except that the difference between the two viewing conditions did not reach significance ($t(8)=1.6\ p>.05$). As expected, when the background remained stationary (sham condition), no postural displacement was observed in either viewing condition.

Results of Experiment 4 showed that the contra-directional postural response during foreground fixation was observed both during monocular and binocular conditions. This indicates this postural response is, in the main, monocularly mediated. The trend for larger binocular than monocular responses is in agreement with previous studies on spontaneous body sway showing improved body stability during binocular than monocular fixation (Jones & Lee 1981; Paulus et al. 1984; Fox 1990; Stoffregen et al. 1999).

Table 2.4: Mean head/COP induced response (average and standard deviation) in mm of the head and the COP in the different visual conditions in Experiment 4.

<table>
<thead>
<tr>
<th></th>
<th>Binocular Fixation</th>
<th>Monocular fixation</th>
<th>Stationary background</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>SD</td>
<td>M</td>
</tr>
<tr>
<td>Head sway</td>
<td>-6.4</td>
<td>2.9</td>
<td>-5.4</td>
</tr>
<tr>
<td>COP</td>
<td>-4.9</td>
<td>2.1</td>
<td>-3.8</td>
</tr>
</tbody>
</table>

Note - A negative value indicates a deviation in the opposite direction of motion.
H. EXPERIMENT 5: Background acceleration

In Experiment 1-3, the initial postural shift evoked by the displacement of the background was slower (i.e. less steep) in the foreground as compared to the background fixation condition. Two factors, not mutually exclusive, could explain this difference. The first one is based on differences in baseline body stability in these two conditions. It is well established that an increased instability gives rise to an increased sensitivity to visual disturbances (Lee & Lishman 1975; Bles et al. 1980). In agreement with the literature (Lee & Lishman 1975; Paulus et al 1984) in Experiment 1 we found that when the background was stationary, body stability (sway path length) was improved by the foreground target as compared to the condition of background alone. In addition, in the background condition, the velocity of the initial postural response evoked by the displacement of the background was strongly correlated with the sway path length measured in that condition with stationary background. Therefore, the steeper postural response observed in the background condition can well be the consequence of an increased baseline postural instability.

The different velocities observed in these two conditions could also be explained in terms of retinal flow. Indeed, in a stable environment, a spontaneous displacement of the head at, say, 1 cm/s, while looking straight at a stationary background placed at 150 cm from the eyes, would produce a retinal image motion of ~0.39°/s. This is approximately half the amount of retinal image motion of the background that subjects experience while fixating a foreground object placed at 50 cm from the eyes (~0.76°/s) (see discussion of chapter 3 for equations). Thus, to produce a similar retinal image motion of the moving background in these two visual conditions, the velocity of the visual background should be twice as fast in the foreground fixation condition as in the background fixation condition. If the second explanation were true, it would indicate that the two components of motion parallax, the relative direction of objects motion and their relative velocity were both taken into account by the visuo-motor system to control posture.
The aim of Experiment 5 was to investigate whether the initial body sway evoked by motion parallax could be modulated by the dynamic characteristics of the moving background and particularly by the acceleration. If relative velocity of object motion is taken into account by the postural control system, then the dynamic characteristics of the postural response should vary with different accelerations of background displacement.

1. Method

1.1. Subjects

Eight subjects with normal or corrected normal vision (normal visual acuity and stereopsis) gave their informed consent to participate in this experiment (18-46 years of age).

1.2. Apparatus and procedure

The apparatus used in Experiment 5 was similar to that used in Experiment 1-4. The background was moved at 150 cm from the subject's eyes along an axis parallel to the inter-aural axis, in an otherwise dark room. After 3s stationary (baseline level), the background was moved with three different accelerations. The maximum velocity was fixed at 18 cm/s. The three accelerations to which each subject were exposed were:

1) 4 cm/s^2 lasting 4.5 sec to reach the maximum velocity of 18 cm/s. Then the background decelerated to stop within one second. The total excursion of the background was 52 cm.

2) 8 cm/s^2 lasting 2.25 sec, to reach a constant velocity of 18 cm/s maintained for 2.25 sec and then decelerated to stop within one second. The total excursion was 75 cm.

3) 24 cm/sec^2. This acceleration lasted 0.75 sec to reach a constant speed of 18 cm/sec for 3.75 sec and then decelerated to stop within one second. The total excursion was 98 cm.

In each visual condition, subjects were asked to fixate a cross placed at the centre of the earth fixed luminescent window frame (30 x 24 cm). This foreground
was distant of 50 cm from subject eyes and 100 cm from the background. Each condition consisted of 10 stimuli, 5 to the right and 5 to the left. The total of 30 stimuli with 10 control stimuli with stationary background were divided in two blocs of 20 pseudo-randomized stimuli.

1.3. Data analysis

The main parameter of interest was the velocity (slope) of the initial lateral head/COP shift opposite to background motion. The velocity expressed in mm/s was measured for a period of 750 ms, 1s after the onset of background motion. The velocity estimate was based on the linear regression fitted on the data points covering the 750ms period. This period was chosen for measurement because it was linear (as shown by the regression coefficient > 80) and it excluded the initial counter-push perceptible at the level of the COP 500-700ms after stimulus onset and also the ambiguity of the rounding off at the bottom of the slope. The analysis period of 750ms from 1s following the onset of background motion was chosen because no further postural correction other than that of interest could be detected within this time. In addition, the mean head/COP induced response were computed for a period of 3s from 1.5s following stimulus onset to stimulus deceleration, time slice after the postural response built up. Responses to rightwards and leftwards stimuli were combined (after reversing all sway responses during leftward motion).

An ANOVA with the within subject factor ‘acceleration’ was performed both for the velocity and the mean induced response parameters. LSD post hoc test was used for pairwise comparisons. A .05 significance level was adopted throughout.

2. Results and discussion

Fig. 2.11 shows the mean head and COP lateral displacements obtained for the 8 subjects for the three accelerations conditions (4cm/s², 8cm/s² and 24cm/s²). Data are reported in table 2.5. Whatever the acceleration considered, the displacement of the background induced a postural readjustment in the opposite direction to motion. Although the latency of the response appeared slightly delayed when the acceleration was minimum, the velocity of the initial response was similar
in the three conditions. The ANOVA indicated that the factor acceleration had no effect on the velocity of both the initial head \( F_{2,14}=0.9 \) \( p>0.05 \) and COP \( F_{2,14}=0.7 \) \( p>0.05 \) displacements in the direction opposite to background motion.

As can be seen in Fig. 2.11, the mean shift following the initial postural response appeared to be greater when the acceleration was minimum as compared to the other two conditions. However, ANOVA analysis indicated that the mean induced response did not differ significantly between the three experimental conditions, neither for the head \( F_{2,14}=1.03 \) \( p>0.05 \) nor for the COP \( F_{2,14}=0.3 \) \( p>0.05 \).

In summary, Experiment 5 showed that the velocity profile of the initial body sway in the opposite direction to background motion when fixating an earth-fixed foreground target was similar in the three conditions of acceleration manipulated. Thus, the initial postural response induced by visual motion appears to be determined by the direction of motion on the retina (as shown in experiment 1-4), but not by more dynamic characteristics of visual motion such as acceleration, at least within the range of acceleration tested. This result also favor the hypothesis that the velocity of the initial postural response evoked by visual disturbances is partly determined by the baseline postural stability.

Table 2.5: Mean head/COP response and slopes (average and standard deviations) in mm in the three conditions of acceleration manipulated of Experiment 5.

<table>
<thead>
<tr>
<th>Condition</th>
<th>M (mm)</th>
<th>SD</th>
<th>Slope (mm/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Head sway</strong></td>
<td>4 cm/s²</td>
<td>-2.9</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>8 cm/s²</td>
<td>-2.9</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>24 cm/s²</td>
<td>-2.1</td>
<td>2.1</td>
</tr>
<tr>
<td><strong>COP</strong></td>
<td>4 cm/s²</td>
<td>-2.4</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>8 cm/s²</td>
<td>-1.9</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>24 cm/s²</td>
<td>-1.8</td>
<td>2.2</td>
</tr>
</tbody>
</table>

Note - A negative value indicates a deviation in the opposite direction of motion.
Figure 2.11: Grand mean lateral translation of the head (upper panel) and the COP (lower panel) evoked by the displacement of the background with different accelerations while subjects were fixating the stationary foreground. Lower traces are the different velocity profiles used in the experiment. Downwards deflections indicate a translation in the opposite direction of stimulus motion.
I. DISCUSSION

1. Motion parallax as a relevant cue for postural control

In the five experiment presented in this chapter, we attempted to define further the significant factors determining the contra-directional postural response previously reported by Bronstein and Buckwell (1997) when a stationary fixated foreground was placed between a moving background and a standing subject. Through Experiment 1-4, results showed that this contra-directional postural response was not just a transient response but could be sustained at least for the 11 sec of background motion. These results indicate that the postural response observed reflects not a transient instability, but a postural repositionning. The results of the experiments presented also provide converging evidence that this contra-directional sway elicited by earth-fixed foreground fixation against a moving background was due to motion parallax. The key arguments are: 1) the presence of an earth-fixed foreground target reversed the postural response induced by the moving background when the direction of displacement of the two objects on the retina mimics what an observer would experience during self-motion in a stable environment (foreground fixation). When the direction of displacement of the two objects on the retina are inconsistent with what a moving observer would experience, the postural response was found to be inconsistent ('fixation through the window' condition). 2) the effect is not mediated by induced movement. Although most of the subjects reported an induced movement illusion when the fixation point was coplanar to the moving background, no systematic contra-directional postural response was observed (Experiment 2). 3) the contra-directional postural response is not caused by ocular convergence / accommodation on a foreground target against a defocused moving background since co-directional sway was elicited with a head-fixed target (Experiment 3). As expected, this contra-directional postural response could be observed monocularly as well as binocularly (Experiment 4). Thus the necessary condition for reversed sway seems to be a differential motion of foreground with respect to the background similar to that which would be provoked by self-motion of the observer.
2. Directionally specific sway in response to an ecological stimulus.

As mentioned above, the possibility remained that the induced movement of the foreground rather than motion parallax was the relevant cue to reverse the postural sway to background motion. The purpose of Experiment 2 was to test this alternative explanation. Although most subjects reported the illusory motion of the fixation point when coplanar to the moving background, no consistent, direction-specific postural response was observed. Unlike motion parallax, induced movement can exist in the absence of an observer’s own motion. Our results do not exclude the possibility that induced movement, in some trials or circumstances, can induce a contra-directional postural response as proposed by van Asten et al. (1988a) for the sagittal plane (i.e. induced motion in depth). However, its contribution in the lateral direction appears to be at least of lesser importance than motion parallax.

No directionally specific postural response was also observed with background fixation through the window (Experiment 1). The relative movement of the two objects in that condition does not correspond to what a subject could see with any real self-body movement. As shown in Figure 1.4, when a subject is moving his head while fixating a far object beyond a near object, the image of the fixated point remains stable on the retina while the image of the near object moves in the opposite direction to head motion. To reproduce what would be seen during self-motion when looking at a far object, (as with background fixation through the window), the near object should move.

These findings suggest that in order to induce consistent and directionally specific responses, the relative motion of objects within the foreground and the background must reflect what a moving observer would experience in a natural 3 D environment. It must be noticed that the retinal displacement of the moving background (21 degrees) in Experiments 1-4 was larger than what a subject would

---

2 It is possible to experience such foreground background displacement but only when passively transported and looking through the window of the vehicle.
experience during spontaneous sway (Bles et al. 1980). However, it has been reported that stimulus amplitude is not a relevant parameter for visuo-postural responses (Lestienne et al. 1977; Van Asten et al. 1988; Masson et al. 1995).

3. A peripheral dominance of postural control?

The retinal periphery has been considered to be dominant for self-motion perception and the control of posture (Brandt et al. 1975; Dichgans & Brandt 1978). Andersen & Dyre (1989) found however, that visually induced body sway could be elicited when stimulation was restricted to a small area of the central visual field (15°). Moreover, optical information for the control of posture appears to be also a function of the geometry of the optical flow field (Stoffregen 1985, 1986; Gielen & Van Asten 1990, Masson et al. 1995). Stoffregen (1985) demonstrated that the retinal periphery itself shows no particular facility for detecting posturally relevant information if the visual flow is radial as opposed to lamellar. The central versus peripheral distinction also applied for near and far vision. Delorme and Martin (1986) found that both the retinal periphery and depth of the visual field played an important role in the visually induced body sway. These authors showed that forward and backward movement of the scene limited to the foreground produced little postural sway in the antero-posterior direction compared with motion located in the background. In the foreground fixation condition in Experiment 1-3, the close (in term of depth) and central object (in terms of retinal location), reversed the driving effect of the peripheral and far visual scene.

Our results suggest that the amplitude of postural readjustment in both the condition of background and foreground fixation was under the control of the moving background as shown by the similar amplitude of both the co-directional and contra-directional sway and also by the significant correlation observed between these conditions. However, the spatial relation between the background, the foreground and the observer’s fixation point determined the direction of the postural readjustment. These results provide new evidence that the control of stance is dependent not only on the retinal location of objects, on the geometrical structure of
the visual flow but also on the observer’s fixation point in a 3 dimensional environment. Then, when present in the visual environment, motion parallax is a powerful cue to specify the direction of sway in the frontal plane.

4. About the nature of the initial body response.

Although the relative direction of objects appears to be critically involved in the control of postural orientation, more dynamic components of motion parallax, such as the relative acceleration between objects as tested in Experiment 5, do not affect the postural re-adjustments. Indeed, at least within the range of acceleration tested in Experiment 5, from $4\text{cm/s}^2$ to $24\text{cm/s}^2$, no difference in the velocity profile of the initial postural response could be detected. An explanation could be that the initial body response to visual stimuli is a 'quantal' behavioural tactic (invariant in amplitude and velocity over a wide range of stimuli) based on the occurrence of motion. To our knowledge, the idea of an initial 'quantal' behavioural tactic as the basis of fundamental mechanism of simple postural re-orientations has not hitherto been suggested. At first glance, the steeper initial postural response observed in Experiment 1 in background condition in comparison to that observed in foreground condition seems to be inconsistent with this idea. However, one must remember that in Experiment 1, the velocity of the initial postural response evoked by the onset of the visual scene displacement was closely linked to the baseline postural stability (at least in background condition). In conclusion, it seems that the initial induced postural response, observed within 0.5 to 1 sec after stimulus onset depends more on the baseline or background stability than on the dynamic characteristics of the visual disturbance.

5. Relation between illusory self-motion and postural adjustment.

In addition to a postural readjustment, a moving visual display can induce an illusion of self-motion, also called vection, in the opposite direction to motion of the visual display (Dichgans & Brandt 1978). An everyday example is the illusion of self-translation induced by perchance sighting of a moving train through the window of a stationary one. As reported by Berthoz et al (1979), the features of fore-aft
postural readjustments and the magnitude estimation of vection induced by a linearly moving visual surround are closely related. In both cases, the influence of the stimulus becomes larger with increasing area, velocity and spatial frequency of the stimulus (Berthoz et al. 1975; Lestienne et al. 1977). Recent work also confirmed the close relationship between these two phenomena (Previc 1992; Kuno et al 1999). On the basis of such similarities, Kuno and collaborators (1999) recently concluded that vection induces visually induced body sway (but not the reverse): the subject perceiving an illusory self-displacement in one direction, compensate by initiating a postural correction in the opposite direction.

Although some relationship might exist between vection and visually induced body sway, some experimental data suggest show that the latter can not be the consequence of the former as do Kuno and collaborators (1999) claim. For instance, subjects may report vection without postural change, or change their posture without reporting vection (Berthoz et al. 1979). Also, vection takes usually a few of seconds to build up, while initiation of visually induced body sway can be observed ~250ms after the onset of stimulus motion (see discussion of chapter 5; also Previc 1992; Previc & Mullen 1990-91). Finally, it has been shown that with a slow moving stimulus, the magnitude of vection, in the direction opposite to background motion, was increased when subjects were fixating a stationary objet in the foreground (Howard & Howard 1994). In agreement, in the different experiment presented in the first chapter of this thesis, a few subjects reported spontaneously a vection in the opposite direction to background motion (stimulus duration: 11sec) but only when they were fixating the foreground object, not when the background was alone. with a stimulus duration of 11s, This anecdotal finding is particularly interesting since it shows that both the illusory sensation of self-motion and the visually induced body sway can be in the same direction, both in the opposite direction to motion. Therefore, although vection might effectively modulate the amplitude of the postural response, it is neither inductive nor can determine its direction.
Chapter 3

Motion parallax and spontaneous body sway

A. ABSTRACT

The experiment related in chapter 2 indicated that motion parallax plays an important role in postural orientation in standing subject. In the present chapter, we investigate whether motion parallax generated during spontaneous body sway in a 3D environment could be used in a closed loop as feedback by the visuo-motor system to control body oscillations. In Experiment 1, motion parallax was investigated in isolation while other parameters such as image angular size and target distance were controlled. Twelve subjects fixated a two-LED target placed at 45cm from their eyes in a dark room. A second similar two-LED target was placed either at 170 cm (Maximum parallax) or at 85 cm (medium parallax) from the fixated target, or in the same plane of the fixated target (0cm, no parallax). Results showed that the amplitude of sway was reduced significantly when the two targets were presented in depth (parallax present) as compared to when they were in the same plane (no parallax). The effect was only present in the lateral direction and for low frequency components of sway (up to 0.5 Hz). We confirmed in Experiment 2 on eight subjects with a design similar to that used in Experiment 1 that the effect of motion parallax on body sway was of monocular origin since observed with monocular and binocular vision.
B. INTRODUCTION

Visual stabilization of posture depends largely on how effectively body oscillations can be detected in a given environment. As mentioned in the first chapter, an important visual cue underlying visual stabilization is the retinal target displacement. Among the different physical and physiological parameters from which depends retinal target displacement, motion parallax has probably received the least interest. However, if one considers a natural 3D environment, with objects placed at different distances from each other, the magnitude of motion parallax can be substantial.

Even when standing up quietly, an observer is always swaying slightly (spontaneous body sway), generating an apparent displacement on the retina of the objects in the environment. In a 3 dimensional environment, with objects placed at different distances from each other, the slight spontaneous body sway generates motion parallax. We have seen in chapter 2 that motion parallax was a relevant cue to regulate postural orientation. Indeed, when we reproduce the motion parallax a subject would experience during spontaneous body sway in a 3D environment, we observed directionally specific postural responses. The aim of Experiment 1 and 2 presented in this chapter was to investigate whether motion parallax cues produced during 'spontaneous body sway' in a stable 3 dimensional environment could be used in a closed loop as feedback by the visuo-motor system to control the overall body oscillations.

Several physical and physiological parameters can affect visual stabilization of the body. However, if the stabilizing effect of each of those parameters were linearly summated, the theoretical stabilization would largely exceed the capability of the postural system. For instance, although the central part of the retina is largely involved in postural stabilization when stimulated in isolation, an optimal visual stabilization can be achieved when the complete visual field except the central area is stimulated (Paulus et al. 1984). Hence, the visual field provides enough redundancy for compensation of scotomas. Similarly, in a rich 3D environment, several parameters such as eye-object distance, object size, in addition to motion
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parallax could affect stability, but probably not in an additive manner. Sakellari (Experiment 1 reported in Guerraz et al. 2000) found that motion parallax when confounded with other factors such as eye-object distance or visual size, did not have a significant effect on equilibrium. Therefore, it is important to investigate motion parallax in isolation from other visual cues.

In an attempt to isolate motion parallax, Fox (1990) used 3 LEDs aligned in depth in a dark environment, distant of 25.4 cm from each other, the first one (the fixation point) being at 145 cm from the subject’s eye. With this set-up, left/right displacement of the observer creates motion parallax and the absolute change in size of the visual display is largely reduced. Comparison between this visual condition and either the condition with only the fixated LED visible or with three LEDs placed at 145 cm from the eye aligned in the frontal plane, showed no significant difference in stability. Accordingly, it was concluded that motion parallax did not affect postural sway. A limitation of this research was that the amount of motion parallax was not optimized. Indeed, motion parallax is proportional to the distance between the different objects and inversely proportional to the distance between the fixated one and the observer. Inversely, Fox used a large distance between the fixation point and the subject (145 cm) and a small one between the different targets (25.4 cm).

In Experiment 1 and 2, motion parallax was isolated from other visual cues as in Fox’s experiment, and both the distance between the observer and the fixation point and the distance between the different LEDs have been optimized as to obtain a great amount of motion parallax during spontaneous body sway. In Experiment 2 we investigated the effect of motion parallax on postural stability both with monocular and binocular vision.
C. GENERAL METHOD

1. Apparatus

In order to isolate motion parallax, the only visual cues available in the different experimental conditions of Experiments 1 and 2 consisted of light emitting diodes (LEDs) mounted on pieces of perspex in an otherwise dark room. Two sets of two LEDs were used; one set was positioned at a fixed distance from the eyes, whilst the other set was placed at variable distances behind the first set (see Fig. 3.1). With this set-up, the absolute change in size of the visual display was largely reduced. Each set of LEDs consisted of a pair of LEDs on the same plane, vertically separated by 2 cm, offering minimal cues to verticality.

2. Procedure

In Experiment 1 and 2, subjects were instructed to ‘stand still and relaxed’ with hands at their side. They stood barefoot on a rigid foot support placed on top of a slab of foam rubber (height 5 cm; specific weight 30 g/dm3) resting on the sway platform. Postural sway in the lateral and sagittal direction was recorded using the AMTI force platform (model BP2436) for COP recordings. Subjects wore also a lightweight helmet, on top of which was mounted an infra-red light emitting diode so that head displacements could be measured. Displacements of the light were transduced by imaging a top view of the subject onto the photo-sensitive surface of the 2-dimensional Schottky barrier photodetector (United Detector Technologies) situated 40 cm above the head. Since the distance between the head mounted infra-red light and the Schottky camera was maintained at 40 cm, head sway values were normalised for subjects’ heights (signal * mean height of group / individual’s height).
3. Parameters of body sway

Postural equilibrium in the lateral and sagittal direction was evaluated as the average deviation, the sway path and also in the frequency domain.

1) The average deviation \( \langle Xm \rangle \) denotes the absolute displacement of the coordinates around the average during the analysis period:

\[
\text{Equation 2: } \langle Xm \rangle = \frac{1}{N} \sum_{i=1}^{N} |x_i - Xo|
\]

where \( N \) is the number of samples, \( x_i \) is the COP/head position for the \( i^{th} \) sample, and \( Xo \) is the average position (COP or head) during the time of recording.

1) The sway path \( (SwP) \) computed for the lateral and sagittal direction is the length of the path described by the COP or the head, and is defined as the sum of the distances between sequential points sampled during the analysis period. See equation 1 in chapter 2.

2) To calculate power spectra, a 50s epoch (1000 points) were detrended using a line of best fit and then windowed with a Hanning function. A fast Fourier transform (FFT) algorithm was then applied (MATLAB Mathworks Inc.). The resulting power spectrum had a frequency resolution of 0.02 Hz (i.e. there were spectral lines at each 0.02 Hz interval), and bandwidth 0 to 10 Hz. For subsequent analysis, only the 0 to 2 Hz range was considered. For statistical analysis the frequency components from 0.02 to 2 Hz were grouped into 8 bands, each spanning 0.25Hz. The Power in each of these bands was then calculated by summing the spectral lines.
D. EXPERIMENT 1: Motion parallax and spontaneous body sway

1. Method

1.1. Subjects

Twelve normal subjects (7 females, 5 males, average age 35 years) with normal or corrected vision (normal visual acuity and stereopsis) gave their informed consent to participate in the experiment in accordance with the local ethics committee. All subjects were healthy without musculoskeletal or neurological disorders.

1.2. Visual Conditions

In the three experimental conditions manipulated in Experiment 1, subjects were instructed to binocularly fixate the LEDs positioned at a constant distance of 45 cm from the eyes, adjusted to the subjective level of the eyes (see fig 3-1). The second set of LEDs, were placed as follow:

- **Maximum parallax**: The second set of LEDs was placed at 170 cm behind the first set of LEDs that the subject was fixating.
- **Medium parallax**: The second set of LEDs was at the distance from the fixated ones of 85 cm.
- **No parallax**: The two sets of LEDs were placed coplanar, 1 cm apart, at 45 cm from the eyes (0 cm).

Sway was also recorded in full room illumination while the subject fixated the LEDs at 45 cm and, also, with eyes closed as control conditions. Recording time for each visual condition was 1 minute. Subjects were standing in a large room (H=4.5 m, L=10 m, W=5 m), facing the front wall at 2.3 m, with lateral walls at approximately 5 m on each side. Signals were sampled at 20 Hz.
2. Results

Since the specific purpose of Experiment 1 was to isolate the motion parallax component, only the experimental conditions, maximum (170 cm), medium (85 cm) and no parallax conditions (0 cm) were subjected to statistical analysis. The other two visual conditions, with full light illumination and with eyes closed, were presented for qualitative comparison. For each parameter of body sway, an analysis of variance (ANOVA) was performed on the three visual conditions. For the analysis of power spectra, a two factor design with repeated measures was used, with the factor ‘frequency’ (8 frequency bands) in addition to the factor ‘visual condition’. LSD post hoc test was used for pairwise comparisons. Figure 3.2 depicts the data from the 12 subjects for both the COP and head displacements in the lateral direction of sway. Mean deviation (top panels) and sway path length data are reported (bottom panels).
Chapter 3: Motion parallax and spontaneous body sway

2.1. Average deviation

In the lateral direction of sway, a large decrease of body sway can be observed when subjects were fixating LEDs in darkness or in full light as compared to the control condition with eyes closed (see Figure 3.2). More interesting, the mean deviation of both the COP and the head decreased with motion parallax. Indeed, the mean deviation was smaller in condition of maximum parallax (170cm) compared to the condition of medium parallax (85cm), the latter in turn being smaller than the no parallax condition (0cm). Body sway was reduced by approximately 33% and 28% for the head and the COP respectively in the condition of maximum parallax as compared to the condition of no parallax. The reduction between the condition of no parallax and that of medium parallax was of 18% and 11% for the head and the COP respectively. ANOVA analysis showed that this decrease in 'average deviation' of the COP with motion parallax was significant ($F_{2,22} = 6.09 \ p < .01$). Post hoc mean comparison (LSD) indicated that only the condition of maximum parallax was significantly different from the other two, medium parallax and no parallax ($p < .01$). The effect of motion parallax was also significant for head sway ($F_{2,22} = 7.38 \ p < .01$) although the only significant difference was between the conditions of maximum parallax and no parallax ($p < .01$). Supplementary analysis, showed that there was no difference between the condition of maximum parallax and the condition of normal light, both for COP ($r(11) = 1.1 \ p = .33$) and head sway ($r(11) = .7 \ p = 0.48$).

In the antero-posterior direction of sway (sagittal plan), increasing the distance between the fixation point and the far LEDs did not affect the amount of sway both for the COP ($F_{2,22} = 0.32 \ p = 0.70$) and the head ($F_{2,22} = 0.3 \ p = 0.73$). Since motion parallax had no effect in the antero-posterior direction of sway, data were not presented.
Figure 3.2: Mean deviation (top) and sway path length (bottom) for the lateral direction of sway, both for the head (left panels) and the COP (right panels) in the condition of maximum, medium and no parallax. The light condition is shown for comparison. The dashed lines correspond to the condition with eyes closed. Errors bars are standard errors of the mean.
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2.2. Sway path length

The bottom panels in Figure 3-2 depict the influence of motion parallax on the sway path length in the lateral direction of sway. As for the mean deviation parameter, there was a clear reduction of the sway path length when visual information were available in comparison with eyes closed, both for the head and the COP. Beyond this well known effect, ANOVA analysis indicated that there was a significant effect of motion parallax for head recordings \(F_{2,22} = 4.9\ p <.05\). Pairwise comparison (LSD) indicated that both the condition of maximum and medium parallax were significantly different from the condition of no parallax \(p <.05\). There was no difference between the condition of maximum and medium parallax \(p >.05\). In contrast, the effect of motion parallax had no effect for COP recordings \(F_{2,22} = 1.5\ p >.05\). Indeed, as can be seen in Figure 3-2, (right panel), the sway path length tend to be even shorter in the condition of no parallax in comparison with the two conditions of parallax.

The apparent discrepancy between the parameter average deviation, affected equally by motion parallax at COP and head sway levels, might be due to the fact that sway path is more influenced by high frequency sway activity. The latter is notoriously more pronounced in COP recordings than in head sway recordings (Koles & Castelein 1980; Day et al. 1993).

As observed previously with the mean deviation, motion parallax had no effect on the antero-posterior sway path both for the head \(F_{2,22} = 0.75\ p >.05\) and the COP \(F_{2,22} = 0.44\ p >.05\).

2.3. Power spectra

An analysis of variance (ANOVA) was used to selectively investigate the effect of the maximum, medium and no parallax conditions at different sway frequencies. The ANOVA model was a two-factor, within-subject design with 'visual condition' and 'frequency' (0-0.25 Hz to 1.75-2 Hz) as factors.
Average power-spectra of both the maximum parallax and no parallax conditions are reported in Figure 3.3 including full-room illumination and eyes closed conditions for comparison. We can see in this figure that both COP and head sway are smaller in the maximum parallax condition than in the no parallax condition for low frequency components of sway, up to 0.5 Hz. For the sake of clarity, power spectra data in the condition of medium parallax was omitted from Fig. 3.3 as these values were always within those of maximum and no parallax conditions.

Figure 3.3: Average power spectrum of displacement of the COP in condition of eyes closed, eyes open with maximum parallax, no parallax and full light. Power spectral density is expressed in arbitrary units with a frequency resolution of 0.02 Hz.
ANOVA analysis revealed that at the level of the head, the main effect of motion parallax did not reach significance ($F_{2,22} = 2.3$ $p >.05$) but interacted significantly with the factor frequency ($F_{14,154} = 1.93$ $p <.05$). This interaction indicated that motion parallax had a significant stabilizing effect on head sway but only at low frequencies, up to 0.5 Hz. Pairwise comparisons showed that the difference between the conditions of maximum and no parallax was significant only for the first two frequency bands analysed (0-0.25 Hz and 0.25-0.5 Hz). As can be seen in Figure 3.3, head oscillations above 1 Hz are extremely limited and no differences between any visual conditions, (including eyes closed and full room illumination) can be detected.

In force platform measurements (COP), the stabilizing effect of motion parallax was also restricted to low frequencies, up to 0.5 Hz (Figure 3.3). At higher frequencies (0.5 - 2 Hz), a reversed tendency was observed, i.e. an increased activity with increasing parallax, but this was not substantiated statistically. The ANOVA revealed that motion parallax was not significant as a main effect ($F_{2,22} = 1.3$ $p <.01$) but interacted significantly with the factor frequency ($F_{14,154} = 3.28$ $p < .01$). Post hoc pairwise comparisons between the maximum and no parallax conditions revealed significant differences only for the lowest two frequency bands, 0 – 0.25 Hz and 0.25-0.5 Hz ($p <.05$).
E. EXPERIMENT 2: Monocular versus binocular vision

The rationale of Experiment 2 was to investigate whether the effect of motion parallax on body sway is present with monocular and binocular vision.

1. Method

1.1. Subjects

Eight normal subjects (2 females, 6 males, average age 33.6 years) with normal or corrected vision participated in Experiment 2. All subjects gave informed consent for the experiments, following approval by the local ethics committee.

1.2. Visual Conditions

As in Experiment 1, motion parallax was manipulated by adding a second set of LEDs behind the fixated LEDs at a distance of 300 cm. This condition with motion parallax was compared to one of fixation of the LEDs placed at 100 cm from the subject without any further visual cues (The two sets of LEDs were coplanar. No parallax). The distance between the fixation point and the eyes was constant at 100 cm from the subject’s eyes. Sway was also recorded with eyes closed and in a condition of background wall illumination while fixating the LEDs at 100 cm. The illuminated background wall, fully textured, was at 550 cm from the fixation point, providing important motion parallax. Subjects were asked to stand still and relaxed in the middle of a large room (H=4.5 m, L=10 m, W=5 m), facing the front wall at 6.5 m.

In addition, subjects were instructed to fixate binocularity or monocularly (dominant eye) the set of LEDs placed at 100 cm. Monocular fixation was obtained by covering with a patch the non-dominant eye. The order of binocular and monocular fixation as well as the order of the visual conditions (motion parallax or no parallax) were counterbalanced. Recording time for each visual condition was 1 minute. Signals were sampled at 125 Hz.
2. Results

2.1. Average deviation

Figure 3.4 shows the data from the 8 subjects respectively for the head and COP displacements. Only the two experimental visual conditions, motion parallax and no parallax conditions with binocular and monocular vision were subjected to statistical analysis.

In the lateral direction, the mean deviation of both the COP and head displacement decreased with motion parallax as compared to the condition of no parallax. This decrease with binocular vision was of 28% and 21% for the head and the COP respectively. With monocular vision, it was of 36% and 28% for the head and the COP respectively. ANOVA indicated that the main effect of parallax was significant for both head (F_{1,7} = 17.2 p < .01) and COP recordings (F_{1,7} = 47.2 p < .01). No difference was found between monocular and binocular viewing, neither as a main effect (Head: F_{1,7} = .84 p > .05; COP: F_{1,7} = .37 p > .05) nor in interaction with the factor parallax (Head: F_{1,7} = .15 p > .05; COP: F_{1,7} = .13 p > .05).

Interestingly, the average standard from the mean position (equation 2) of both the head and the COP in the condition of no parallax does not differ from that observed in the condition with eyes closed (see Fig. 3.4). This indicates that an eye-target distance of 100cm, with a single set of LEDs as the only visible object, is already too long to give rise to efficient stabilization of the body.

In the antero-posterior direction of sway, neither the main effect of parallax nor the main effect of vision was significant for both COP and head recordings. However, a interaction between these two factors reached significance for the head (F_{1,7} = 6.1 p < .05) but not for the COP (F_{1,7} = 4.2 p > .05). This interaction was due to a reduction of the amplitude of head sway with binocular vision as compared to monocular vision in the condition of no parallax. No difference appeared in the condition of motion parallax.
Figure 3.4: Mean deviation (top panels) and sway path length (bottom panels) in the lateral direction of sway both for the head (left panels) and the COP (right panels) with monocular and binocular vision. Visual conditions consisted of no parallax, motion parallax and full room illumination (Light). The dashed lines represent the mean deviations with eyes closed. Error bars represent the standard deviation.
2.2. Sway path length

Sway path length analysis confirmed the absence of difference between binocular and monocular vision in the lateral direction both for COP and head recordings, as a main effect as in interaction with the factor parallax. The effect of motion parallax was small and at the level of significance for head sway ($F_{1,7} = 5.4 \ p = 0.05$) and was not significant at the level of the COP ($F_{1,7} = 0.3 \ p = 0.61$).

2.3. Power spectra

Spectrum analysis was obtained as in Experiment 2. The ANOVA model was a three-factor, within-subject design with vision (binocular vs monocular vision), ‘visual condition’ (motion parallax and no parallax) and ‘frequency’ (0-0.25 Hz to 1.75-2 Hz) as factors.

Spectrum analysis confirmed 1) the absence of difference in the lateral direction between binocular and monocular vision both at the level of the head and COP, as a main effect as in interaction with the other two factors (motion parallax and frequency) 2) a significant effect of motion parallax at the level of the COP in interaction with the factor frequency ($F_{7,49} = 4.9 \ p < 0.01$) indicating that the effect of motion parallax was restricted to low frequency components of sway ($< 0.5 \ Hz$). At the level of the head, the interaction was only close to significance ($F_{7,49} = 1.9 \ p = 0.09$).
F. DISCUSSION

The main findings in this study were that lateral sway was reduced by the presence of motion parallax cues. The effect of motion parallax was observed both in condition of monocular and binocular vision. In experiment 1 and 2, motion parallax was manipulated in isolation by keeping angular size and eye-fixation target distance constant. A decrease of lateral body sway was observed with increasing distance between the fixated LEDs and the distant LEDs both with binocular (Experiment 1 and 2) and monocular vision (Experiment 2). This effect was observed for the sway parameter ‘average deviation’ and for the additional lateral ‘sway path’ parameter. For the former the effect was observed both for COP and head sway whereas, for the latter, it was statistically significant for head sway only. This difference was likely due to the higher sensitivity of the parameter ‘sway path’ to high frequency activity, which are particularly important in force plate recordings, as compared to the parameter ‘average deviation’. Indeed, spectral analysis revealed that motion parallax did reduce low frequency components of sway (0 to 0.5 –0.5 Hz), both for force plate and head sway recordings, but not higher frequency components.

In Experiment 1, subjects were fixating the different targets with binocular vision. Thus, in addition to motion parallax information, retinal disparity information was also available. Both motion parallax and binocular disparity provide information about the three-dimensional structure of the visual environment. However, unlike motion parallax, binocular disparity is essentially static and relies on discrete difference between the image of objects on each retina. When subjects fixate binocularly a close target, objects further away or closer to the fixated target are perceived as double. The similarity between monocular and binocular vision observed in Experiment 2, reveal the monocular origin of the stabilising effect provided when additional depth cues were provided, attesting that motion parallax was the relevant visual cues used by the subject to stabilise their posture.
Chapter 3: Motion parallax and spontaneous body sway

1. Afferent and efferent visual control of body sway

Two different mechanisms subserving visual stabilization of posture in the lateral direction were proposed by Paulus et al. (1989) and Rushton et al. (1989): afferent and efferent motion perception. As depicted in Figure 3.5 (top diagram), when a subject is fixating a visual target, the eyes will track it while the head is moving sideways. If we assume that the tracking is perfect during self-motion, the lateral head movement is visually detected by the amplitude of the eye movement (extra-retinal signal): efferent motion perception. Little or no retinal shift of the fixated target occurs on the retina. The value of the angle $\alpha$ (eye movement) is a trigonometric function of eye-target distance and is represented in Fig. 3.5 (top) by:

$$\alpha = \text{Arc tan} \left( \frac{d}{x} \right)$$

where $d$ represents lateral head movement and $x$ represents eye-target distance. As mentioned above, fixation of a tiny light spot (LED) in an otherwise completely dark surround stabilises posture up to a limit of 2m - 2.5m (Bles et al. 1980; Brandt et al. 1980; Paulus et al. 1984; 1989). Then, as can be seen in Figure 3.5, the amplitude threshold for efferent motion perception (extra-retinal motion perception), is an angle $\alpha$ of approximately 0.3 degrees for 1 cm head sway amplitude that is in the physiological range of postural sway in the lateral direction.

The presence of a second target behind the point of fixation generates relative motion between the two objects when the observer is moving, i.e. motion parallax. Then, the magnitude of head movement can be detected not only by the amplitude of the eye movements (efferent motion perception) but also by pure retinal information provided by the relative motion of the two objects: afferent motion perception (see also Rushton et al. 1989). The amplitude of the relative motion of the two objects (Fig. 3.5, bottom), angle $\delta$, is related to the distance between the two objects ($D$) and to the distance between the fixation point and the subject ($x$). Angle $\delta$ is given by:
\delta = \text{Arc tan} \left( \frac{dD}{x(x + D)} \right)

The results of Experiment 1 and 2 are in accordance with the presence of two modes of visual stabilization in the control of posture. The improvement of lateral body sway by fixating LEDs in the same plane (0 cm) as compared to eyes closed attests principally to the efferent motion perception mechanism. The decreasing sway observed with increasing depth between LEDs attests to the afferent (retinal) motion perception mechanism in action.

It should be noted that, for geometrical reasons, \( \delta \) (relative movement of the two objects on the retina), is always smaller than \( \alpha \) (Figure 3.5). However, the threshold of perception for relative motion between two objects is lower than that of absolute motion of a single object (Abadi et al. 1999; Johnson et al. 1982; Snowden 1992). Therefore, we can postulate that the threshold of visual detection of body sway is lower for afferent motion perception (angle \( \delta \)) than that efferent motion perception (angle \( \alpha \)). One might envisage that when eye-target distance is large enough not to provide the required amount of extra-retinal information (> 2m-2.5m), the relative movement between the foreground and a background far away could still provide pure retinal information about body sway. In Experiment 2, when the fixated LED is at a distance of 1m, seen in isolation, this LED did provide little or no stabilisation of the body as compared to the condition with eyes closed (see Fig. 3.4). In contrast, when a second set of LED was placed 3 m behind the fixation point, body sway as measured with the average deviation was improved in comparison to body sway with eyes closed. Thus, for sufficiently large body sway with respect to eye-target distance, the afferent and the efferent perception systems would provide two sources of visual information about body displacements while the afferent system might remain the only one used for small lateral body sway.
Figure 3.5: Geometrical relationship between the eye and a fixation target (cross) during lateral head sway over a distance ‘d’. TOP (no background, no parallax): the amplitude of eye displacement (angle $\alpha$) is plotted as a function of eye-target distance. BOTTOM (background object and parallax present): The angle $\delta$, which represents the angle travelled by the background object on the retina, is plotted as a function of eye-fixation target distance for three different inter-object distances ‘D’. For these plots ‘d’ = 1cm.
2. Motion parallax affects only slow body re-orientation

The effect of motion parallax appears to be limited to low frequency components of sway (< 0.5Hz) both for the head and the COP. On the basis of this frequency specificity (Experiment 1 and 2), and the readjustment of body orientation observed in Experiment 1-5 (chapter 2), it seems that motion parallax is particularly involved in slow re-orientations of the body but to a lesser extent, if so, in rapid stabilization (>0.5 Hz), particularly important for the COP. These results are similar to those observed with stroboscopic light. Indeed, under stroboscopic light with flashes at a frequency lower than 6Hz, slow re-orientation of the body is maintained (Isableu et al 1997; Kapteyn et al. 1979) but not rapid stabilization (Amblard et al. 1985). A possible explanation for this similarity is that motion parallax is used to control posture, but on the basis of discrete visual cues (static-geometric cues) instead of on continuous visual flow (dynamic cues). This explanation, more extensively discussed in the discussion chapter of this Ph.D., would also fit with the absence of effect of the relative acceleration between the foreground-background on the initial postural readjustment in Experiment 5 in chapter 2. As suggested previously, the relative direction of motion (geometric cues) of objects on the retina seems to be more important for the control of posture than dynamic characteristics of visual motion (visual flow). More direct evidence would require experiments with stroboscopic illumination in order to reduce the amount of dynamic cues available. Indirect evidences will be provided in the following chapter (chapter 4), with subjects with congenital nystagmus.

In conclusion, the experiments show that motion parallax is used by the postural system to reduce body sway during quiet, upright standing in a static three-dimensional visual environment. The findings provide support for the view that there are two modes (afferent and efferent) of visual detection of body sway. The effect is only observed for lateral sway and is particularly pronounced for low frequency components of body sway (up to 0.5 Hz).
Chapter 4

Influence of action and predictability on visual control of posture

A. ABSTRACT

In the fourth chapter, we investigated how active control or predictability of the displacement of a visual scene affects the visually induced postural response. Centre of foot pressure (COP) and head displacement were recorded using a sway platform and a tracking system, respectively. The subjects faced a visual scene (1m x 1m, at a distance of 45 cm) which moved transiently (with a velocity of 1 cm/s) in a direction parallel to the interaural axis. When the displacement of the visual scene was under the active control of the subjects, visually induced body sway was strongly reduced, in comparison with the response to unpredictable stimuli. Prior knowledge of the characteristics of the forthcoming displacement was sufficient, in most subjects, to reduce postural re-adjustment, even when subjects did not exert active control. Finally, the visually induced postural response was strongly reduced even when subjects only triggered the stimulus, without any knowledge about the direction of motion. In conclusion, it appears that although vision is of primary importance in the control of postural orientation, high level processes such as expectation can modulate its impact by providing cues as to whether forthcoming visual flow is the consequence of self-motion or object-motion.
B. INTRODUCTION

Vision provides an important source of information for the control of posture. We have seen in the previous chapters that the particular pattern of optic flow a subject experiences depends on both the nature of his environment and how he moves therein. However, visual motion signals are relative: displacement of either the subject or an external object can yield a similar retinal motion stimulus (unlike vestibular information, for example, which codes unambiguously motion of the head). Therefore, visual control of posture depends largely on the ability to differentiate optical flow due to self-motion from that due to object-motion. The visually induced body sway reported originally by Lee and Lishman (1975), indicates that the visuo-motor system may misinterpret the displacement of the visual environment as a displacement of the self and initiate a postural response.

Gibson (1962, 1966) reminds us that, quotidian, perception usually involves an active observer. This author examined the benefit of active perception as compared with passive perception in tactile perception. In his experiment (1962), subjects were presented with irregular shapes placed in their palm. In one condition, the shape could be explored by moving the hand over the shape (active touch) while in the other condition, the hand remained stationary and the shape was physically moved over the palm (passive touch). Results showed that blinded subjects were more accurate at identifying the shapes when they were allowed to actively explore them. Similarly, Stappers (1989) reported that visual recognition of a computer-generated shape was enhanced if the observers can actively control the motion of the object with a mouse, as compared to motion controlled by the computer. More recently, Larish and Andersen (1995) reported that subjects who actively locomoted (via a joystick) within a virtual 3 D environment were more accurate in predicting dynamic spatial orientation than subjects who passively viewed the replayed 3 D visual display. Thus, action appears to be an important parameter affecting how subjects perceive their environment and themselves in their environment.
In the context of visual control of posture, action has also been shown to play a significant role. White and collaborators (1979) showed elegantly that body sway induced by retinal flow depends on whether the movement of the retinal image is voluntarily produced by a saccadic eye movement or externally produced: The visual flow accompanying saccades had little or no influence on body sway while the similar externally produced visual flow induced a systematic postural re-adjustment (White et al. 1979). This experiment showed that voluntary action allows the observer to differentiate efficiently optical flow due to self-motion (eye movement in this example) from that due to object-motion and more generally revealed the dynamic interaction between the active observer and subsequent changes in stimulation in a closed-loop system. In line with this statement, the following experiments address how active control of the visual flow due to object motion affects postural responses. Experiment 1 compares postural responses to actively controlled displacements of a visual scene with those evoked by passive observation of unpredictable displacements of the visual scene.

Predictability of forthcoming events has also been shown to influence perception. For instance, expectation of forthcoming object motion modulates the threshold of motion detectability (Ball & Sekuler 1980; Sekuler 1995). Therefore the expectation or predictability which is inherent in the active control might be more important than the active control per se. Experiment 2 investigates whether motor action to drive the visual scene is necessary for inhibition of inappropriate postural responses or whether predictability of the forthcoming scene displacement is sufficient. In Experiment 3, we investigate whether active-triggering of the visual scene displacement, without any expectation of the direction of motion, is sufficient to inhibit the inappropriate postural readjustment.
C. GENERAL METHOD

1. Subjects

Eight subjects took part in each experiment. Experiment 1 involved 2 women and 6 men, aged 23-52 years. Experiment 2 involved 12 women and 5 men, aged 23-48, including 3 subjects from Experiment 1. Finally, Experiment 3 involved 3 women and 5 men, aged 24-46 years, including 6 subjects who had participated in either Experiment 1 or 2. All subjects were right handed (Edinburgh Inventory; Oldfield 1971). None of the subjects had any relevant medical history and all had normal or normal-corrected vision. Informed consent was obtained prior to the experiments according to the Declaration of Helsinki.

2. Apparatus

In these experiments, body sway was recorded in response to the linear displacement of a 2 dimensional visual scene. The visual scene consisted of a flat board (1m x 1m, 96° of visual angle) covered in randomly distributed fluorescent discs of 2 cm diameter, placed 45 cm from the subject, at eye level, in an otherwise dark room. The board was mounted on a motorized miniature train on a linear track and moved at a constant velocity of 1 cm/s along an axis parallel to the inter-aural axis, when driven via a PC or a joystick. The experimental set-up is represented in Figure 4.1. The motor used to move the train was a low noise stepper motor coupled with rubber-belts. The noise coming from the motor (0.5dB (c) recorded in a sound proof booth) was not perceptible within the background noise of the laboratory (60dB (c)) which was largely attributable to air conditioning and afforded adequate masking. Therefore, the onset of stimulus motion was not cued by the mechanics of motion.

Subjects stood on a force-platform (internal malleoli 3 cm apart), which measured the position of the centre of foot pressure (COP) in the lateral and anterior-
posterior directions. They also wore a lightweight helmet carrying the receiver-coil of a 3-D magnetic search coil system (Polhemus 3space Fastrak: resolution of 0.5 mm) which transduced the linear component of head displacement in both lateral and anterior-posterior directions. Output signals from the sway platform and the Fastrak were acquired with a computer at a sampling rate of 125 Hz.

Figure 4.1: Experimental setup of Experiment 1-3. Subjects were standing in front of a flat board covered in randomly distributed fluorescent discs, which could be driven in the frontal plane, either by the subject (via a joystick) or by the experimenter. The small train used is seen ghosted.

3. Procedure

In all experiments, subjects were instructed to stand still and relaxed with both hands holding a manipulandum (a small box fitted with either a joystick or buttons) whatever the visual condition. They were asked to maintain fixation of a luminescent dot fixed in the centre of the display at eye level.
4. Eye movement recordings

In order to control subjects' fixation, electro-oculographic recordings of horizontal eye movements were also performed during Experiments 2 and 3 using bi-temporal electrodes. Resolution of eye position was ±1 degree. Inspection of recordings showed that, within this resolution, subjects complied with the task and no rejections due to inappropriate fixations were necessary.

5. Data analysis

For each subject, the averaged body sway under each condition was calculated by averaging all recordings taken for that condition. The time of stimulus onset was used to synchronize the recordings from each trial. Responses to rightward and leftward stimuli were combined after reversing the lateral components of the responses to leftward stimuli.

On the averaged response for each subject calculations were made of: the mean position of COP/head over the 2.5s before stimulus onset and the mean position of COP/head over a 1.8s period, from 1.2s to 3s after the onset of stimulus motion. The difference between these two means is the mean amplitude of the COP/head response (mean response); a measure of how much COP/head deviates in response to the stimulus. The first 1.2s following stimulus onset were excluded from the computation of the mean response because of delay in the development of the postural response.
D. EXPERIMENT 1. Effect of action

1. Procedure and visual conditions

Experiment 1 comprised three conditions:

1) 'Unpredictable condition': the visual scene was moved by the computer, leftwards or rightwards at a velocity of 1 cm/s for 3 seconds. Prior to each trial, subjects did not know whether or not, when and in what direction the visual scene would move.

2) 'Active condition': subjects drove the displacement of the visual scene with a joystick. By moving and holding the joystick deflected to the right or left, the subject could start the visual scene moving and maintain its velocity at 1 cm/s. Subjects were instructed to move the visual scene for 'a few seconds' soon after the experimenter gave the verbal command 'joystick'. Only the first 3s of motion were considered for analysis, and trials with scene movement lasting less than 3s were discarded. Subjects were not allowed to switch from one direction to the other within a single trial and were asked to alternate the direction of motion between trials.

3) 'Control conditions': no displacement of the visual scene.

Each subject underwent 20 trials in the ‘unpredictable’ condition (10 with scene motion to the right and 10 to the left), 20 trials in the ‘active’ condition and 10 trials in the ‘control’ condition. The 50 trials for each subject were divided into two blocks of 25 trials. Within each block, the order of stimulus presentation was pseudorandomized. The two blocks were presented successively with a rest period of 10 minutes between the two. Prior to data recording, two ‘active’ and two ‘unpredictable’ trials were given to each subject in normal room illumination.
Chapter 4: Action and predictability

2. Results (Experiment 1)

No significant differences were observed in the anterior-posterior direction of sway between the experimental conditions with a moving visual display and the control conditions with a stationary display. This finding is in agreement with the literature (Gielen & van Asten 1990; Wolsley et al. 1996) which shows that there are no directionally specific postural responses orthogonal to the displacement of a visual scene. Therefore, only data concerning lateral sway will be reported.

The averaged head and COP sway in the lateral direction for each subject, in both the unpredictable and the active conditions are reported in Figure 4.2. Mean induced head/COP responses over the 8 subjects are reported in table 4.1.

In the unpredictable condition, motion of the visual scene induced a postural displacement in the same direction as the stimulus in 7 out of the 8 subjects tested; a corrective postural adjustment was observed after stimulus offset. As can be seen in Figure 4.2, COP and head displacements followed a similar trend, apart from a transient COP response opposite to the main direction of sway which occurred 250-300 ms after both stimulus onset and stimulus offset. This transient is caused by the foot pressure responsible for the ensuing body sway (Bronstein & Buckwell 1997; Day et al. 1997). The latency of the head sway response was 300-400 ms from stimulus onset. One sample t-test analysis indicated that the mean response during stimulus motion was different from the baseline level (zero) for both the COP ($t(7) = 3.3 \ p < 0.05$) and the head ($t(7) = 3.9 \ p < 0.01$).

Table 4.1: Mean head/COP lateral induced response (average and standard deviation) in mm of the head and the COP in the different visual conditions in Experiment 1.

<table>
<thead>
<tr>
<th></th>
<th>Unpredictable condition</th>
<th>Active condition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>SD</td>
</tr>
<tr>
<td>Head sway</td>
<td>5.2</td>
<td>3.7</td>
</tr>
<tr>
<td>COP</td>
<td>4.3</td>
<td>3.6</td>
</tr>
</tbody>
</table>

Note - A positive value indicates a deviation in the direction of motion.
Figure 4.2: Individual's averaged sway responses to unpredictable versus actively controlled motion of a visual scene. The records show average position of the COP and the head (in mm) computed for each subject in both the unexpected and active conditions of Experiment 1. Upward deflections indicate deviation in the direction of stimulus motion.
In the active condition, stimulus motion induced a small postural response in the same direction in most subjects for both the COP and the head, with latencies of approximately 350 ms and 400 ms respectively. This postural adjustment had a smaller amplitude than that observed in the unpredictable condition, and it was followed by a corrective adjustment during stimulus motion, which shifted both the COP and the head back to the baseline level, or even (in some subjects), in the opposite direction to the stimulus. No clear anticipatory postural response (in the opposite direction to the expected stimulus) was observed during the 2.5 seconds preceding stimulus motion (baseline). One sample t-tests indicated that the mean response during stimulus motion was not different from baseline (zero), neither for the COP ($t(7) = 0.5 \ p > 0.05$) nor for the head ($t(7) = 0.54 \ p > 0.05$). Comparison between COP and head displacements during stimulus motion showed that the active condition responses were significantly different from those in the unpredictable condition (paired t-test, COP: $t(7) = 3 \ p < 0.05$; head $t(7) = 2.9 \ p < 0.05$).

No postural displacement was observed in the control condition with a stationary visual display ($p > 0.05$).

In summary, results showed that when the displacement of the visual scene was under the active control of the subjects, visually induced body sway measured both as head and COP displacement, was markedly reduced, in comparison with the response to unpredictable stimuli.
E. EXPERIMENT 2: Predictability versus action

Results of Experiment 1 showed that the postural readjustment induced by the displacement of a moving scene was markedly reduced when subjects were controlling actively that displacement. The rational of Experiment 2 was to test whether this inhibition is due to the active control per se or to the expectation-predictability which is inherent in the active control.

1. Procedure and visual conditions

Experiment 2 involved four conditions:

1) ‘unpredictable’ condition: identical to that of Experiment 1.

2) ‘Active’ condition: subjects triggered the computer-generated stimulus by pushing one of two buttons (for rightward or leftward scene motion). After the verbal instruction ‘button’ from the experimenter, the subject had to press within a few seconds. Subjects were asked to alternate right and left between trials.

3) ‘predictable’ condition: subjects were told that the scene would move to the right or to the left 3 to 5s before the onset of motion. They were also given an audible beep (50 ms duration, 500Hz tone) 500 ms before stimulus onset. Thus, in the ‘predictable’ condition, subjects knew when and in which direction the scene would move.

4) Control condition: no displacement of the visual scene.

The stimulus was the same in the three motion conditions, consisting of a displacement of the visual scene leftwards or rightwards at a velocity of 1 cm/s for 3 seconds. Each subject underwent 10 trials in each condition (with equal numbers of visual scene displacement rightward and leftward). The 40 trials for each subject were divided into two blocks of 20 trials, presented successively with a rest period of
10 minutes between the two. Within each block the order of stimulus presentation was pseudo-randomized.

Prior to the experiment, we tested whether the act of pressing the button by itself had a significant postural effect. After being informed that the visual scene would not move, subjects pressed the right or left button alternatively (n=10). Results indicated that the active push (left or right) had no effect on the COP / head position (p >0.05).

2. Results (Experiment 2)

No significant differences were observed in the anterior-posterior direction of sway, between the experimental conditions with a moving visual display and the control conditions with a stationary display. Therefore, only data concerning lateral sway will be reported. The averaged head sway in the lateral direction for each subject in the ‘unpredictable’, ‘predictable’ and ‘active’ conditions are given in Figure 4.3. Mean induced head/COP responses over the 8 subjects are reported in table 4.2.

As in Experiment 1, unpredictable displacement of the visual scene induced a postural re-adjustment in the direction of motion. Except for the early transient COP response (latency of ~280 ms) opposite to stimulus motion, COP displacement followed a similar trend to that of the head. In contrast to the unpredictable condition, no significant postural readjustment was observed when the displacement of the visual scene was triggered by the subjects themselves (active condition) neither for the head nor for the COP (p > 0.05). It is however interesting to notice that approximately 2.5sec after stimulus onset, a displacement of the head (and COP) in the direction of stimulus motion is initiated (see Fig 4.3). A resetting towards the initial baseline position is observed soon after stimulus offset. This late initiation of postural correction indicates that the beneficial effect of self-triggering the stimulus is limited to the first 2-2.5sec of stimulation.
Figure 5.3: Individual’s averaged sway responses to unpredictable, predictable and actively controlled motion of the scene. The drawings on the left side show the experimental set-up for each stimulus condition. Although subjects were holding the manipulandum in all conditions, it has been removed from the drawings of the unpredictable and predictable conditions for the sake of clarity.
In the *predictable* condition, the displacement of the moving scene failed to induce clear postural re-adjustment in six out of the eight subjects tested. In one of the two remaining subjects, the predictable displacement of the moving scene induced a postural re-adjustment in the direction of motion, of a similar amplitude to that elicited in the unpredictable condition. In the other subject, an anticipatory postural response could be observed within 2.5 s of baseline period, followed by a postural adjustment in the opposite direction to stimulus motion. A similar response pattern was observed for this subject in the active condition. When all subjects were considered together, the mean response of both the head and the COP during stimulus motion was not different from the baseline level (p > 0.05).

An analysis of variance (ANOVA) was performed on the three stimulus conditions (*unpredictable, predictable* and *active*) and the LSD test was used for pairwise comparisons. The ANOVA showed a significant effect of experimental condition, for both the head ($F_{2,14} = 16.4 \ p < 0.01$) and the COP ($F_{2,14} = 21.8 \ p < 0.01$). *Post hoc* mean comparison indicated that the *unpredictable* condition was systematically different from the other two conditions, for both the head and the COP (p < 0.01). No difference was observed between the *active* and the *predictable* conditions (p > 0.05).

No postural displacement was observed in the control condition with a stationary visual display (p > 0.05).

Table 4.2: Mean lateral head/COP induced response (average and standard deviation) in mm of the head and the COP in the different visual conditions in Experiment 2.

<table>
<thead>
<tr>
<th></th>
<th>Unpredictable condition</th>
<th>Predictable condition</th>
<th>Self-triggered condition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>SD</td>
<td>M</td>
</tr>
<tr>
<td>Head sway</td>
<td>5.3</td>
<td>1.9</td>
<td>0.17</td>
</tr>
<tr>
<td>COP</td>
<td>3.8</td>
<td>1.3</td>
<td>-0.07</td>
</tr>
</tbody>
</table>

Note - A positive value indicates a deviation in the direction of motion.
F. EXPERIMENT 3: Directionally specific information

1. Procedure and visual conditions

Experiment 3 involved four conditions: The 'unpredictable', 'active' and 'control' conditions were identical to those of Experiment 2. The other condition, 'active unspecific', was similar to the active condition except that subjects held a single push-button for triggering motion and they did not know in which direction the visual scene would move when they pushed the button. Each condition consisted of 10 trials, 5 with motion to the right and 5 with motion to the left (in the conditions with scene movement). The 40 trials for each subject were divided into four blocks of 10 trials. There were 2 or 3 'unpredictable' and 2 or 3 'control' trials per block. 'Active' trials completed two of the blocks (5 trials in each) and 'active-unspecific' trials completed the other two blocks. This division was chosen to avoid changing push-buttons with a block. The order of stimulus presentation was pseudo-randomized within each block. The presentation of the four blocks was counterbalanced.

2. Results (Experiment 3)

The averaged head sway for each subject in the unpredictable, active and active-direction unspecific conditions are shown in Figure 4.4. Mean induced head/COP responses over the 8 subjects are reported in table 4.3.

As in Experiment 1 and 2, unpredictable displacements of the visual scene induced a postural re-adjustment (head and COP) in the direction of motion, while little or no postural re-adjustment was observed when subjects were triggering the stimulus themselves with a directionally specific trigger (active condition). In this latter condition, one subject showed a postural re-adjustment in the opposite direction to motion. In both conditions, head and COP followed a similar trend during the displacement of the scene.
Figure 5.4: Individual’s averaged sway responses to unpredictable visual motion and actively controlled visual motion, with and without directionally-specific information. The traces show the average position of the head (in mm) for each subject in the three experimental conditions of Experiment 5.3.
In the active-unspecific condition, a slight tendency to lean in the direction of stimulus motion was observed in most subjects. However, comparison between the mean response during stimulus motion and the baseline level (zero) failed to reach significance both for the head ($t(7) = 2.1$, $p = 0.078$) and the COP ($t(7) = 2.04$, $p = 0.081$).

An ANOVA was performed on the three stimulus conditions (unpredictable, active and active-unspecific) and the LSD test was used for pairwise comparisons. The ANOVA showed a significant effect of experimental condition both for the head ($F_{2,14} = 17.1$, $p < 0.01$) and the COP ($F_{2,14} = 22.4$, $p < 0.01$). Mean comparison indicated that the unpredictable condition was significantly different from the other two conditions both for the head and the COP ($p < 0.01$) and correlation coefficient between these two conditions did not reach significance neither for the head ($r = 0.32$) nor for the COP ($r = 0.59$). No difference was observed between the active and the active-unspecific conditions ($p > 0.05$). No postural displacement was observed when the visual display was stationary.

Subjective report:

Following data collection, subjects were questioned about their subjective impression of the experiment and, more specifically, were asked whether the three stimulus conditions lead to the same percept. The eight subjects of Experiment 3 reported that the perception of visual scene motion was much more ambiguous when they could not predict the displacement than when they triggered the stimulus. Three subjects reported that they could not systematically perceive the visual scene as moving in the unpredictable condition. One subject mentioned that he realised that the visual scene was moving in unpredictable trials, but only after becoming aware that his body was being driven by the moving scene. Only one subject reported a perceptual difference between the active and the active-unspecific conditions.
Table 4.3: Mean lateral head/COP induced response (average and standard deviation) in mm of the head and the COP in the different visual conditions in Experiment 3.

<table>
<thead>
<tr>
<th>Condition</th>
<th>M</th>
<th>SD</th>
<th>M</th>
<th>SD</th>
<th>M</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Head sway</strong></td>
<td>6.2</td>
<td>3.1</td>
<td>-0.05</td>
<td>3.1</td>
<td>1.2</td>
<td>1.4</td>
</tr>
<tr>
<td><strong>COP</strong></td>
<td>4.3</td>
<td>2.08</td>
<td>-0.3</td>
<td>1.8</td>
<td>0.6</td>
<td>0.8</td>
</tr>
</tbody>
</table>

Note - A positive value indicates a deviation in the direction of motion.

G. DISCUSSION

The results of Experiment 1 showed that the visually induced body sway observed in response to the unpredictable displacement of a visual scene was markedly suppressed when that displacement was actively controlled by the observer. The results of Experiment 2 indicated that the active control of driving the scene was not necessary to inhibit the visually induced body sway since predictability alone was sufficient in seven subjects out of eight. Except in one subject, no anticipatory response could be identified in either the active (Experiment 1-3) or in the expected (Experiment 2-3) conditions. Finally, an incomplete, but nevertheless substantial, reduction in visually induced body sway was also observed when subjects merely triggered the stimulus, without prior knowledge of the direction of motion (Experiment 3).

The finding that minimal motion, below the threshold for motion perception (as in some of our subjects and in previous studies; Lee & Lishman 1975; Stoffregen 1986) is sufficient to induce postural readjustments is in favour of a low level postural control system requiring little contribution from high level processes (Bertenthal et al 1997). However, our data show that when the displacement of the visual scene is predictable, (active and predictable conditions, Experiments 2-3), the postural readjustment is strongly reduced. Thus, high level functions, such as expectation, can have a decisive impact on the visuo-motor system controlling
posture. As shown in Experiment 3, when subjects were triggering the displacement of the scene without any directionally specific information (active-unspecific), the suppression of the postural re-adjustment was almost complete. The absence of difference between the two active conditions, with or without directionally specific information, indicates that knowledge about ‘when’ the stimulus is going to move is sufficient to strongly reduce the influence of visual inputs on postural control.

The cognitive processes affecting suppression of visually induced body sway remain unclear, but active control does not appear to be necessary, as suggested by the similarity between the active and the predictable conditions in Experiment 2. The beneficial effect of active control of the displacement of the visual scene is not due to action per se but to the prediction of the future event. As discussed above, visual control of posture depends largely on how the visual flow is interpreted by the visuo-motor system, either as self-motion or as object-motion. High level processes, such as expectation or attention are known to reduce the threshold for perceiving motion (Ball & Sekuler 1980; Sekuler 1995). Subjective reports collected systematically after data collection in Experiment 3 are in agreement with this statement; all subjects reported that the displacement of the visual scene was much more ambiguous when unpredictable than when actively triggered, both in the active and active-unspecific conditions. Therefore, if the visual flow due to the displacement of the scene can be implicitly or explicitly attributed to object motion instead of self motion, there is no need for the visuo-motor system to initiate a postural re-adjustment; the visual flow is disregarded. Accordingly, this is what was found in the active and predictable conditions in Experiment 1-3.

In our study subjects swayed most, and had an ambiguous perception of self versus object-motion, when the visual stimuli were unpredictable. Predictability and sway must act on a subject’s perception of what is happening in a circular fashion: the action perception cycle. From our own experiences of the experiments, we feel that sway was minimal because we perceived the visual stimuli most accurately; i.e. when it was predicted. However, it would be hazardous to say categorically whether sway was suppressed because perception was certain or whether little sway
facilitated accurate perception since the threshold for object-motion perception has been shown to be raised by concurrent head motion (Brandt 1981).

Previous reports also favour an effect of high level processes on visual control of posture. Lestienne et al (Lestienne et al. 1976, 1977) reported that subjects who were insensitive to linear visual flow became sensitized when performing a concurrent arithmetic task (dual task). More recently, using the moving room paradigm, Bronstein (1986) showed that prior exposure to visual stimulus induces adaptation of the visually evoked response from the first to the second trials. Interestingly, the reduction of the postural readjustment (antero-posterior direction of sway) was accompanied with a reduction in EMG responses. These data indicate that the reduction of the visually induced postural response observed by Bronstein (1986) was not due to an increased stiffness of leg muscles to counteract the disturbance but was more likely due to down-regulation of irrelevant visual inputs. Therefore, in light of Bronstein's results (1986) it is reasonable to assume that the inhibition of inappropriate postural responses was not the consequence of an increased stiffness of leg muscles. Unfortunately, in contrast to the antero-posterior direction of sway (Day et al. 1997), EMG activity is not sensitive enough to detect the rather small visually evoked body sway in the lateral direction.

The latencies of visually induced body sway reported in the literature vary greatly. The short latencies we observed are similar to those reported previously for low stimulus velocities (Bronstein & Buckwell 1997). They are also closer to the latencies at which vision contributes to rapid automatic postural responses (EMG activity around 100 ms) following the displacement of the support surface (Berthoz et al 1979; Sundermier & Woollacott 1998). In contrast latencies as long as 1 sec (Lestienne et al 1977) or even more (Dichgans et al 1972) have been reported. Differences in the dynamics of the various transduction devices used would not account for the large variations in response latency. The more likely factor being that these latter studies used high velocity visual stimuli which would give an unambiguous percept of object motion when the stimulus started to move.
In conclusion, it appears that although vision is of primary importance in the control of postural orientation, high level processes such as expectation or predictability can modulate its impact by providing decisive cues as to whether the visual flow is the consequence of self-motion or object motion.
Chapter 5

Visual control of postural orientation and stabilization in congenital nystagmus

A. ABSTRACT

The aim of Experiment 1 and 2 was to investigate how subjects with congenital nystagmus (CN) use visual information, including motion parallax, to stabilize and orient their bodies in space. Center of foot pressure (COP) and head displacements in the lateral plane were recorded using a sway platform and Schottky barrier photodetector respectively. In Experiment 1, a comparison was made of the oscillatory characteristics of body sway with eyes open as compared to eyes closed. Experiment 2 studied the postural readjustments made in response to simple motion (background fixation condition) or motion parallax (Foreground fixation condition) of objects in the visual scene, generated by lateral displacement of background scenery. Results of Experiment 1 revealed that CN subjects made poor use of visual information to stabilize their COP but were able to stabilize their head at frequencies lower than 1 Hz. Experiment 2 showed that in response to the displacement of a visual display, for both simple motion (background fixation) and motion parallax (foreground fixation), CN subjects re-oriented their body in space in a similar manner to control subjects. The results suggest that despite involuntary eye movements, CN subjects were able to use orientation cues, including motion parallax, to control their posture, but not dynamic cues useful to control rapid oscillations which are particularly important at the level of the COP. These findings suggest that in CN, visual control of posture is restricted by low frequency sampling of the visual scene. It does also suggest that although motion parallax is essentially dynamic, discrete sampling of the positional changes involved may provide adequate cues to control body orientation.
Chapter 5: Postural control and congenital nystagmus

B. INTRODUCTION

Congenital nystagmus (CN) is an ocular motor disorder characterized by involuntary oscillatory eye movements that disrupt foveal target fixation. The onset of nystagmus occurs during the first six months of life (Dell’Osso & Daroff 1975). Typically, the nystagmus is in the horizontal plane and each cycle is initiated by slow phases with exponentially increasing velocity, taking the eyes off the target. A fast phase returns the eyes to the object of regard, at which time there is usually a period of transient stability: a ‘foveation period’ of 10 to > 100 ms duration within which the target is visually ‘sampled’ (Dell’Osso & Leigh 1992). A electro-nystagmographic recording of horizontal eye movements during fixation of a target in a patient with congenital nystagmus is presented in Figure 5.1. Despite almost constant eye movement, and therefore, large amount of retinal image slip, patients with congenital nystagmus rarely complain of either oscillopsia (spatial constancy) or impairment of visuo-motor coordination (Leigh et al. 1988). Oscillopsia refers to the illusion of world motion usually experienced by patients with acquired spontaneous nystagmus or abnormal vestibulo-ocular reflex (Dell’osso & Leigh 1992a,b).

Figure 5-1: A recording of horizontal eye movement for 2 sec in a patient with congenital nystagmus during fixation of a target in primary gaze. The foveation periods, the slow phases to the right with exponentially increasing velocity and finally the fast phases to the left (jerk left) can be identified.
As stressed throughout this manuscript, visual information is an essential factor in the multi-sensory control of movement and balance. Unlike vestibular information, visual motion signals are relative: that is, a displacement of the subject or an external object can yield similar patterns of retinal motion stimuli. Hence, visual control of posture depends largely on the ability to differentiate optical flow due to self-motion from that due to object motion. Such a differentiation could be compromised in individuals with involuntary eye movements such as CN. Accordingly, in addition to increased thresholds for motion detection (Dieterich & Brandt 1987; Eggert et al. 1997; Shallo-Hoffmann et al. 1998), individuals with CN make less use of visual information to control stance, measured as displacement of the COP, than control subjects (Eggert et al. 1997; Di Girolamo et al. 1999).

In Experiment 1 and 2, we present detailed investigations of the dynamics of visual postural control in CN subjects. Experiment 1 sought to identify the frequency bands in which visual control of equilibrium (the oscillatory component of body sway) is disturbed by CN. Since oscillations of the COP have a higher frequency range than upper parts of the body (Day et al. 1993; Benda et al. 1994) one might expect that visual regulation of head oscillations in CN is different from that of COP oscillations. Therefore, both COP and head oscillations were recorded. The second experiment determined the extent to which subjects with CN re-orient (i.e. tilt or displace in a given direction) their bodies in space in response to visual flow. We know from the previous chapters and Experiments that normal subjects lean in the direction of motion when viewing a moving background and that this postural adjustment reverses in direction when a stationary target providing motion parallax cues is placed between the standing subject and the moving background. Because of the intrinsic visual instability and raised thresholds for motion detection in CN, we hypothesized that these subjects may have disturbed patterns of postural response to such visual motion stimuli.
C. GENERAL METHOD

1. Subjects

Nine adult subjects with horizontal CN conforming to the criteria of Gresty et al. (1984) and Snellen visual acuity of at least 0.33 in one eye were studied. Six took part in Experiment 1 (subjects 1-6 in Table 5.1) and all underwent Experiment 2 (Subjects 1-9 in Table 5.1).

Table 5.1. Clinical details of the nine subjects with CN who took part in Experiment 1 (Subjects 1-6) and 2 (Subjects 1-9).

<table>
<thead>
<tr>
<th>Subject</th>
<th>Age / sex</th>
<th>Snellen Acuity</th>
<th>Frequency Hz</th>
<th>Stereopsis (sec of arc)</th>
<th>Dominant Waveform</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>38 M</td>
<td>0.5; 0.5</td>
<td>4.5</td>
<td>50&quot;</td>
<td>jerk left</td>
</tr>
<tr>
<td>2</td>
<td>40 F</td>
<td>&lt;0.1; 0.5</td>
<td>4</td>
<td>Nil</td>
<td>Alternating</td>
</tr>
<tr>
<td>3</td>
<td>57 M</td>
<td>0.67; 0.67</td>
<td>4</td>
<td>80&quot;</td>
<td>Pendular</td>
</tr>
<tr>
<td>4</td>
<td>33 M</td>
<td>0.33; &lt;0.1</td>
<td>4</td>
<td>Nil</td>
<td>jerk left</td>
</tr>
<tr>
<td>5</td>
<td>24 F</td>
<td>0.17; 0.67</td>
<td>4.5</td>
<td>Nil</td>
<td>jerk right</td>
</tr>
<tr>
<td>6</td>
<td>41 M</td>
<td>0.67; 0.67</td>
<td>5</td>
<td>140&quot;</td>
<td>jerk left</td>
</tr>
<tr>
<td>7</td>
<td>30 M</td>
<td>0.33; 0.33</td>
<td>4</td>
<td>800&quot;</td>
<td>jerk right</td>
</tr>
<tr>
<td>8</td>
<td>30 M</td>
<td>0.33; 0.33</td>
<td>3.5</td>
<td>Nil</td>
<td>jerk left</td>
</tr>
<tr>
<td>9</td>
<td>56 M</td>
<td>0.67; 0.5</td>
<td>4</td>
<td>100&quot;</td>
<td>jerk left</td>
</tr>
</tbody>
</table>

Fourteen healthy, aged matched, subjects participated in Experiment 1. Six of these control subjects (mean age: 38.5 years) had their visual acuities artificially reduced to match those of the CN subjects (acuity control group). These subjects wore spectacles with ‘fogging’ lenses (x1 magnification lenses with ground surfaces) for 15 minutes prior to the start of the experiment. Since two CN subjects had extremely low vision on one eye (< 0.1), two control subjects were tested.
monocularly in addition to fogging. The other eight subjects (mean age: 40.5 year) were tested with normal vision (‘normal control group’). Fourteen healthy adults, aged matched to the CN subjects (mean age: 38 years) with normal Snellen acuity took part in Experiment 2. Patients gave their written informed consent to the study according to the Declaration of Helsinki.

2. Postural recordings

The studies focus on postural adjustments in the lateral plane, in response to lateral movements of both the visual scene and the eyes, since a number of published studies have shown that postural responses are co-planar with the visual motion stimuli deployed (Gielen et al 1990; Wolsley et al. 1996; Thurrell et al. 2000). Postural movements in other directions are not correlated. In both experiments, subjects stood barefoot on a rigid board placed on top of a slab of foam rubber (height 5 cm; specific weight 30g/dm³) resting on the AMTI force platform (model BP2436) which transduced postural sway as displacement of the COP in the lateral direction. Feet were splayed at 30° with heels together.

Subjects also wore a lightweight helmet, on top of which was mounted an infra-red light emitting diode. Displacements of the light were transduced by imaging a top view of the subject onto the 2-dimensional Schottky barrier photodetector (United Detector Technologies Inc) situated 40 cm above the head (see chapter 3 for a description of the camera). Head sway values were normalized for each subjects’ height (signal * mean height of group / individual’s height). All signals were filtered with a passband < 30 Hz and digitally sampled at 125 Hz.

3. Eye movement recording

Bi-temporal, direct coupled, electro-oculographic recordings of horizontal eye movements were performed on all CN subjects during Experiments 1 and 2, to monitor the predominant fast phase direction and the frequency of the nystagmus.
D. EXPERIMENT 1: Visual Control of Equilibrium

1. Method

1.1. Procedure and visual conditions

CN, acuity-control and normal control subjects were tested under two conditions: ‘eyes open’ and ‘eyes closed’. With eyes open, subjects were asked to fixate a small cross (1 x 1 cm) placed at the center of an earth-fixed window frame (30 x 24 cm) at a distance of 50 cm from the eyes with a stationary background 100cm away from the foreground window frame. The visual environment was similar to that used in Experiment 1-5 in chapter two except that the room was normally illuminated. The order of presentation of the eyes open, eyes closed conditions was counterbalanced. In both conditions, subjects were instructed to ‘stand still and relaxed with hands at their side’. Each condition was presented for one minute, from which the last 50s were analyzed.

1.2. Data analysis

Postural equilibrium in the lateral direction was evaluated as sway path and also in the frequency domain. The sway path is the length of the path described by the COP or the head, and is defined as the sum of the distances between sequential points sampled during the analysis period (50s).

To calculate power spectra, the 50s epochs were detrended using a line of best fit and then windowed with a Hanning function. A fast Fourier transform (FFT) algorithm was then applied to the entire 6250 point signal (MATLAB Mathworks Inc). The resulting power spectrum had a frequency resolution of 0.02 Hz and bandwidth from 0 to 62.5 Hz. For subsequent analysis, only the 0 to 5 Hz range was considered. For statistical analysis the frequency components from 0.02 to 5 Hz were grouped into 20 bands, each spanning 0.25Hz with 12 or 13 (alternating) discrete frequency components per band. The Power in each of these bands was then calculated by summing the frequency components.
Analysis of variance (ANOVA) was used to investigate the effects of 'vision' in the three subject groups. A two factor design was employed for sway path analysis (3 X 2) with 'group' as the between subject factor (CN, acuity-controls and normal controls) and 'vision' as the within subject factor (eyes closed versus eyes open). The Tukey test was used for post hoc comparison. A three factor design was employed for spectral analysis (3 x 2 x 20), with 'frequency' (0-0.25 Hz to 4.75-5 Hz) as a second within subject factor.

2. Results (Experiment 1)

The sway path data measured from COP and head recordings for CN and the two control groups are given in Table 5.2.

Table 5.2. Mean sway path length (in cm) and standard deviations of both the COP and the head for the eyes closed and eyes open conditions in CN, acuity and normal controls.

<table>
<thead>
<tr>
<th></th>
<th>Eyes closed</th>
<th></th>
<th>Eyes open</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>SD</td>
<td>M</td>
<td>SD</td>
</tr>
<tr>
<td><strong>Head</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CN subjects</td>
<td>67.8</td>
<td>13.2</td>
<td>49.1</td>
<td>12.1</td>
</tr>
<tr>
<td>Acuity-control subjects</td>
<td>56.5</td>
<td>12.2</td>
<td>35.9</td>
<td>9.5</td>
</tr>
<tr>
<td>Normal-control subjects</td>
<td>53.2</td>
<td>17.5</td>
<td>31.9</td>
<td>13.3</td>
</tr>
<tr>
<td><strong>COP</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CN subjects</td>
<td>115.1</td>
<td>15.6</td>
<td>92.4</td>
<td>23.1</td>
</tr>
<tr>
<td>Acuity-control subjects</td>
<td>111.3</td>
<td>23.9</td>
<td>45.8</td>
<td>10.1</td>
</tr>
<tr>
<td>Normal-control subjects</td>
<td>128.1</td>
<td>55.1</td>
<td>50.3</td>
<td>11.5</td>
</tr>
</tbody>
</table>
2.1. Effect of vision on the COP

a. Sway path length

Comparisons between the sway path lengths measured in the eyes open and eyes closed conditions indicated that visual stabilization of the COP was more effective in the two control groups than in the CN subjects. The sway path of the COP with eyes open was reduced only by 19% in the CN subjects as compared to 59% and 57% in the acuity control and normal-control subjects respectively. Figure 5.2 (left panel) illustrates the improvement of stability (%) with vision for each individual CN and acuity-control subject. The significant interaction between the ‘group’ factor (CN, acuity and normal controls) and the ‘vision’ factor (eyes closed versus eyes open) confirmed that vision was more stabilising in the two controls groups as compared to the CN group (ANOVA: F_{2,17} = 4.1 \ p < 0.05). Post hoc comparison indicated that there was no difference between the three groups with eyes closed (p > 0.05). In the eyes open condition, the sway path was longer in CN subjects than in the other two control groups (p < 0.01). No differences of any kind were observed between the acuity-control and normal-control subjects (p > 0.05).

Figure 5.2: Percentage improvement (%) of stability (sway path) with vision calculated for each subject with CN and acuity control for both the COP (left panel) and the head (right panel) in Experiment 1. The improvement was calculated as 
\[ \frac{(\text{eyes closed score} - \text{eyes open score})}{\text{eyes closed score}} \times 100 \].

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Power spectra

Spectral analysis of COP for the CN and the acuity-control subjects is shown in Figure 5.3. The frequency characteristics of the visual effect on COP displacements can be inferred from a comparison of the spectra of sway obtained with eyes closed versus eyes open (Dichgans et al. 1976; Lestienne et al. 1977). In CN, visual stabilization of the COP was restricted to frequencies lower than 1 Hz (Fig. 5.3). In contrast, for acuity-control subjects (and normal control subjects), vision had an effective stabilizing influence on COP throughout the frequency range 0 to 5 Hz (Fig. 5.3 for acuity-control subjects). Visual stabilization of the COP was significantly more effective in the control subjects (acuity control and normal control subjects) than in the CN subjects as reflected by the significant interaction between the ‘group’ factor and the ‘vision’ factor (ANOVA: $F_{2,17} = 4.9 \ p < 0.05$). ANOVAs examining for within group effects indicated that the effect of vision in the CN subjects failed to reach significance either as a main effect ($F_{1,5} = 3.7 \ p = 0.11$) or in interaction with the frequency factor ($F_{19,95} = 0.9 \ p = 0.58$). The effect of ‘vision’ was similar in the two control groups with a significant main effect of vision ($p <0.05$) and no interaction with the ‘frequency’ factor ‘ ($p > 0.05$).
Figure 5.3: Average power spectra of displacement of the COP (bottom panels) and the head (top panels) in CN (left panels) and acuity control subjects (right panels) with eyes closed (red line) and eyes open (blue dashed line). Power spectra density is in $\log_{10} (\text{cm}^2)$ with a frequency resolution of 0.02 Hz. Error bars are the standard deviation for each frequency band. Note that the decay in power with increasing frequency for oscillatory head movement is greater than for oscillations of the COP.
2.2. Effect of vision on head sway

a. Sway path length

Comparisons between the eyes open and the eyes closed conditions indicated that the sway path length was shorter in the three groups of subjects when their eyes were open than when eyes were closed (see Table 5.2). The sway path length with vision was reduced by 27% in the CN subjects, 34% in the acuity-control subjects and 38% in the normal-control subjects, as compared to eyes closed. As can be seen in Fig. 5.2, the improvement in stability with vision was similar to that of acuity-controls in five out of the six CN subjects. Statistical analysis (ANOVA) confirmed that the reduction of the sway path length with vision was similar in the three groups of subjects ($F_{2,17} = 0.1 \ p > 0.05$). Post hoc comparisons indicated that there was no difference between the three groups in the eyes closed condition ($p > 0.05$). With eyes open a significant difference between the CN and the normal-control subjects was observed ($p < 0.05$) but no other comparison reached significance.

b. Power spectra

Spectral analysis showed that visual stabilization of the head in the three groups primarily affected low-frequencies of head movement. In the CN subjects (Fig. 5.3) visual stabilization of the head was restricted to < 1 Hz while in the two control groups, visual stabilization of the head was apparent up to 2-3 Hz (Fig. 5.3 for acuity-control subjects). Although visual stabilization of the head appears to have a higher frequency dynamic in the acuity-control and normal control groups, the magnitude of visual stabilization of head sway was similar in the three groups. This was shown by the absence of significant interactions in the ANOVA examining interactions between group, vision and frequency factors ($p > 0.05$). The stabilizing effect of vision was significant in the three groups of subjects, as a main effect and in interaction with the factor frequency ($p < 0.05$).
E. EXPERIMENT 2: Visually Induced Body Sway

Experiment 2 aimed to provoke postural adjustments (postural re-orientation) by presenting the standing subject with the 2-dimensional visual background which could, either remain stationary or move in a controlled translation in the lateral plane. Both the conditions of background (simple motion) and foreground fixation (motion parallax) were manipulated. The effect of these target dispositions on oscillatory component of unperturbed body sway (no background motion) was also examined.

1. Method

1.1. Apparatus

Postural re-orientation was provoked by moving background visual scenery. The scenery was similar to that used in Experiment 1-5 in chapter 2, with a flat board (2m x 3m) subtending 67° height x 90° width of visual angle, oriented in the transverse plane, 150 cm from the subject. Photoluminescent yellow-green stripes fixed to the board defined the outline of a house (see experimental set-up in Fig. 5.4) in an otherwise dark room. The board was mounted on a motorized wheeled chassis running on a linear track. For background motion, the board first accelerated for 1.25s, rightwards or leftwards, and then maintained a constant velocity of 6 cm/s for 8.5s. The overall displacement was 58 cm, subtending 21° at the subject’s viewing position.

1.2. Procedure and visual conditions

The two visual conditions to which each subject was exposed were the background and foreground fixation conditions as in Experiment 1 in chapter 2.

1) Background fixation (simple motion): Subjects were instructed to 'look straight ahead', binocularly, at the house in the background without following it when it moved. The luminescent background was the only visible display in the otherwise completely dark room.
2) Foreground fixation (motion parallax): Subjects had to fixate a cross (1 x 1 cm) placed at the centre of a purpose built earth fixed luminescent window frame (30 x 24 cm), 50 cm distant from the subject's eyes. This foreground was placed 100 cm in front of the background.

Under each condition, subjects underwent fifteen pseudo-randomized trials, five with background motion to the right, five to the left and five control trials with the background stationary.

1.3. Data analysis

Postural re-orientation in the lateral direction (mean amplitude head/COP response) was evaluated as the shift in the mean head/COP position during the constant velocity part of stimulus motion (a 8.5s period, from 1.25s to 9.75s after the onset of stimulus motion), relative to a 4s baseline preceding background motion. Trials were averaged for each subject and visual condition. Student t-tests were used to compare CN with control subject data.

Supplementary analysis on trials with stationary background was made using the sway path length (in the lateral direction) in order to test the effect of the target disposition on oscillatory component of unperturbed body sway. From the averaged sway path length per subject for each visual condition, the percentage difference between background and foreground conditions was computed by the ratio [(background score - foreground score) / (background score)*100].
2. Results (Experiment 2)

1.1. Visually induced body sway

Since no differential effect between the two directions of motion was observed, postural responses to leftward and rightward stimuli were combined by reversing responses to leftward stimuli. Figure 5.4 shows sample records of head displacement for a CN subject in both the condition of background and foreground fixation. Individual mean amplitude of head/COP response in both visual conditions are plotted in Figure 5.5.

As can be seen in the sample record in Figure 5.4 from a CN subject, in the background fixation condition (simple motion), the displacement of the background induced a displacement of the head (and also of the COP) in the same direction as motion, followed by a return to baseline posture on cessation of the stimulus. In both the CN and the control subjects, a postural adjustment in the direction of motion was observed in response to simple motion in background fixation condition, with a similar amplitude in the two groups, both for the COP \( t = 0.13 \ p > 0.05 \) and for the head \( t = 0.21 \ p > 0.05 \). Individual mean amplitude of the head/COP response in background fixation condition for both CN (blue circles) and control subjects (red diamonds) are represented on the X axis of head/COP scatters in Figure 5.5.

With a foreground target, i.e. motion parallax, a shift of head position (and also of the COP) in the opposite direction to stimulus motion was induced (Fig. 5.4). These postural adjustments in the opposite direction to background motion were significant departures from baseline in the two groups of subjects. Individual mean amplitude of head/COP responses for both CN and control subjects are plotted on the Y axis of head/COP scatters in Figure 5.5. Statistical analysis indicated that the mean response was of similar amplitude in the two subject groups, both for the COP \( t = 0.27 \ p > 0.05 \) and for the head \( t = 0.38 \ p > 0.05 \).
Figure 5.4: Sample records of head displacement of a subject with congenital nystagmus under conditions of both background and foreground fixation. Upward deflections indicate deviation in the direction of stimulus motion. The drawings show the set-up for experiment 2.
Figure 5.5: Mean induced response for the head (top panel) and the COP (bottom panel) in of background fixation condition (vertical axis) plotted against that in the foreground fixation condition (horizontal axis) for both the CN (blue circles) and the control subjects (red diamonds).
An additional analysis was made of the results from the 7 CN subjects who had sustained uni-directionally beating nystagmus to test whether the direction of nystagmus affected the postural readjustment to leftward and rightward stimuli. The postural responses were inverted in the two CN subjects with right-beating nystagmus to make their data comparable to that of the other five CN subjects with left-beating nystagmus. Student’s t-tests comparing response amplitudes in the same versus opposite direction to the nystagmus fast phase showed that the nystagmus direction had no effect neither on COP nor on head data, either for simple motion or motion parallax (p > 0.05).

1.2. Sway path length with stationary background

Figure 5.6 shows the individual percentage difference in the averaged sway path length between background and foreground conditions with stationary background \[\frac{(\text{background score} - \text{foreground score})}{\text{background score}} \times 100\] in CN and control subjects both for the head and the COP.

At the level of the head (Fig. 5.6), a positive percentage difference was observed in CN (18 %) as in control subjects (23.9 %). These positive values indicated that when a foreground was placed directly in front of the subjects, sway oscillations of the head decreased as compared to the condition of stationary background alone. One sample t-test indicated that the stabilizing effect of the additional foreground was significant in both groups (CN: \(t(8) = 4.1\ p < 0.01\); controls: \(t(13) = 7.1\ p < 0.01\)). No difference between CN and control subjects was observed \(t(21) = 1.1\ p = 0.29\).

For the COP, the was not percentage difference in sway path length between background and foreground conditions in CN subjects (-0.6%) \(t(8) = 0.1\ p = 0.9\). In contrast, in controls subjects, a significant percentage difference of 24.2 % between these two visual conditions was observed \(t(13) = 4.9\ p < 0.01\). An independent t-test revealed a significant difference between the CN and control subjects \(t(21) = 3.3\ p < 0.01\).
Figure 5.6: Percentage improvement (%) of stability (sway path) with the addition of a foreground in front of the stationary background for each subject with CN and control for both the COP (left panel) and the head (right panel) in Experiment 2. The improvement was calculated as \[ \frac{\text{background score} - \text{foreground score}}{\text{background score}} \times 100 \].

To summarize Experiment 2, it was found that in response to background motion, both in a 2 (background condition) or 3 dimensional environment (foreground condition) CN subjects re-oriented their head and COP in space in a similar manner to control subjects. Measures of postural stability in the condition of stationary background revealed that CN subjects were able to make use of additional visual information (visual foreground) to stabilize their head in space as control subjects, but not to stabilize their COP, in accordance with results of Experiment 1.
F. DISCUSSION

Experiment 1 showed that visual control of equilibrium in the lateral direction in CN subjects appears to have greatest efficacy for low-frequency components of sway (<1Hz). However, visual control of equilibrium was less effective in CN than in control subjects. We could detect a marginal loss of visual stabilization of high-frequency head movements in CN subjects as compared to controls. However high-frequency components to head movement were minimal in both the CN and the control subjects (acuity and normal controls) and thus had little implication for postural stability as measured. Center of foot pressure had more power at high-frequencies than head movement. The reduction of COP instability due to vision, was smaller in CN subjects than in controls across all frequencies, but particularly at frequencies >1Hz. No difference was observed between the two control groups tested (acuity-controls and normal controls) indicating that the differences between the CN and the control subjects was not a consequence of the slightly reduced visual acuity of the CN subjects included in Experiment 1.

Although the paradigm used in Experiment 2 (foreground / background) was different to that used in experiment 1 (eyes closed / eyes open), both showed that CN subjects did not make use of visual information to control the rapid oscillations visible at the level of the COP but use them to stabilise their head in space. Indeed, analysis of body stability (sway path) in Experiment 2, showed that placing an additional foreground object well in front of the stationary background improved head stability as in normal subjects, but not COP stability. With eyes closed COP and head stability were similar in the CN and control subjects. These results are consistent with previous observations (Eggert et al. 1997) which support the thesis that somatosensory and vestibular controls of posture in CN subjects are normal.

Experiment 2 showed that the use of visual information to control body orientation in space (i.e. overall tilt) was normal in CN. Visually induced body sway under conditions of simple motion (background fixation) and motion parallax (foreground fixation) did not differ between subject groups. Consistent with reports
in the literature and our previous experiments, absolute motion induced ipsi-directional body sway (Dijkstra et al. 1994; Lestienne et al. 1977; Lee & Lishman 1975), whereas juxtaposing a stationary target between subject and background provoked sway contra-directional to background motion (Experiment 1-5 in chapter 2; Bronstein & Buckwell 1997). Thus, despite their nystagmus, subjects with CN made normal use of visual motion cues, including motion parallax, to control postural orientation.

Insight into the impairment of visual control of high-frequency postural instability in CN is given by the behavior of normal subjects in stroboscopic light, when the flashes are presented at a strobing frequency of 3-5 Hz (Amblard & Crémiieux 1976; Amblard & Carblanc 1980; Amblard et al. 1985; Isableu et al. 1998; Kapteyn et al. 1979; Paulus et al. 1984). This frequency range is similar to the nystagmus frequency in this sample of CN subjects (see Table 5.1). Isableu et al. (1998) showed that subjects with normal vision, standing in front of a tilted frame, leaned in the direction of tilt under normal or stroboscopic lighting (2.8 Hz). Displacement of an oscillating background under strobed light also causes a continuous modulation of low frequency postural sway (Kapteyn et al. 1979). These results indicate that discrete visual sampling is sufficient for controlling body orientation.

Unlike body orientation, normal equilibrium appears to be degraded under stroboscopic vision at frequencies lower than 6 Hz (Amblard & Crémiieux 1976; Amblard et al. 1985; Paulus et al. 1984). Measured at different levels, from ankle to head, the destabilizing effect of such discrete visual sampling principally affects the lower parts of the body (Amblard et al 1985). The latter authors concluded that discrete visual information ('static cues') were sufficient to control the upper part of the body, which has predominantly low-frequency dynamics. Visual motion cues ('dynamic cues') control oscillations of the lower part of the body which extend through a higher frequency range. Thus, CN subjects appear to be similar to normal subjects in stroboscopic light, in that they share some ability to orient and control low-frequency head instability, but are less able to control the higher frequency
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instabilities of the COP with the visual cues available. Dynamic visual cues, requiring continuous visual feedback, appear to be particularly crucial for fast stabilization of the COP.

The similarity between normal subjects in stroboscopic light and CN subjects is consistent with the concept that the waveform of CN affords intermittent, low-frequency, visual sampling at the time of the 'foveation' periods. CN subjects do not behave as if they were exposed to continuous visual motion because of their nystagmus, and this intermittent sampling of vision to control posture may be related to the mechanism whereby they suppress oscillopsia. These results are particularly interesting in that they indicate that although motion parallax is by essence a dynamic cue, it might be recovered and used on the basis of discrete visual information. This issue will be discussed in more details in the general discussion section of the thesis.

The mechanisms proposed for suppressing oscillopsia in CN include: 1) A reduced sensitivity to retinal image motion (Abadi & Sandikcioglu 1975, Dieterich & Brandt 1987; Shallo-Hoffmann et al. 1998). 2) An ability to extract visual information during the foveation periods (the parts of the nystagmus waveform when the eyes are quiescent and images are most stable on the fovea) and to ignore the smeared vision during high velocity slow phases (Abadi & Worfolk 1989; Dell’Osso & Leigh 1992a,b). 3) The use of extraretinal signals, i.e., efference copy of the CN waveform, to negate the visual effects of the oscillation (Abadi et al 1999; Bedell & Currie 1993; Dell’Osso et al. 1997). The mechanism of efferent copy has long been proposed as the mechanism by which normal observers can distinguish object or world-motion from the retinal slip produced by intended eye movements (see Carpenter 1988). It has been proposed that the use of extra-retinal signals to suppress oscillopsia implies that the unknown source of congenital nystagmus lies within the efference copy-loop (see Dell’Osso 1997 for a model).
Of these, the most recent evidences suggest that the efference copy of the CN waveform appears to be the major factor in oscillopsia suppression (Abadi et al. 1999; Dell’Osso et al. 1997). Indeed, Dell’Osso et al. (1997) reported recently that well-developed foveation in nystagmus is neither necessary nor sufficient for oscillopsia suppression. In addition, Abadi et al (1999) showed that when the image is maintained stationary on the eyes, by an eye-position feedback system, patients with CN then experience oscillopsia. Although foveation periods may not be primarily responsible for oscillopsia suppression, they are important for visual acuity (Dell’Osso et al. 1997) and they may be responsible for the discrete sampling of visual cues to postural orientation in CN.
Chapter 6

General discussion

The results of each set of experiments have been discussed in the appropriate chapter. In the general discussion, a summary of the results is presented followed by a general overview.

1. Motion parallax is a relevant cue for postural control

The first two experimental chapters of this thesis were concerned with the role of motion parallax in postural control. Motion parallax refers to the relative displacement of objects on the retina during self-motion. Although it can be considered as an ecological stimulus experienced during self-motion in everyday life environments, its impact on postural control has received surprisingly little interest. Most of the research aimed at provoking body re-orientation has manipulated the displacement of a whole 2 or 3 dimensional real or simulated environment. As reported above, such displacements evoke compensatory body sway in the direction of motion, either in the anterior-posterior or in the lateral direction of sway. Recently, Bronstein and Buckwell (1997) showed that introducing an earth-fixed foreground in front of a moving background scenery, could reverse the direction of the evoked lateral sway response as long as the observer fixated this foreground object. This readjustment in the opposite direction to background motion is consistent with the motion parallax a standing subject experiences during self-motion in a stationary environment. However, alternative hypotheses such as induced motion, ocular convergence on a close objects needed to be addressed. In addition, since motion parallax is of monocular origin, it appeared important to replicate this observation with monocular vision. In the first chapter we replicated Bronstein and Buckwell’s finding, and showed that this effect was sustained for at least the 11 sec of stimulation. This indicates that this phenomenon does not reflect a transient instability, but a ‘repositioning’ of the body with respect to the visual environment. In addition, we excluded alternative hypotheses by showing that neither induced motion of the foreground, convergence
on a near object nor binocular vision were necessary for this phenomenon to occur. Therefore, we concluded that the postural readjustment opposite to background motion, was determined primarily by motion parallax.

2. *Discrete visual cues or visual flow?*

The second experimental chapter of the thesis presented findings indicating that the motion parallax a subject generates during spontaneous body sway can be used as feedback by the visuo-motor system to control body oscillations. The greater the gradient of parallax (manipulated by changing the distance between the fixated LEDs and the distant ones) was, the less the subjects oscillated. This stabilizing effect was however limited to the low frequency components of sway (< 0.75Hz) both for the head and the COP. In contrast, the effect of vision with full light illumination extended to higher frequency components such as 2-3Hz for the head and even more for COP recordings (see Experiment 4-1 in chapter 4). Based on this frequency specificity and the effect of motion parallax on visually induced body sway (chapter 2), we conclude that motion parallax is particularly involved in slow re-orientations of the body but to a lesser extent in rapid stabilization (>0.5 Hz). This frequency specificity is similar to that reported under stroboscopic illumination. With flashes at a frequency lower than 6Hz, slow re-orientation of the body is preserved (Kapteyn et al. 1979; Isableu et al. 1997) but not rapid stabilization (Amblard et al. 1985). Accordingly, motion parallax might be used more on the basis of static-geometric cues controlling slow body re-orientation instead of continuous visual flow. More insight into this question was gained by studying postural control in patients with congenital nystagmus.

Despite involuntary eye movements, we showed that patients with congenital nystagmus (CN) were able to use motion parallax to control their postural orientation as normal subjects do. On the contrary, in a stationary room with full light illumination, these patients were not able to control rapid oscillations which are particularly important at the level of the COP. The similarity between the behavior of CN patients and that of normal subjects in stroboscopic light suggest that in CN, visual control of posture is restricted by low frequency sampling of the
visual scene (foveation periods). It does also provide more evidence that although motion parallax is by essence a dynamic cue, it could be used to control body orientation on the basis of solely discrete visual samples. Therefore, the velocity component of motion parallax per se might not be the medium for postural control. Instead, relative direction of motion and also geometrical static cues might serve the task. The absence of differences observed in the visually induced response with different background acceleration in chapter 2 (Experiment 5) would also favour this idea.

In theory, as with any motion (Koendering and van Doorn 1975, Longuet-Higgins & Prazdny 1980), motion parallax cues could be adequately obtained from discrete visual samples (providing serial position changes) as long as there is a sufficient number of samples. Continuous perception (continuous velocity information) is not strictly necessary. Direct evidence would require experiments involving manipulation of discrete visual cues (i.e. stroboscopic illumination) in order to suppress the amount of dynamic cues (visual flow) available. Interestingly, it has recently been shown that the visual flow was not necessary to find the direction of heading (Vishton and Cutting 1995; Rushton et al 1998). For instance, Vishton and Cutting (1995) showed that performance in wayfinding could be performed adequately on the basis of discrete visual samples (frequency of 1.5Hz) without continuous visual flow. Their findings together with our own data reveal that the role of visual flow may have been overestimated in the literature of the past 2-3 decades. Although it is likely that human subjects do exploit the visual flow in some spatial activities such as stabilization, static-geometric cues might predominantly be guiding other activities, such as way-finding or controlling of postural orientation.

An alternative explanation could account for the absence of stabilizing effect of motion parallax above 0.5 Hz. As mentioned in introduction, depth information is gained from the magnitude of displacement or relative angular velocity of the retinal image of the objects. A precise estimation of the distance between objects on the basis of motion parallax cues requires however a precise estimation of the displacement of the head of the observer. Conversely, the precise estimation of head displacement on the basis of relative motion between objects requires a
precise estimation of the distance between the objects present in the environment. This mutual interdependency between depth and self-motion perception in impoverished visual environments (e.g., single LED without size cues or blurring) is likely to engender uncertainty. Therefore, in such environments, motion parallax could be used as a gross indicator about self-motion but might not, and probably could not, provide sufficient accuracy to control high frequency components of sway.

3. Postural orientation and postural stabilization

Postural control is charged with two important behavioral goals: postural orientation and equilibrium (stabilization). These two aspects of postural activity are particularly difficult to disentangle in the unperturbed spontaneous body sway of standing subjects: both act to maintain the body parallel to the gravitational vertical. Amblard et al. (1985) proposed that body orientation and stabilization could be differentiated on the basis of the frequency components of sway. They suggested that separate mechanisms could be in charge of postural orientation and stabilization. The first one, resistant to stroboscopic 'interruption', operating below 1-2 Hz, could control the orientation of the upper part of the body on the basis of static visual cues. The second one, 'strobe-vulnerable', operating above 2 Hz, could immobilize the body on the basis of dynamic cues, working upwards from the feet. Although the critical point at ~2Hz between orientation and stabilization is questionable, the model remains heuristic.

Although the data provided in this thesis offer converging evidence that motion parallax is used for the control of postural orientation, its role in stabilization remains an open question. The key elements are 1) the body response evoked by motion parallax simulation (contradirectional body sway) is sustained for a period as long as 11 sec (chapter 2), reflecting a ‘repositioning’ of the body with respect to the visual environment and not a transient instability. 2) in spontaneous body sway (chapter 3), motion parallax affects the low components of body sway (<0.75 Hz), frequency band which, according to the model of Amblard et al. (1985), reflects body re-orientation.
4. Do we use motion parallax in natural environments?

Throughout the different experiments presented in this thesis, motion parallax has played a significant role in postural regulation. In a natural environment, in addition to motion parallax, an observer has at his disposal a large amount of visual information, including binocular disparity, gradient of texture, convergence, accommodation, occlusions and even more. Although all these cues could affect postural sway when manipulated in a highly constrained situation, it seems unlikely that the observer would necessarily always compute and use all this information. Accordingly, under normal viewing conditions, outside laboratories, subjects may make little use of motion parallax! As mentioned in chapter 3, Stoffregen et al. 1999 and Sakellari (Experiment 1 in Guerraz et al. 2000) failed to substantiate the influence of motion parallax on spontaneous body sway in rich visual environments.

An important aspect of motion parallax is that it does not depend on the nature of the objects themselves but on the spatial disposition or relationship between these objects. The objects merely serve as marks that enable the observer to extract the relative displacements or optic flow. It might therefore be quite resistant to visual alterations such as visual defects or blur and low luminosity) such as at night time or in London smog. Accordingly, motion parallax has been shown to provide useful depth information in normal subjects with simulated deficits in acuity, contrast sensitivity or field loss (Jobling et al. 1997) and also in patients with low vision due to low visual acuity, contrast sensitivity or field loss. Similarly, motion parallax generated by active head movements could significantly improve the performance of prehension tasks requiring the analysis of visual depth in patients without binocular vision (Marotta et al. 1995; Dijkerman et al. 1999). It has also been reported as a likely cue in studies of mobility with reduced viewing conditions (Pelli 1987 reported by Jobling et al. 1997). Pelli showed that the accuracy and time taken to walk through a 3D maze providing important motion parallax, were only impaired in very severe visual degradation. Therefore, although the involvement of motion parallax in natural environment remains questionable, it likely plays an important role in locomotor and postural tasks in impoverished...
environments as one would encounter at night time or in patients with visual defects.
REFERENCES


References


References


Appendix

Appendix A: Declaratory note

Most of the work described in the preceding chapters has already been accepted for publication in specialised literature. The articles which have already been published or are still in press are gathered in appendices B-E. An additional review article written by Adolfo M. Bronstein (principal supervisor) and myself has been provided in appendix F.

Dr Adolfo M. Bronstein co-authored all papers and Michael A. Gresty co-authored three of them.


Effect of visual surrounding motion on body sway in a three-dimensional environment

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Unidirectional motion of a uniplanar background induces a codirectional postural sway. It has been shown recently that fixation of a stationary foreground object induces a sway response in the opposite direction (Bronstein & Buckwell, 1997) when the background moves transiently. The present study investigated factors determining this contradirectional postural response. In the experiments presented, center of foot pressure and head displacements were recorded from normal subjects. The subjects faced a visual background of 2 × 3 m, at a distance of 1.5 m, which could be moved parallel to the interaural axis. Results showed that when the visual scene consisted solely of a moving background, the conventional codirectional postural response was elicited. When subjects were asked to fixate an earth-fixed foreground (window frame) placed between them and the moving background, a consistent postural response in the opposite direction to background motion was observed. In addition, we showed that this contradirectional postural response was not transient but was sustained for the 11 sec of background motion. We investigated whether this contradirectional postural response was the consequence of the induced movement of the foreground by background motion. Although induced movement was verbally reported by subjects when viewing an earth-fixed target projected onto the moving background, the contradirectional sway did not occur. These results indicate that foreground—background separation in depth was necessary for the contradirectional postural response to occur rather than induced movement. Another experiment showed that, when the fixated foreground was attached to the head of the observer, the contradirectional sway was not observed and was therefore unrelated to vergence. Finally, results showed that the contradirectional postural response was, in the main, monocularly mediated. We conclude that the direction of the postural sway produced by a moving background in a three-dimensional environment is determined primarily by motion parallax.

Movement of visual surroundings (real or projected) induce postural adjustments in human subjects. Real visual environments used to study this phenomenon have been tilting rooms (Bles, Kapteyn, Brandt, & Arnold, 1980), rotating disks (Dickgans, Held, Young, & Brandt, 1972), and translating rooms (Bronstein, 1986; Lee & Lishman, 1975). Projected visual displays have simulated moving walls, tunnels, floors, and ceilings (Dijkstra, Schöner, & Gielen, 1994; Fluckiger & Baumberger, 1988; Lestienne, Schoechting, & Berthoz, 1977; van Asten, Gielen, & Dienner van der Gon, 1988). Those experiments have shown that motion of a single surface background (in the simplest case, two dimensional) induces a codirectional postural sway.

Postural adjustments in the opposite direction to motion of the surrounding (contradirectional sway) have also been reported. Bronstein and Buckwell (1997) found systematic postural adjustments in the opposite direction of display motion when a stationary object of fixation was placed in the foreground. In their experiment, a visual background was moved behind a stationary window (foreground) with a velocity and amplitude that created an optic flow comparable to what a standing subject would experience during spontaneous quiet sway in a three-dimensional (3-D) environment. As shown in Figure 1, when an observer moves laterally while fixating a distant object, the direction of motion of the images of nearer objects is in the opposite direction of head movement. When the observer fixes a nearer object, the direction of motion of the images of distant objects moves in the same direction as the head. Then, the postural adjustment in the opposite direction of background motion is consistent with the direction of image movement on the retina that a moving subject would experience in a 3-D environment. Useful in the determination of depth (see Howard & Rogers, 1995, for review) and locomotion (Bardy, Warren, & Kay, 1996; Warren, Kay, & Yilmaz, 1996), motion parallax (i.e., the relative movement of images across the retina) also appears to be a potential source of information to stabilize standing posture. Since a short-duration (2-sec) stimulus was used by Bronstein and Buckwell (1997), the aim of our first experiment was to determine whether this postural response is only a transient phenomenon or whether it can sustain for a longer period. This would parallel findings on the codirectional anteroposterior sway observed with a uniplanar moving visual environment (Lestienne et al., 1977).

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Figure 1. When the observer moves his/her head from right to left while fixating a stationary point, the image of the flower in the foreground moves from the left to the right relative to the line of sight. The image of the tree in the background moves from the right to the left, relative to the line of sight. The nearer object (flower) then appears to move in the opposite direction of head movement, whereas the distant object (tree) appears to move in the same direction as the head.

A perceived movement of the fixated foreground induced by the moving background ("induced movement"; see Reinhardt-Rutland, 1988, for review) could also be responsible for the contradirectional sway observed by Bronstein and Buckwell (1997). Van Asten et al. (1988) investigating visually induced body sway in the anteroposterior direction reported that when the central part of their linearly moving display was masked, anteroposterior sway was in the opposite direction of background motion (moving forward-backward) in 25% of the trials. Since the stationary inner part of their display was perceived as moving in the opposite direction of motion (induced movement in depth), the authors interpreted the sway opposite of motion as determined by induced movement of the stationary inner part of the display. Thus, the perceived movement of a target rather than its retinal image movement can be a relevant cue for controlling posture. Analogously, it has been shown that perceived motion can generate nystagmic eye movements with slow phases in the direction of induced movement both in monkeys (Waespe & Schwarz, 1987) and in humans (Collewijn, Curio, & Grüßer, 1982; Heywood, 1973; Yasui & Young, 1975).

The present study was divided into four experiments. Experiment 1 investigated whether the contradirectional postural adjustments observed with a foreground target can be sustained for longer than 1–2 sec. The purposes of Experiments 2 and 3 were to investigate whether the contradirectional sway observed in a 3-D environment is due to induced movement of the fixated foreground, motion parallax, or simply convergence of the eyes on a close target in front of a moving background. Finally, Experiment 4 investigated whether binocular vision was necessary for the contradirectional postural response to occur.

GENERAL METHOD
Apparatus
In Experiments 1–4, we recorded body responses in the lateral direction for different visual conditions. Since the main goal of the study was to characterize the direction of visually evoked postural responses, discrete unidirectional motion of a visual background was the chosen stimulus (Bronstein, 1986; Bronstein & Buckwell, 1997). The visual background consisted of a 2 × 3 m flat board (67° × 90° of visual angle). Photoluminescent yellow-green stripes (7.5c·scd/m²) were used to create the picture of a house with a peaceful garden (Figure 2). Background displacement was achieved by mounting the flat board on a chassis with four pneumatic wheels (bogie) running on a linear track. The bogie was driven by a pair of linear induction motors that generated thrust against a reaction plate situated along the middle of the track. The background was moved at 150 cm from the subject's eyes along an axis parallel to the interaural axis in an otherwise dark room. It was moved 58 cm (21°) leftward or rightward. A constant velocity of 6 cm/sec was reached after approximately 1.25 sec of acceleration onset and sustained for 8.5 sec before the deceleration occurred. After each trial, the subjects were asked to close their eyes while the background was moved.
back to its starting position and reilluminated with a lamp to keep a constant level of luminance.

Procedure

In all experiments, the subjects were instructed to "stand still and relaxed" with hands at their sides. They stood barefoot on a rigid foot support placed on top of a slab of foam rubber (height, 5 cm; specific weight, 30 g/dm³) resting on the sway platform. The aim was to increase the instability of the subjects so that any effect of visual condition on the subjects' sway could be more easily observed (Bies et al., 1980; Bronstein, 1986; Lee & Lishman, 1975). Postural sway in the lateral direction was recorded using a force platform for center of pressure (COP) recordings. The subject wore a lightweight helmet carrying an infrared LED so that head displacements could be measured with a Shottky barrier photodetector camera (resolution of 0.1 mm, linear up to ±8 cm) mounted 40 cm above the subject's scalp. Since the distance between the head-mounted infrared light and the Shottky camera was maintained at 40 cm, head-sway values were normalized for the subjects' heights (signal X mean height of group/individual's height). A computer was used to generate the command signal to the linear motors of the bogie and to acquire the output signals from the sway platform and the Shottky camera at a sampling rate of 125 Hz. The sway signals were also continuously monitored on line on an oscilloscope. The experimenter familiarized himself with the spontaneous sway amplitude of each subject and delivered the stimuli at points of average or smaller than average sway amplitude.

Measurements taken from COP and head position signals included average position (Equation 1), which measures body orientation relative to the prestimulus position value (Xbaseline) in the lateral direction. Average position indicates the directionally specific effect of any stimulus on head or COP position in space:

\[ X_n = \frac{1}{N} \sum_{i=1}^{N} (x_i - X_{\text{baseline}}) \]  

where N is the number of samples, \( x_i \) is the COP/head position for the ith sample, and \( X_{\text{baseline}} \) is the average position (COP or head) during the 4 sec preceding stimulus onset. It was calculated for each single trial during the 8.5 sec of constant velocity and then averaged for each subject and visual condition. Stimulus onset was used to synchronize the recordings during averaging. This allowed the specific component of sway due to the visual stimuli to emerge. Since no differential effect between the two directions of motion was expected, responses to rightward and leftward stimuli were combined (after reversing all sway responses during leftward motion).

One-sample t tests were used to obtain the significance of the effect of a given visual condition on average COP and head position values for each individual or for the group. Paired-samples t tests were used for all comparisons of the mean values, based on individual averages. Spearman correlation coefficients were used to assess any relation between sway magnitudes for different conditions of visual fixation. A .05 significance level was adopted throughout.

EXPERIMENT 1

Method

Subjects. Twelve normal subjects with normal or corrected vision (normal visual acuity and stereopsis) gave their informed consent to participate in the experiment. The subjects ranged in age...
from 25 to 50 years old. All subjects were healthy, without musculo-skeletal or neurological disorders.

**Visual conditions.** The three visual conditions to which each subject was exposed were the following: (1) looking straight ahead at the background that was the only visible display (background fixation)—the subjects were instructed to look straight ahead, binocularly, at the house in the background without following it when it moved; (2) fixating a cross (1 X 1 cm) placed at the center of a purpose-built earth-fixed luminescent window frame (30 X 24 cm), at a distance of 50 cm from the subject's eyes (Figure 2; foreground fixation); and (3) looking straight ahead at the background through the earth-fixed window frame 50 cm away (background fixation through the window). Each visual condition consisted of 24 trials—8 with motion to the right, 8 to the left, and 8 with stationary background (shams)—equally divided into two groups of 12 pseudo-randomized stimuli. The first three blocks (one per visual condition), followed by the second three blocks, were presented in a Latin-square design. A rest of 15 min was given to the subjects between the two test sessions.

**Results and Discussion**

Figure 3 shows a typical sample record of head and COP displacements during background and foreground fixation conditions. Head and COP displacements followed a similar trend during the whole recording in the three different visual conditions. Values for the COP and the head displacements are reported in Table 1.

When the subjects were looking straight at the background as shown in the sample record in Figure 3 (background fixation condition, left panel), an initial postural readjustment was observed in the direction of motion with a latency of approximately 800 msec. This initial response was followed by a resetting, which brought the COP and the head toward their initial baseline positions. The postural resetting was then followed by an increasing displacement of the COP and the head in the direction of background motion until the end of the stimulus, as shown in the sample record in Figure 3. When the movement of the visual background stopped, a postural correction bringing the COP and the head toward their initial baseline was observed. By synchronizing stimulus onset, the initial postural response can be clearly identified in the average from individual data (Figure 4, n = 12). The mean slopes of the initial postural response computed for each individual subject were 6.7 mm/sec for the COP and 4.1 mm/sec for the head. As shown in Figure 4, the initial codirectional postural response during background fixation was followed by a postural correction in the op-

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**Figure 3.** A sample record of a postural response induced by the moving background in background fixation condition (right panel) and in foreground fixation condition (left panel). Upward deflections indicate deviation in the direction of stimulus motion.
posite direction, bringing the COP (and the head) to baseline levels. The position of both the COP and the head at this point, computed for each individual subject, did not differ from the baseline level [COP, \( t(11) = 0.1, p = .94 \); head, \( t(11) = 0.98, p = .34 \)]. One-sample \( t \)-tests, based on the average position of each subject during the 8.5 sec of constant background velocity, confirmed the significance of deviation in the direction of background motion [COP, \( t(11) = 3.8, p < .01 \); head, \( t(11) = 2.9, p < .05 \)]. Seventy-six percent of single trials were found to be in the direction of stimulus motion. Three of the 12 subjects tested showed no statistically significant postural adjustment.

During fixation of the foreground target (foreground fixation condition), a displacement of the COP and of the head was observed in the opposite direction of background motion as shown in the sample recording presented in Figure 3 (right panel). The mean latency of the postural response was around 850 msec (Figure 4) and was not significantly different from that observed in the condition of background fixation [COP, \( t(11) = 1.9, p = .08 \); head, \( t(11) = 0.9, p = .40 \)]. The slopes of the initial postural response were \(-3.1\) mm/sec and \(-2.1\) mm/sec for COP and head displacements, respectively, and were significantly less steep than the slopes of the initial postural response observed in the condition of background fixation [COP, \( t(11) = 3.8, p < .01 \); head, \( t(11) = 2.8, p < .05 \)]. The initial postural displacement in the opposite direction to that of the visual stimulus was not followed by a sharp postural correction toward the baseline (Figure 4). Instead, the subjects continued to lean in the opposite direction of stimulus motion until it stopped. The average peak displacements in the opposite direction of motion were \(6\) mm and \(8\) mm for the COP and the head, respectively. One-sample \( t \)-test analysis confirmed that the displacements of both the COP and the head in the opposite direction of background motion were statistically significant [COP, \( t(11) = 9.4, p < .01 \); head, \( t(11) = 6.9, p < .01 \)]. The postural readjustments in the opposite direction of motion were significant in all subjects except one. Eighty-nine percent of responses to the single trials were in the opposite direction of stimulus motion. The COP and head displacements recorded during foreground and background fixation were negatively correlated [COP, \( r = -.62, p < .05 \); head, \( r = -.60, p < .05 \)]. Therefore, the more a subject deviated in the direction of motion during background fixation, the more this subject deviated in the opposite direction during foreground fixation (Figure 5).

During the condition of background fixation through the window, a slight tendency to lean in the opposite direction of background motion was observed (Figure 4). This effect was statistically significant when individual averages were considered [COP, \( t(11) = 2.2, p < .05 \); head, \( t(11) = 2.7, p < .05 \)] but was not consistent since it was significant in only 4 of the 12 subjects tested. Sixty percent of responses were in the opposite direction of stimulus motion. The amplitude of the postural displacement observed in this visual condition was statistically different from that observed in background [COP, \( t(11) = 3.7, p < .01 \); head, \( t(11) = 3.1, p < .01 \)] and foreground [COP, \( t(11) = 3.6, p < .01 \); head, \( t(11) = 4.3, p < .01 \)] conditions. No significant correlations with the other two conditions were observed for either the COP or the head recordings.

No difference in average position was found between the three sham conditions (trials for each visual fixation condition with stationary background). All trials were combined to obtain a single average per subject, and no consistent body movement to the right or left appeared when the background was stationary (Figure 4).

The slower (i.e., less steep) initial postural displacement observed during foreground fixation, relative to that during background fixation, would be consistent with the visual flow experienced by a subject swaying in a stable environment. A spontaneous displacement of the head at \(1\) cm/sec when fixating a stationary background placed at \(150\) cm from the eyes produces a retinal image motion (0.39°/sec). This is approximately half the amount of retinal image motion of the background that subjects experience when fixating a foreground object placed at \(50\) cm from the eyes (0.76°/sec) (see Guerczak, Sakellari, Burchill, & Bronstein, 2000). Thus, to produce a similar retinal image motion of the background that subjects experience when fixating a foreground object, it would be twice as fast in the foreground fixation condition as in the background fixation condition.

Table 1: Average Position (Mean and Standard Deviation; in Millimeters) of the COP and the Head According to the Visual Condition in Experiment 1

<table>
<thead>
<tr>
<th>Condition</th>
<th>Background</th>
<th>Foreground</th>
<th>Background Window</th>
<th>Sham</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( M ) SD</td>
<td>( M ) SD</td>
<td>( M ) SD</td>
<td>( M ) SD</td>
</tr>
<tr>
<td>Head sway</td>
<td>3.41 4.01</td>
<td>-3.38 2.70</td>
<td>-2.42 3.07</td>
<td>0.27 0.61</td>
</tr>
<tr>
<td>COP</td>
<td>2.96 2.67</td>
<td>-4.01 1.63</td>
<td>-1.27 1.97</td>
<td>0.26 0.74</td>
</tr>
</tbody>
</table>

Note—A positive value indicates a deviation in the direction of motion, whereas a negative value indicates a deviation in the opposite direction of motion.
Background fixation

Foreground fixation

Fixation through the foreground

No stimulus

Figure 4. COP displacements evoked by a moving visual background during the background condition, the foreground condition, and through the window fixation condition. COP displacement with a stationary background is also reported at the bottom of the figure. The average positions and standard deviations of the COP displacements in the 12 normal subjects are shown. Upward deflections indicate a displacement in the direction of stimulus motion; downward deflections indicate a displacement in the opposite direction of motion.

tently reported in the field of visual control of balance (Crémieux & Mesure, 1994; Isableu, Ohlmann, Cré-}

mieux, & Amblard, 1998; Lacour et al., 1997; Lestienne et al., 1977; Masson, Mestre, & Pailhous, 1995; Warren et al., 1996). For instance, Lestienne et al. (1977) reported that 20% of subjects tested with linear motion of the visual scene did not show any postural readjustment. Although the reason is not well understood (see Isableu et al., 1998), a postural response could be induced in some of these nonresponsive subjects when they were asked to do a mental arithmetic task at the same time as the postural task (Lestienne et al., 1977), indicating that attentional mechanisms could affect the postural response. The 3 above-mentioned subjects showing no visually induced body sway in response to background motion in Experiment 1 were not included in subsequent experiments.

In summary, we replicated the observation of Bronstein and Buckwell (1997) showing that by fixating a stationary foreground placed between the subject and a moving background, the postural response induced by motion of the background is reversed in direction. In ad-
when the foreground and background are at 100 cm from each other.

**Method**

**Subjects.** Eight normal subjects with normal or corrected vision gave their informed consent to participate in these experiments. The subjects ranged in age from 24 to 50 years old. Three of these subjects had participated in Experiment 1.

**Visual conditions.** Parameters of background motion were the same as those in Experiment 1. The subjects were exposed to three visual conditions: (1) looking straight ahead at the background as in Experiment 1 (background fixation condition); (2) fixating a laser point projected on a small earth-fixed black dot (1 cm of diameter) taped on a piece of Perspex and adjusted at eye level—the fixation point was at 50 cm from the subject's eyes and at 100 cm from the background (foreground condition); and (3) fixating an earth-fixed laser point projected directly on the background (coplanar condition).

Each condition consisted of 21 trials—7 to the right, 7 to the left, and 7 sham (no motion) stimuli—divided into two groups of 10 or 11 pseudo-randomized stimuli. The first three blocks (one per condition) followed by the second three blocks were presented in a Latin-square design. The subjects were asked at the end of each block for the two visual conditions with laser-point fixation to tell the experimenter whether or not and how the laser point appeared to move with respect to the background.

**Results and Discussion**

In the coplanar condition, 7 subjects reported seeing either systematically or from time to time the earth-fixed laser point moving in the opposite direction of background motion. In the foreground condition, only 1 subject reported seeing the laser point moving. Values for the COP and the head displacements are reported in Table 2.

When the subjects were looking straight at the background (background condition), the motion stimulus induced a body readjustment in the direction of motion (Figure 6, top trace). The pattern of sway was similar to that observed in Experiment 1. One-sample t-test analysis confirmed that this deviation in the direction of motion was statistically significant [COP, \(t(7) = 5.02, p < .01\); head, \(t(7) = 3.3, p = .01\)]. This deviation was not significant in 2 of the 8 subjects tested.

In the foreground fixation condition, the linear motion of the background induced a clear postural readjustment in the opposite direction of motion (Figure 6, middle trace) as in Experiment 1. One-sample t-test analysis confirmed

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**Table 2**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Background</th>
<th>Motion Parallax</th>
<th>Induced Movement</th>
<th>Sham</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M  SD</td>
<td>M  SD</td>
<td>M  SD</td>
<td>M  SD</td>
</tr>
<tr>
<td>Head sway</td>
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<td>-3.68 2.27</td>
<td>0.68  2.31</td>
<td>0.64  1.04</td>
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<tr>
<td>COP</td>
<td>3.1  1.7</td>
<td>-2.8 1.53</td>
<td>1.08  1.7</td>
<td>0.42  0.6</td>
</tr>
</tbody>
</table>

Note—A positive value indicates a deviation in the direction of motion, whereas a negative value indicates a deviation in the opposite direction of motion.
EXPERIMENT 2

The results of Experiment 2 suggest that, in the lateral direction, motion parallax is a more relevant cue to elicit a contradirectional sway response than is induced motion.

EXPERIMENT 3

The aim of Experiment 3 was to examine whether the possibility that the contradirectional postural response described in Experiments 1 and 2 was due to ocular con-
vergence (in front of the background) rather than to motion parallax. Convergence on a fixation point in the foreground produces a defocused double image of the visual background behind. The defocusing reduces spatial frequency corresponding to a reduction in visual acuity, which has been found to play a significant role in the regulation of lateral sway in a stable environment (Paulus, Straube, & Brandt, 1984).

Method

Subjects. Seven subjects with normal or corrected vision gave their informed consent to participate in this experiment. The subjects ranged in age from 21 to 52 years old. Three of the 7 subjects had participated in either Experiment 1 or Experiment 2. One subject had to stop in the middle of the experiment because of nausea. Since this subject took part in the first three blocks of the experiment (one block per visual condition), his data were included in the analysis of the experiment.

Visual conditions. Parameters of background motion were the same as those in Experiment 1. The subjects were exposed to three visual conditions: (1) looking straight ahead at the background, as in Experiments 1 and 2 (background condition); (2) fixating an LED placed on a piece of Perspex adjusted to eye level—the fixation point was at 40 cm from the subject’s eyes and at 110 cm from the background (earth-fixed foreground condition); and (3) fixating an LED at 40 cm from the subject’s eyes, attached to the helmet with a rod (head-fixed foreground condition). For both head-fixed and earth-fixed foreground, convergence and accommodation remained the same, and the background remained out of focus. Unlike the condition of direct background fixation, when the fixation point is coupled with head movement, it does not produce motion parallax. When moving the head to one side, the background will be perceived as moving in the opposite direction of head motion as in the condition of direct background fixation. Then, as for the condition of direct background fixation, a sway codirectional to background motion was expected.

Each condition consisted of 12 stimuli—4 to the right, 4 to the left, and 4 shams (no motion)—divided into two groups of 6 pseudo-randomized stimuli. The first three blocks (one per condition) were followed by the second three blocks, which were counterbalanced. Each subject took part in the first three blocks of the experiment (one block per visual condition), his data were included in the analysis of the experiment.

Discussion

Visual conditions. The motion of the background condition and the earth-fixed foreground fixation condition was the same as in Experiment 1 (Figure 2). The subjects were fixating the foreground binocularly or monocularly with their dominant eye, the second eye being covered by a patch. Three subjects had a left dominant eye, and 5 had a right dominant eye. Each condition consisted of 15 stimuli—5 to the right, 5 to the left, and 5 shams (no motion)—divided into two groups of 7 or 8 pseudo-randomized stimuli. The first two blocks (one per condition) followed by the second two blocks were counterbalanced. A rest of 15 min was given to the subjects between the two test sessions.

Table 3

<table>
<thead>
<tr>
<th>Condition</th>
<th>Background</th>
<th>Head-Fixed Foreground</th>
<th>Earth-Fixed Foreground</th>
<th>Sham</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>COP</td>
<td>M  0.67</td>
<td>M  0.72</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.64 4.02</td>
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<td>2.66 2.5</td>
<td>4.49 1.9</td>
<td>-3.66 4.03</td>
</tr>
</tbody>
</table>

Note—A positive value indicates a deviation in the direction of motion, whereas a negative value indicates a deviation in the opposite direction of motion.
Results and Discussion

For both viewing conditions, the linear visual motion induced a clear displacement in the opposite direction of background motion, as in Experiments 1–3 (Table 4). The amplitude of the contradirectional sway response was slightly but significantly larger during binocular fixation than during monocular fixation for the COP [t(8) = 3.4, p < .05]. Similar results were observed for head position, except that the difference between the two viewing conditions did not reach significance [t(8) = 1.6, p = .15]. As expected, when the background remained stationary (sham condition), no postural displacement was observed in either viewing condition (one = sampled t test, p > .05); thus, binocular and monocular conditions did not differ [COP, t(8) = 0.4, p = .69; head, t(8) = 0.3, p = .71].

The results of Experiment 4 showed that the contradirectional postural response observed during foreground fixation was observed during both monocular and binocular conditions. This indicates that the contradirectional response is, in the main, monocularly mediated. The trend for larger binocular responses than monocular responses is in agreement with previous studies on spontaneous body sway showing improved body stability during binocular fixation relative to that during monocular fixation (Fox, 1990; Jones & Lee, 1981; Paulus et al., 1984; Stoffregen, Smart, Bardy, & Pagulayan, 1999).

**GENERAL DISCUSSION**

In the present study, we attempted to further define the significant factors determining the contradirectional postural response previously reported by Bronstein and Buckwell (1997) when a stationary fixed foreground was placed between a moving background and a standing subject. The results of Experiments 1–4 show that this contradirectional postural response was not just a transient response but could be sustained at least for the 11 sec of background motion. The results of these experiments also provide converging evidence that this contradirectional sway elicited by earth-fixed foreground fixation against a moving background was due to motion parallax. The key arguments are the following: (1) The presence of an earth-fixed foreground target reversed the postural response induced by the moving background when the direction of displacement of the two objects on the retina mimics what an observer would experience during self-motion in a stable environment (foreground fixation). When the direction of displacement of the two objects on the retina are inconsistent with what a moving observer would experience, the postural response was found to be inconsistent (fixation through the window condition). (2) The effect is not mediated by induced movement. Although most of the subjects reported an induced movement illusion when the fixation point was coplanar to the moving background, no systematic contradirectional postural response was observed (Experiment 2). (3) The contradirectional postural response is not caused by ocular convergence/accommodation on a foreground target against a defocused moving background, since codirectional sway was elicited with a head-fixed target (Experiment 3). Finally, this contradirectional postural response could be observed monocularly and binocularly (Experiment 4). Thus, the necessary condition for reversed sway seems to be a differential motion of foreground with respect to the background similar to that which would be provoked by self-motion of the observer.

As suggested recently, control of stance is not independent of other suprapostural behavioral tasks (Riccio & Stoffregen, 1988; Stoffregen et al., 1999). For instance, in order to shoot a target with a gun, one requires minimizing sway in order to aim successfully. Thus, the fixation task can significantly affect the control of stance. The data presented here would suggest that one of the ways in which this could come about is by using parallax cues emerging as a result of the new fixation task. Disentangling suprapostural fixation task from parallax-mediated effects can, however, prove difficult. As mentioned above, the visual flow that a subject would experience in a 3-D environment is modulated by the fixation point. As shown in Figure 1, when a moving subject is fixating a given object, nearer objects move on the retina in the opposite direction of self-motion, whereas far objects move in the direction of motion. Thus, one could argue that the reversal of body sway observed in the foreground conditions of Experiments 1–4 and previously (Bronstein & Buckwell, 1997) could be the consequence of the fixation task per se rather than motion parallax.

Data from Experiment 1 and recent research (Guerraz...
et al., 2000), however, do not support this hypothesis. In Experiment 1, the fixation task in the condition of background fixation and in the condition of background fixation through the window was the same: The subjects looked straight at the background. If the fixation task was the relevant factor controlling postural readjustment, a similar postural response should be observed in these two conditions. On the contrary, the postural readjustment triggered by motion of the background was entirely different. When fixating the background with no objects in the foreground, the subjects showed the well-established codirectional postural response (Lee & Lishman, 1975; Lestienne et al., 1977). When subjects fixate the background through the foreground window, the response is significantly smaller in amplitude, inconsistent, and with a contradirectional preference, as shown in the present study and a previous study (Bronstein & Buckwell, 1997).

In addition, we have recently shown that motion parallax plays a specific role in the control of spontaneous body sway in a stable 3-D environment (Guerraz et al., 2000), in which the effect of motion parallax was observed when depth information was manipulated and the fixation task was always kept constant. In those experiments, subjects always fixated an LED at 30 cm from the eye while motion parallax was increased by placing additional LED targets at different distances from the fixated LED. The results showed that the low-frequency components of sway (<0.5 Hz) were significantly reduced with increasing distance between LEDs. Thus, although the fixation task can be an important factor affecting postural responses, it can explain neither the effect of depth information observed on spontaneous body sway (Guerraz et al., 2000) nor that observed on visually induced body sway (Experiments 1–4 reported here).

The retinal periphery has been considered to be dominant for self-motion perception and the control of posture (Brandt, Wist, & Dichgans, 1975; Dichgans & Brandt, 1978). However, Andersen and Dyre (1989) found that visually induced body sway could be elicited when stimulation was restricted to a small area of the central visual field (15°). Moreover, optical information for the control of posture also appears to be a function of the geometric structure of the light rays that form the optical flow field (Gielen & van Asten, 1990; Masson et al., 1995; Stoffregen, 1985, 1986). Stoffregen (1985) demonstrated that the retinal periphery itself shows no particular facility for detecting posteriorly relevant information if the visual flow is radial as opposed to lamellar. The central versus peripheral distinction also applied for near and far vision. Delorme and Martin (1986) found that both the retinal periphery and the depth periphery played important roles in the visually induced body sway. They showed that forward and backward movement of the scene limited to the foreground produced little postural sway in the anteroposterior direction relative to motion located in the background. In the foreground fixation condition in Experiments 1–3, the "central object," in terms of both retinal area and depth, reversed sustainably the driving effect of the "peripheral stimulus." Our results suggest that the amplitude of postural readjustment in both background and foreground fixation conditions was under the control of the moving background, as shown by the similar amplitude of both the codirectional and the contradirectional sway and by the significant correlation observed between these conditions (Figure 5). However, while the amplitude of postural readjustment appeared to be under the control of the moving background, the spatial relation between the background, the foreground, and the observer's fixation point determined the direction of the postural readjustment. These results provide more evidence that the control of stance is dependent not only on the retinal location of objects and on the geometric structure of the visual flow but also on the observer's fixation point in a 3-D environment. Then, when present in the visual environment, motion parallax is a powerful cue to specify the direction of sway in the frontal plane.

As mentioned above, it remained possible that the induced movement of the foreground rather than motion parallax was the relevant cue to reverse the postural sway to background motion. The purpose of Experiment 2 was to test this alternative explanation. Although most subjects reported the illusory motion of the fixation point when coplanar to the moving background, no consistent direction-specific postural response was observed. Unlike motion parallax, induced movement can exist in the absence of an observer's own motion. Our results do not exclude the possibility that induced movement, in some trials or circumstances, can induce contradirectional postural response, as proposed by van Asten et al. (1988) for the sagittal plane (i.e., induced motion in depth), but its contribution in the lateral direction appears to be less important than that of motion parallax.

The absence of direction-specific postural response was also observed in the condition of background fixation through the window (Experiment 1). As in the coplanar condition (Experiment 2), the relative movement of the two objects in the condition of background fixation through the window does not signal any real self-body movement the subject could experience in the condition of stationary background. However, motion parallax in this condition could signal passive motion (e.g., a subject seated in a car or in a bus). As shown in Figure 1, when a subject is moving his/her head while looking beyond a near object, the image of the fixated point remains stable on the retina while the image of the near object moves in the opposite direction of head motion. To mimic more realistic self-movement when the subject is looking at a far object, as in the condition of background fixation through the window, there should be movement of the near object. These findings suggest that in order to induce consistent and directionally specific responses, the relative motion of objects within the foreground and the background must reflect what a moving observer would experience in a stable 3-D environment. Note that the retinal displacement of the moving background (21°) in Ex-
experiments 1–4 was larger than what a subject would experience during spontaneous sway (Bles et al., 1980). However, it has been reported that stimulus amplitude is not a relevant parameter for visuopostural responses (Lestienne et al., 1977; Masson et al., 1995; van Asten et al., 1988).

In conclusion, the results of the present experiments clearly demonstrate that motion parallax can be a significant factor in postural orientation in standing subjects, as it has been found earlier in walking subjects (Bady et al., 1996; Warren et al., 1996). Despite strong biomechanical differences, the visual control of standing and walking in a 3-D environment appears to be regulated by similar visual cues among which motion parallax is of particular importance.

REFERENCES


(Manuscript received April 27, 1999; revision accepted for publication May 10, 2000.)
Influence of motion parallax in the control of spontaneous body sway

Abstract Visual control of postural sway during quiet standing was investigated in normal subjects to see if motion parallax cues were able to improve postural stability. In experiment 1, six normal subjects fixated a fluorescent foreground target, either alone or in the presence of full room illumination. The results showed that subjects reduced body sway when the background was visible. This effect, however, could be mediated not only by parallax cues but also by an increase in the total area of visual field involved. In experiment 2, other parameters such as image angular size and target distance were controlled for. Twelve subjects fixated a two light-emitting diode (LED) target placed at 45 cm from their eyes in a dark room. A second similar two-LED target was placed either at 170 cm (maximum parallax) or at 85 cm (medium parallax) from the fixated target, or in the same plane of the fixated target (0 cm, no parallax). It was found that the amplitude of sway was reduced significantly, by approximately 20%, when the two targets were presented in depth (parallax present) as compared to when they were in the same plane (no parallax). The effect was only present in the lateral direction and for low frequency components of sway (up to 0.5 Hz). We confirmed in experiment 3 on eight subjects with a design similar to that used in experiment 2 that the effect of motion parallax on body sway was of monocular origin since observed with monocular and binocular vision.

Introduction

Vision provides important information for the control of posture. This is illustrated, for instance, by the fact that the amplitude of spontaneous sway increases by as much as 50% when subjects close their eyes (Edwards 1946; Travis 1945). Vision carries information about displacements and movements of the observer relative to a stable environment as well as about displacements of external objects. Thus, visual stabilisation of posture depends on the ability to differentiate optical flow due to ego motion from that due to object motion.

Displacement of an observer in a three-dimensional visual environment generates a spatiotemporal pattern on the retina specific to observer's motion (Gibson et al. 1955). When two or more objects are at different distances, the projections of these objects on the retina move in relation to each other as the observer moves. This horizontal optical motion of objects on the retina is referred to as motion parallax. An important factor affecting motion parallax is the distance in depth between the observer and the fixation point and also the distance between the different objects in the environment. Thus, motion parallax is proportional to the distance between the different stimuli and inversely proportional to the distance between the fixated object and the observer.

Motion parallax has long been recognised as a source of information about the relative distances of objects in the environment (see Howard and Rogers 1995), but only recent research has yielded its utility in the control of posture (Bronstein and Buckwell 1997; Guerraz et al. 1999) and locomotion (Bardy et al. 1996; Warren et al. 1996). By simulating motion parallax that an observer would experience in a stable three-dimensional environment, Bronstein and Buckwell (1997) showed that specific postural readjustment to motion parallax can be induced. In this research, the role of motion parallax in the control of stance was investigated with techniques rely-
ing on visual destabilisation (moving visual scene). The aim of the present research was to investigate the role of motion parallax in spontaneous body sway in a stable three-dimensional environment.

Materials and methods

Experiment 1

Six normal subjects (two females, four males, average age 30 years) with normal or corrected vision were tested. In this experiment the effect of motion parallax interacting with target distance was investigated. Subjects fixated a fluorescent foreground window at distances of 50, 100, 150, 200 and 250 cm from the eyes, in an otherwise dark room or in the presence of a background (250 cm from subjects eyes) and room illumination. The foreground consisted of a piece of 16x18 cm clear perspex with a fluorescent rectangular border, 1 cm wide, placed at 1 m from the eyes. A fixation point consisting of a small cross (1 by 1 cm, 2 mm wide) was present in the centre of the fluorescent window. Photoluminescent yellow-green stripes (luminance of 0.075 cd/m^2) were used to create the window frame. The background consisted of an outline of a landscape scene, covering the entire 2.9x1.5 m wall; the room size was 2.9 m high, 4 m long and 1.5 m wide. Since the background was always at 250 cm from the subjects eyes and the distance between the foreground and the background varied between 0 to 50, 100, 150 or 200 cm, the amplitude of motion parallax induced by body sway was inversely proportional to eye-foreground distance.

Experiment 2

Twelve normal subjects (seven females, five males, average age 33.6 years) with normal or corrected vision participated in the experiment. In order to isolate motion parallax, the distance between the eyes and the fixation point was fixed (45 cm) and the only visual cues available consisted of light-emitting diodes (LEDs) mounted on a piece of perspex in an otherwise dark room. Two sets of two LEDs were used; one set was positioned at 45 cm from the eyes whilst the other set was placed at one of three different distances from the fixed LEDs, 170 cm (‘maximum parallax’), 85 cm (‘medium parallax’) and at the same distance (0 cm, ‘no parallax’) (Fig. 1). The set of LEDs consisted of a pair of LEDs on the same plane, vertically separated by 2 cm, offering a minimum of verticality cues. The subjects were instructed to binocularly fixate the top LED at 45 cm, adjusted to the subjective level of their eyes. With this set-up, the absolute change in size of the visual angle point was fixed (45 cm) and the only visual cues available consisted of light-emitting diodes (LEDs) mounted on a piece of perspex in an otherwise dark room. Two sets of two LEDs were used; one set was positioned at 45 cm from the eyes whilst the other set was placed at one of three different distances from the fixed LEDs, 170 cm (‘maximum parallax’), 85 cm (‘medium parallax’) and at the same distance (0 cm, ‘no parallax’) (Fig. 1). The set of LEDs consisted of a pair of LEDs on the same plane, vertically separated by 2 cm, offering a minimum of verticality cues. The subjects were instructed to binocularly fixate the top LED at 45 cm, adjusted to the subjective level of their eyes. With this set-up, the absolute change in size of the visual display was largely reduced. Sway was also recorded in full room illumination while the subject fixated the LEDs at 45 cm and, also, with eyes closed. Subjects were standing in a large room (4.5 m high, 10 m long and 5 m wide), facing the front wall at 2.3 m, with lateral walls at approximately 5 m on each side.

Experiment 3

The rationale of experiment 3 was to investigate whether any effect of motion parallax on body sway is present with monocular and binocular vision. Eight normal subjects (two females, six males, average age 33.6 years) with normal or corrected vision participated in experiment 3. Subjects were standing in the middle of a large room (4.5 m high, 10 m long and 5 m wide), facing the front wall at 6.5 m. As in experiment 2, the only visual cues available consisted of two LEDs mounted on a piece of perspex in an otherwise dark room. The distance between the fixation point and the eyes was constant at 100 cm from the subjects eyes with a second set of two LEDs placed at 300 cm from the fixation point (motion parallax). This condition was compared to one of fixation of a target at 100 cm from the subject (no parallax). The subjects fixated binocularly or monocularly (non-dominant eye patched) the set of LEDs placed at 100 cm. The order of binocular and monocular fixation was counterbalanced. Sway was also recorded with eyes closed and in a condition of background wall illumination while fixating the LEDs at 100 cm. The illuminated background wall, fully textured, was at 550 cm from the fixation point, providing important motion parallax.

In experiments 1–3, subjects were instructed to stand still with hands at their side and feet 3 cm apart, at the level of the internal malleoli. They stood barefooted on a rigid foot support placed on top of a slab of foam rubber (height 5 cm; specific weight 30 g/dm^3) resting on the sway platform. The aim was to increase the instability of the subjects so that any effect of visual condition on the subjects’ sway could be more easily observed (Bles et al. 1980; Bronstein 1986; Bronstein and Buckwell 1997; Kunkel et al. 1998). Lateral and sagittal deviations of the centre of foot pressure (COP) were obtained but, because of the interposition of the foam, these measurements are only an estimate of the real displacement of the COP. The measurements are therefore relative but, since all experiments were carried out on foam, and the study was planned with a within subject design, they are unlikely to influence comparisons between different conditions. In addition, a pilot experiment showed that optical recordings of the vertical displacement of the foot support surface were highly correlated (r>0.90) with the force platform signals. Head sway was also recorded with a three-dimensional search coil (Polhemus 3space fastrak, experiment 1) and with an optical system (Schotky camera, experiments 2 and 3). Due to software changes, the signals were sampled at 20 Hz in experiments 1 and 2 and at 125 Hz in experiment 3, and normalised to allow for each subject’s mass and height. Recording time for each visual condition was 1 min. All subjects gave informed consent for the experiments, following approval by the local ethics committee.

Average deviation of the COP and the head in the lateral and sagittal plane were measured in experiments 1–3. Additional measurements and statistical procedures will be indicated in the Results section in experiments 2 and 3.

Results

Experiment 1

Figure 2 shows the data from all subjects for the COP and head displacements. Data were analysed with an
ANCOVA (5 distance × 2 display) with repeated measures in the lateral and anteroposterior direction of sway.

In the lateral direction (Fig. 2 left panels), a reduced 'average deviation' was observed when ambient visual information was provided in addition to the visual foreground. This main effect was significant both for COP (F_{1,5}=92, P<0.01) and head displacements (F_{1,5}=29, P<0.01). The main effect of eye-target distance was also found to be highly significant both for the COP (F_{4,20}=6.1, P<0.01) and the head (F_{4,20}=7.8, P<0.01). The effect of eyes-target distance was particularly clear between 50 and 100–150 cm for the COP and for the head. No significant interaction was found between these two factors (COP: F_{4,20}=0.54, P=0.71; head: F_{4,20}=0.81, P=0.53).

In the anteroposterior direction of sway, the main effect of additional ambient visual information was significant (COP: F_{1,5}=36.5, P<0.01; head: F_{1,5}=43.3, P<0.01). The main effect of distance was close to significance for head sway (F_{4,20}=2.16, P=0.1) but not for COP sway (F_{4,20}=0.57, P=0.68). No interaction between the two factors was found both for the COP and the head.
**Experiment 2**

**Average deviation**

Figure 3 shows the data from the 12 subjects for the COP and head displacements. As can be seen in Fig. 3, a clear decrease of body sway can be observed when subjects were fixating LEDs in darkness or in full light as compared to the condition of eyes closed. Since the specific purpose of this experiment was to isolate the motion parallax component, only the experimental conditions, maximum (170 cm), medium (85 cm) and no parallax conditions (0 cm) were subjected to statistical analysis.

In the lateral direction, the ‘average deviation’ of the COP and head displacement decreased when motion parallax was available. Indeed, the ‘average deviation’ was smaller in the condition of maximum parallax (170 cm) compared to the condition of medium parallax (85 cm), the latter in turn being smaller than the no parallax condition (0 cm). ANOVA showed that this decrease in ‘average deviation’ of the COP with motion parallax was significant \(F_{2,22}=6.09, P<0.01\). One way ANOVA showed that only the condition of maximum parallax was significantly different from the other two, medium parallax \(F_{1,11}=9.8, P<0.01\) and no parallax \(F_{1,11}=17.2, P<0.01\). The reduced ‘average deviation’ with parallax was also significant for head sway \(F_{2,22}=7.38, P<0.01\) but one-way ANOVA analysis showed that the only significant difference was between the conditions of maximum parallax and no parallax \(F_{1,11}=44.8, P<0.01\). Further analysis showed that there was no difference between the condition of maximum parallax and the condition of normal light, both for COP \(t_{11}=1.1, P=0.33\) and head sway \(t_{11}=0.7, P=0.48\).

In the anteroposterior direction of sway, increasing the distance between the fixation point and the far LEDs did not affect the amount of sway (COP: \(F_{2,22}=0.32, P=0.70\); head \(F_{2,22}=0.3, P=0.73\)).

**Sway path**

In order to further quantify the effect of motion parallax, further analyses of the data were undertaken. We measured ‘sway path’ length in the different experimental conditions manipulated in experiment 2 (Table 1). ‘Sway path’ is the length of the displacement of the COP or the
Table 1  Sway path length (mean and SD in cm) at the level of the centre of foot pressure (COP) and the level of the head in the three experimental conditions of experiment 2 and the two control conditions, with eyes closed and full light illumination

<table>
<thead>
<tr>
<th></th>
<th>Full illumination</th>
<th>Maximum parallax (170 cm)</th>
<th>Medium parallax (85 cm)</th>
<th>No parallax (0 cm)</th>
<th>Eyes closed</th>
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<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td>Head</td>
<td>16.8</td>
<td>2.51</td>
<td>20.9</td>
<td>3.75</td>
<td>21.6</td>
</tr>
<tr>
<td>COP</td>
<td>32.5</td>
<td>5.1</td>
<td>46.2</td>
<td>15.8</td>
<td>44.8</td>
</tr>
</tbody>
</table>

Fig. 4 Average power spectrum of displacement of the COP for 4 experimental conditions, including maximum parallax (170 cm) and no parallax (0 cm). Power spectral density is expressed in arbitrary units with a frequency resolution of 0.02 Hz.

head during the recorded time, normalised by subject's weight and height. ANOVA performed on the three experimental conditions showed that increasing motion parallax reduced lateral sway path at the level of the head ($F_{2,22}=4.9, P=0.02$) but not at the level of the COP ($F_{2,22}=1.5, P=0.25$). The apparent discrepancy with the parameter 'average deviation', affected equally by motion parallax at COP and head sway levels, might be due to the fact that sway path is more influenced by high frequency sway activity. The latter is notoriously more pronounced in COP recordings than in head sway recordings (Day et al. 1993; Koles and Castelein 1980).

**Power spectra**

Spectrum analysis was also obtained with a standard fast Fourier transform program in MATLAB (Mathworks) with a frequency resolution of 0.02 Hz from 0 to 2 Hz. For statistical analysis the spectrum was divided into eight bands spanning 0.25 Hz each. An analysis of variance (ANOVA) was used to selectively investigate the effect of the maximum, medium and no parallax conditions at different sway frequencies. The ANOVA model was a two-factor, within-subject design with 'visual condition' and 'frequency' as factors. Average power spectra of both the maximum parallax and no parallax conditions are reported in Fig. 4, including full room illumination and eyes closed conditions for comparison. This figure shows that both COP and head sway are smaller in the maximum parallax condition than in the no parallax condition for low frequency components of sway, up to 0.5 Hz. For the sake of clarity, power spectra data in the condition of medium parallax was omitted from Fig. 4, as these values were always within those of maximum and no parallax conditions.

ANOVA analysis revealed that, at the level of the head, the main effect of motion parallax was significant ($F_{2,22}=4.5, P<0.05$) and interacted significantly with the factor frequency ($F_{4,44}=4.03, P<0.01$). This interaction confirmed that motion parallax had a significant stabilising effect on head sway but only at low frequencies, up to 0.5 Hz. As can be seen in Fig. 4, head oscillations above 1 Hz are extremely limited and no differences between any visual conditions can be detected.
In force platform measurements, the stabilising effect of motion parallax was restricted to low frequencies, up to 0.5 Hz (Fig. 4). At higher frequencies (0.5–2 Hz), sway activity appeared increased in the maximum parallax condition but this was not substantiated statistically (see below). The ANOVA revealed that motion parallax was significant as a main effect ($F_{2,22}=6.8, P<0.01$) and in interaction with the factor frequency ($F_{4,14}=5.9, P<0.01$). Paired comparisons between the two conditions revealed significant differences only for the lowest two frequency bands, $<0.25$ Hz ($t_{11}=2.7, P<0.05$) and $0.25–0.5$ Hz ($t_{11}=2.1, P=0.05$).

Experiment 3

Average deviation

Figure 5 shows the data from the eight subjects for the head and COP displacements. Only the two experimental conditions, motion parallax and no parallax conditions with binocular and monocular vision were subjected to statistical analysis.

In the lateral direction, the ‘average deviation’ of the COP and head displacement decreased by approximately 28 and 40%, respectively, when motion parallax was present in the visual environment with respect to the condition of no parallax, both monocularly and binocularly. The ‘average deviation’ was smaller in the condition of motion parallax as compared to the condition of no parallax. ANOVA showed that the main effect of parallax was significant for both COP and head recordings (COP: $F_{1,7}=47.2, P<0.01$; head: $F_{1,7}=17.2, P<0.01$). No difference was found between monocular and binocular viewing, neither as a main effect (COP: $F_{1,7}=0.37, P=0.56$; head: $F_{1,7}=0.84, P=0.39$) nor in interaction with the factor parallax (COP: $F_{1,7}=0.13, P=0.73$; head: $F_{1,7}=0.15, P=0.71$).

In the anteroposterior direction of sway, neither the main effect of parallax nor the main effect of vision was significant for both COP and head recordings. An interaction between these two factors reached significance at the level of the head ($F_{1,7}=6.1, P<0.05$) but not at the level of the COP ($F_{1,7}=4.2, P=0.08$). This interaction was due to a reduction of the amplitude of head sway with binocular vision as compared to monocular vision in the condition of no parallax while no difference appeared in the condition of motion parallax.

Fig. 5 Influence of motion parallax on lateral (L-R) and anteroposterior (A-P) sway (measured as ‘average deviation’) at the level of the head (top) and at the level of the COP (bottom). The condition with background wall illumination (Light) and the eyes closed condition (horizontal dashed line) are also shown for comparison.
Sway path length

Sway path length analysis confirmed the absence of difference between binocular and monocular vision in the lateral direction both for COP and head recordings, as a main effect as in interaction with the factor parallax. As in experiment 2, the effect of motion parallax was restricted to head sway ($F_{1,7}=5.4, P=0.05$) and was not significant at the level of the COP ($F_{1,7}=0.3, P=0.61$).

Power spectra

Spectrum analysis was obtained as in experiment 2. The ANOVA model was a three-factor, within-subject design with vision (binocular vs monocular vision), 'visual condition' (motion parallax and no parallax) and 'frequency' as factors.

Spectrum analysis confirmed: (1) the absence of difference in the lateral direction between binocular and monocular vision both at the level of the head and COP, as a main effect as in interaction with the other two factors (motion parallax and frequency) and (2) a significant effect of motion parallax both at the level of the head and the COP in interaction with the factor frequency (head: $F_{7,42}=3.6, P<0.01$; COP: $F_{7,42}=15.6, P<0.01$), indicating that the effect of motion parallax was restricted to low frequency components of sway (up to 0.5 Hz).

Discussion

The main findings in this study were that lateral sway was reduced by viewing nearer targets, by the presence of a visual background and, more specifically, by the presence of motion parallax cues. The effect of motion parallax was observed both in the condition of monocular and binocular vision.

In experiment 1, lateral sway decreased significantly with decreasing eye-target distance, both in full room illumination and with just a single fixated foreground. This effect was particularly significant between 50 and 150 cm, in accordance with the literature (Paulus et al. 1984, 1989), but it failed to reach significance in anteroposterior sway. In addition to this eye-target distance effect, a better stability was observed in both lateral and anteroposterior directions of sway when background visual information was added to the small fixated foreground. In the ambient visual condition, central and peripheral vision were fully stimulated whereas mostly central vision was stimulated by the fixated window frame. Although the differential role of central and peripheral vision in postural stabilisation remains controversial (Nougier et al. 1997; Straube et al. 1994), the results in experiment 1 agree with the literature in that full vision reduces body sway more effectively than central vision alone (Paulus et al. 1984).

The addition of a visual background does not only increase the angular size of the visual display but also introduces motion parallax. The extent of motion parallax between the background and the foreground is proportional to the distance in depth between the two objects. Thus, in experiment 1, a greater reduction in lateral body sway was expected when small eye-target distances (i.e. bigger foreground–background distances) were involved. Although, the results confirmed the effect of additional ambient visual information and the eye-target distance effect, the expected interaction between these two factors did not reach significance (Fig. 2). There are several reasons why such interaction was not statistically significant, including the reduced number of subjects and a possible ceiling effect (i.e. that no further reduction of sway was possible with targets at such close distance in a small, fully illuminated room). For this reason we investigated the parallax contribution directly in experiments 2 and 3, as opposed to indirectly through an interaction as in experiment 1.

In experiments 2 and 3, motion parallax was manipulated in isolation by keeping angular size and eye-fixture target distance constant. A decrease of lateral body sway was observed with increasing distance between the fixated LEDs and the distant LEDs both with binocular (experiments 2 and 3) and monocular vision (experiment 3). This effect was observed for the sway parameter 'average deviation' and for the additional lateral 'sway path' parameter. For the former the effect was observed both for COP and head sway whereas, for the latter, it was statistically significant for head sway only. This difference was likely due to the higher sensitivity of the parameter 'sway path' to high frequency activity, which is particularly important in force plate recordings, as compared to the parameter 'average deviation'. Indeed, spectral analysis revealed that motion parallax did reduce low frequency components of sway (0–0.5 Hz), both for force plate and head sway recordings, but not higher frequency components.

On the basis of this frequency specificity, it seems that motion parallax would be particularly involved in slow reorientations of the body. This is in agreement with experiments investigating visually induced body sway in response to slowly moving visual scenes (Bronstein and Buckwell 1997; Guerraz et al. 1999). However, direct evidence for a role of motion parallax in controlling high frequency sway components would require experiments with stroboscopic illumination (Amblard et al. 1985; Paulus et al. 1984), in order to reduce the amount of dynamic cues available.

The effect of motion parallax was restricted to the lateral direction, as expected, since lateral displacement of the subject's head induces large relative motion of the two targets in the lateral direction (motion parallax). Sagittal head displacement, however, mainly generates disparity and image size cues (Paulus et al. 1989) and, in agreement, a trend for better postural stability in the sagittal plane was observed during binocular as opposed to monocular vision (experiment 3).

In experiments 1 and 2, subjects were fixating the different targets with binocular vision. Thus, in addition
to motion parallax information, retinal disparity information was also available. Both motion parallax and binocular disparity provide information about the three-dimensional structure of the visual environment. However, unlike motion parallax, binocular disparity is essentially static and relies on discrete differences between the image of objects on each retina. When subjects fixate binocularly a close target, objects further away or closer to the fixated target are perceived as double. The similarity between monocular and binocular vision observed in experiment 3, reveal the monocular origin of the stabilising effect provided when additional depth cues were provided, attesting that motion parallax was the relevant visual cues used by the subject to stabilise their posture.

Two different mechanisms subserving visual stabilisation of posture in the lateral direction were proposed by Paulus et al. (1989) and Rushton et al. (1989): efferent and efferent motion perception. As depicted in Fig. 6 (top diagram), when a subject is fixating a visual target, the eyes will track it while the head is moving sideways.

If we assume that the tracking is perfect during self-motion, the lateral head movement is visually detected by the amplitude of the eye movement (extraretinal signal): efferent motion perception. Little or no retinal shift of the fixated target occurs on the retina. The value of the angle \( \alpha \) (eye movement) is an exponential function of the eye-target distance and is represented in Fig. 6 (top) by:

\[
\alpha = \text{ARC} \tan \left( \frac{d}{x} \right)
\]

where \( d \) represents lateral head movement and \( x \) represents eye-target distance. As mentioned above, fixation of a tiny light spot (LED) in an otherwise completely dark surround stabilises posture up to a limit of 2–2.5 m (Bles et al. 1980; Brandt et al. 1980; Paulus et al. 1984, 1989). Then, as can be seen in Fig. 6, the amplitude threshold for efferent motion perception (extraretinal motion perception), is an angle \( \alpha \) of approximately 0.3° for 1-cm head sway amplitude that is in the physiological range of postural sway in the lateral direction.

The presence of a second target behind the point of fixation generates relative motion between the two objects when the observer is moving, i.e. motion parallax. Then, the magnitude of head movement can be detected not only by the amplitude of the eye movements (efferent motion perception) but also by pure retinal information provided by the relative motion of the two objects: efferent motion perception (see also Rushton et al. 1989). The amplitude of the relative motion of the two
objects (Fig. 6 bottom), angle $\delta$, is related to the distance between the two objects ($D$) and to the distance between the fixation point and the subject ($x$). Angle $\alpha$ is given by:

$$\delta = \text{ARC} \tan \left( \frac{dD}{x(x + D)} \right)$$  \hspace{1cm} (2)

The results of experiments 2 and 3 are in accordance with the presence of two modes of visual stabilisation in the control of posture. The improvement of lateral body sway by fixating LEDs in the same plane (0 cm) as compared to eyes closed attests principally to the efferent motion perception mechanism. The decreasing sway observed with increasing depth between LEDs attests to the afferent (retinal) motion perception mechanism in action.

It should be noted that, for geometrical reasons, $\delta$ (relative movement of the two objects on the retina), is always smaller than $\alpha$ (Fig. 6). However, the threshold of perception for relative motion between two objects is lower than that of absolute motion of a single object (Abadi et al. 1999; Johnson and Scobey 1982; Snowden 1992). Therefore, we can postulate that the threshold of visual detection of body sway is lower for afferent motion perception (angle $\delta$) than for efferent motion perception (angle $\alpha$). One might envisage that when eye-target distance is large enough not to provide the required amount of extraretinal information (>2–2.5 m), the relative movement between the foreground and a background far away could still provide pure retinal information about body sway. Thus, for sufficiently large body sway with respect to eye-target distance, the afferent and the efferent perception systems would provide two sources of visual information about body displacements while the afferent system would remain the only one used for small lateral body sway.

In conclusion, the experiments show that motion parallax is used by the postural system to reduce body sway during quiet, upright standing in a static three-dimensional visual environment. The effect is only observed for lateral sway and is particularly pronounced for low frequency components of body sway (up to 0.5 Hz). The findings provide support for the view that there are two modes (afferent and efferent) of visual detection of body sway.

Acknowledgements Financial support from the ‘CEC Access to Large Scale Facility’ grant is gratefully acknowledged.

References


Research report

Influence of action and expectation on visual control of posture

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Accepted 21 November 2000

Abstract

Previous studies have shown that human subjects presented with a moving visual environment initiate a postural re-adjustment in the direction of motion. The present study investigated how active control or expectation of the displacement of a visual scene affects this postural response. Center of foot pressure (COP) and head displacement were recorded using a sway platform and a tracking system, respectively. The subjects faced a visual scene (1x1 m, at a distance of 45 cm) which moved transiently (with a velocity of 1 cm/s) in a direction parallel to the interaural axis. When the displacement of the visual scene was under the active control of the subjects, visually induced body sway was strongly inhibited, in comparison with the response to unexpected stimuli. Prior knowledge of the characteristics of the forthcoming displacement was sufficient, in most subjects, to reduce postural re-adjustment, even when subjects did not exert active control. Finally, the visually induced postural response was strongly reduced even when subjects did not trigger the stimulus, without any knowledge about the direction of motion. In conclusion, it appears that although vision is of primary importance in the control of postural orientation, high level processes such as expectation can modulate its impact by providing cues as to whether forthcoming visual flow is the consequence of self-motion or object-motion. © 2000 Elsevier Science B.V. All rights reserved.

Theme: Motor systems and sensorimotor integration

Keywords: Action; Expectation; Postural control; Vision; Motion perception

1. Introduction

Vision provides an important source of information for the control of posture. The particular pattern of optic flow a subject experiences depends on both the nature of his environment and how he moves therein. However, visual motion signals are relative: displacement of either the subject or an external object can yield a similar retinal motion stimulus (unlike vestibular information, for example, which codes absolute motion of the head). Therefore, visual control of posture depends to some extent on the ability to differentiate optical flow due to self-motion from that due to object-motion [20].

As reported originally by Lee and Lishmann [17], and replicated by many investigators [1,10,18,23] motion of the visual environment, which is analogous to that produced by postural sway induces a postural adjustment in the direction of motion. Lateral sway can be reversed in direction by placing a stationary fixation point between the moving background and the subject, indicating that motion parallax cues are used in the visual control of posture [7,14,15]. Small displacements of the visual environment, below the threshold for conscious perception, are sufficient to induce postural sway [17,23]. These observations indicate that the visuo-motor system may misinterpret the displacement of the scene as a displacement of the self and initiate an postural response.

Gibson [11,12] reminds us that, quotidian, perception usually involves an active observer. Larish and Andersen [16] showed that subjects who actively locomoted within a virtual 3-D environment were more accurate in predicting orientation than subjects who passively viewed the 3-D visual display. Thus, action appears to be an important parameter affecting how subjects perceive self-motion in the visual environment and could inhibit postural responses due to object-motion. The following studies address how active control of visual motion affects postural responses. Experiment 1 compares postural responses to actively controlled displacements of a visual scene with those...
evoked by passive observation of unexpected scene displacements.

Expectation of forthcoming events has also been shown to influence perception. For instance, expectation of forthcoming object motion modulates the threshold of detectability [2, 22]. Therefore the expectancy which is inherent in the active control might be more important than the active control per se. Experiment 2 investigates whether motor action to drive the visual scene is necessary for inhibition of inappropriate postural responses or whether expectation (predictability) of the forthcoming scene displacement is sufficient. In Experiment 3, we investigate whether active-triggering of the visual scene displacement, without any expectation of the direction of motion, is sufficient to inhibit the inappropriate postural readjustment.

2. Materials and methods

2.1. Subjects

Eight subjects took part in each experiment. Experiment 1 involved two women and six men, aged 23–52 years. Experiment 2 involved three women and five men, aged 23–48, including six subjects from Experiment 1. Finally, Experiment 3 involved three women and five men, aged 24–46 years, including six subjects who had participated in either Experiment 1 or 2. All subjects were right handed (Edinburgh Inventory [21]). None of the subjects had any relevant medical history and all had normal or normal-corrected vision. Informed consent was obtained prior to the experiments according to the Declaration of Helsinki.

2.2. Apparatus

In these experiments, body sway was recorded in response to the linear displacement of a visual scene. The visual scene consisted of a flat board (1 x 1 m, 96° of visual angle) covered in randomly distributed fluorescent discs of 2 cm diameter, placed 45 cm from the subject, at eye level, in an otherwise dark room. The board was mounted on a motorized train on a linear track and moved at a constant velocity of 1 cm/s along an axis parallel to the inter-aural axis, when driven via a PC or a joystick. The motor used to move the train was a low noise stepper motor coupled with rubber-belts. The noise coming from the motor (0.5 dB (c) recorded in a sound proof booth) was not perceptible within the background noise of the laboratory (60 dB (c)) which was largely attributable to air conditioning and afforded adequate masking. Therefore, the onset of stimulus motion was not cued by the mechanics of motion.

Subjects stood on a force-platform (internal malleoli 3 cm apart), which measured the position of the centre of foot pressure (COP) in the lateral and anterior–posterior directions. They also wore a lightweight helmet carrying the receiver-coil of a 3-D magnetic search coil system (Polhemus 3 space Fastrak: resolution of 0.5 mm) which transduced the linear component of head displacement in both lateral and anterior–posterior directions. Output signals from the sway platform and the Fastrak were acquired with a computer at a sampling rate of 125 Hz.

2.3. Procedure

In all experiments, subjects were instructed to stand still and relaxed with both hands holding a manipulandum (a small box fitted with either a joystick or buttons) whatever the visual condition. They were asked to maintain fixation of a luminescent dot fixed in the centre of the display at eye level.

2.3.1. Experiment 1: Effect of action

Experiment 1 comprised three conditions. (1) ‘Unexpected condition’: the visual scene was moved by the computer, leftwards or rightwards at a velocity of 1 cm/s for 3 s. Prior to each trial, subjects were naive as to whether or not, when and in what direction the visual scene would move. (2) ‘Active condition’: subjects drove the displacement of the visual scene with a joystick. By moving and holding the joystick deflected to the right or left the subject could start the visual scene moving and maintain its velocity at 1 cm/s. Subjects were instructed to move the visual scene for a few seconds’ soon after the experimenter gave the verbal command ‘joystick’. Only the first 3 s of motion were considered for analysis and trials with scene movement lasting less than 3 s were discarded. Subjects were not allowed to switch from one direction to the other within a single trial and were asked to alternate the direction of motion between trials. (3) ‘Control condition’: no displacement of the visual scene. Each subject underwent 20 trials in the ‘unexpected’ condition (ten with scene motion to the right and ten to the left), 20 trials in the ‘active’ condition and ten trials in the ‘control’ condition. The 50 trials for each subject were divided into two blocks of 25 trials. Within each block the order of stimulus presentation was pseudo-randomized. The two blocks were presented successively with a rest period of 10 min between the two. Prior to data recording, two ‘active’ and two ‘unexpected’ trials were given to each subject in normal room illumination.

2.3.2. Experiment 2: Expectation versus action

Experiment 2 involved four conditions. (1) ‘Unexpected condition’: identical to that of Experiment 1. (2) ‘Active’ condition: subjects triggered the computer-generated stimulus by pushing one of two buttons (for rightward or leftward scene motion). After the verbal instruction ‘button’ from the experimenter, the subject had to press within a few seconds. Subjects were asked to alternate right and left between trials. (3) ‘Expected’ condition: subjects were told that the scene would move to the right or to the left 3–5 s before the onset of motion. They were
also given an audible beep (50 ms duration, 500 Hz tone) 500 ms before stimulus onset. Thus, in the expected condition, subjects knew when and in which direction the scene would move. The stimulus was the same in these three motion conditions, consisting of a displacement of the visual scene leftwards or rightwards at a velocity of 1 cm/s for 3 s. (4) Control condition: no displacement of the visual scene. Each subject underwent ten trials in each condition (with equal numbers of visual scene displacement rightward and leftward). The 40 trials for each subject were divided into two blocks of 20 trials, presented successively with a rest period of 10 min between the two. Within each block the order of stimulus presentation was pseudo-randomized.

Prior to the experiment, we tested whether pressing the buttons had a significant postural effect by itself. After being informed that the visual scene would not move, subjects pressed the right or left button alternatively (n = 10). The active push (left or right) had no effect on the average position of both the COP and the head (P > 0.05).

**3. Results**

In the anterior–posterior direction, no significant differences were observed between the experimental conditions with a moving visual display and the control conditions with a stationary display. This finding is in agreement with the literature [1, 9, 13, 25] which shows that there are no directionally specific postural responses orthogonal to the displacement of a visual scene. Therefore, only data concerning lateral sway will be presented.

**3.1. Effect of action (Experiment 1)**

The averaged head and COP sway in the lateral direction for each subject, in both the unexpected and the active conditions are reported in Fig. 1. In the unexpected condition, motion of the visual scene induced a postural displacement in the same direction as the stimulus in seven out of the eight subjects tested; a corrective postural adjustment was observed after stimulus offset. As can be seen in Fig. 1, COP and head displacements followed a similar trend, apart from a transient COP response opposite to the main direction of sway which occurred 250–300 ms after both stimulus onset and stimulus offset. This transient is caused by the foot pressure responsible for the ensuing body sway [7, 8]. The latency of the head sway response was 300–400 ms from stimulus onset. One sample t-test analysis indicated that the mean response during stimulus motion was different from the baseline level (zero) for both the COP (t(7) = 3.3, P < 0.05) and the head (t(7) = 3.9, P < 0.01).

In the active condition, stimulus motion induced a small postural response in the same direction in most subjects for both the COP and the head, with latencies of approximately 350 and 400 ms, respectively. This postural adjustment had a smaller amplitude than that observed in the unexpected condition, and it was followed by a corrective adjustment during stimulus motion, which shifted both the COP and the head back to the baseline level, or even (in some subjects), in the opposite direction to the stimulus. No clear anticipatory postural response (in the opposite...
Unexpected condition

Fig. 1. Averaged sway responses to unexpected versus actively controlled motion of a visual scene. The records show average position of the COP and the head (in mm) computed for each subject in both the unexpected and active conditions of Experiment 1. Upward deflections indicate deviation in the direction of stimulus motion.

direction to the expected stimulus) was observed during the 2.5 s preceding stimulus motion (baseline). One sample t-tests indicated that the mean response during stimulus motion was not different from baseline (Zero) neither for the COP (t(7)=0.5 P>0.05) nor for the head (t(7)=0.54 P>0.05). Comparison between COP and head displacements during stimulus motion showed that the active condition responses were significantly different from those in the unexpected condition (paired t-test, COP: t(7)=3 P<0.05; head: t(7)=2.9 P<0.05).

No postural displacement was observed in the control condition of a stationary visual display (P>0.05).

3.2. Effect of expectation (Experiment 2)

The averaged head sway in the lateral direction for each subject in the unexpected, expected and active conditions are given in Fig. 2.

As in Experiment 1, unexpected displacement of the visual scene induced a postural re-adjustment in the direction of motion. Except for the early transient COP response (latency of ~280 ms) opposite to stimulus motion, COP displacement followed a similar trend to that of the head. In contrast to the unexpected condition, no significant postural readjustment was observed when the displacement of the visual scene was triggered by the subjects themselves (active condition) neither for the head nor the COP (P>0.05).

In the expected condition, the displacement of the moving scene failed to induce clear postural re-adjustment in six out of the eight subjects tested. In one of the two remaining subjects, the expected displacement of the moving scene induced a postural re-adjustment in the direction of motion, of a similar amplitude to that elicited in the unexpected condition. In the other subject, an anticipatory postural response could be observed within 2.5 s of baseline period, followed by a postural adjustment in the opposite direction to stimulus motion. A similar response pattern was observed for this subject in the active condition. When all subjects were considered together, the mean response of both the head and the COP during stimulus motion was not different from the baseline level (P>0.05).

An analysis of variance (ANOVA) was performed on the
Unexpected condition

Active condition

Expected condition

Fig. 2. Averaged sway responses to unexpected, expected and actively controlled motion of a visual scene (Experiment 2). The traces show average position of the head (in mm) for each subject. The drawings on the left side of the figure show the experimental set-up for each stimulus condition.

Although subjects were holding the manipulandum in all the visual conditions in Experiment 2, the manipulandum has been removed from the drawings of the unexpected and expected conditions for the sake of clarity.

Three stimulus conditions (unexpected, expected and active) and the Bonferroni test was used for pairwise comparisons. The ANOVA showed a significant effect of experimental condition, for both the head ($F_{2,14}=16.4, P<0.01$) and the COP ($F_{2,14}=21.8, P<0.01$). Post hoc mean comparison indicated that the unexpected condition was systematically different from the other two conditions, for both the head and the COP ($P<0.05$). No difference was observed between the active and the expected conditions ($P>0.05$).

In addition, the mean head/COP response in the active condition was significantly correlated (Pearson) with that in the expected condition (head: $r=0.84$; COP: $r=0.78$). No correlation was observed between the unexpected condition and the other two. No postural displacement was observed in the control condition with a stationary visual display ($P>0.05$).

3.3. Directionally specific information (Experiment 3)

The averaged head sway for each subject in the unexpected, active and active-unspecific conditions are shown in Fig. 3.

As in Experiment 2, unexpected displacements of the visual scene induced a postural re-adjustment (head and...
The ANOVA showed a significant effect of experimental condition both for the head ($F_{2,14}=17.1, P<0.01$) and the COP ($F_{2,14}=22.4, P<0.01$). Mean comparison indicated that the unexpected condition was significantly different from the other two conditions both for the head and the COP ($P<0.01$) and correlation coefficient between these two conditions did not reach significance neither for the head ($r=0.32$) nor for the COP ($r=0.59$). No difference was observed between the active and the active-unspecific conditions ($P>0.05$). No postural displacement was observed when the visual display was stationary.

Following data collection, subjects were questioned about their subjective impression of the experiment and, more specifically, were asked whether the three stimulus conditions lead to the same percept. The eight subjects of Experiment 3 reported that the perception of visual scene motion was much more ambiguous when they did not expect the scene to move than when they triggered the stimulus. Three subjects reported that they could not systematically perceive the visual scene as moving in the unexpected condition. One subject mentioned that he realized that the visual scene was moving in unexpected trials, but only after becoming aware that his body was being driven by the moving scene. Only one subject reported a perceptual difference between the active and the active-unspecific conditions.

### 4. Discussion

The results of Experiment 1 showed that the visually induced body sway observed in response to the displacement of a visual scene was strongly inhibited when that displacement was actively controlled by the observer. The results of Experiment 2 indicated that the active control of driving the scene was not necessary to inhibit the visually induced body sway since expectation alone was sufficient in seven subjects out of eight. Except in one subject, no anticipatory response could be identified in either the active (Experiments 1–3) or in the expected (Experiments 2–3) conditions. Finally, an incomplete, but nevertheless substantial, reduction in visually induced body sway was also observed when subjects merely triggered the stimulus, without prior knowledge of the direction of motion (Experiment 3).

The finding that minimal motion, bellow the threshold for motion perception (as in some of our subjects and in previous studies [17,23]) is sufficient to induce postural readjustments is in favour of a low level postural control system requiring little contribution from high level processes [3]. However, our data show that when the displacement of the visual scene is expected, (active and expected conditions, Experiments 1–3), the inappropriate postural readjustment is strongly reduced. Thus, high level functions, such as expectation, can have a decisive impact on the visuo-motor system controlling posture. As shown in

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**Fig. 3.** Averaged sway responses to unexpected visual motion and actively controlled visual motion, with and without directionally specific information. The traces show the average position of the head (in mm) for each subject in the unexpected, active and active-unspecific conditions of Experiment 3.
Experiment 3, when subjects were triggering the displacement of the scene without any directionally specific information (active-unspecific), the suppression of the postural re-adjustment was almost complete. The absence of difference between the two active conditions, with or without directionally specific information, indicates that knowledge about ‘when’ the stimulus is going to move is sufficient to strongly reduce the influence of visual inputs on postural control.

The cognitive processes affecting suppression of visually induced body sway remain unclear, but active control does not appear to be necessary, as suggested by the similarity between the active and the expected conditions in Experiment 2. As discussed above, visual control of posture depends to some extent on how the visual flow is interpreted by the visuo-motor system, either as self-motion or as object-motion. High level processes, such as expectation or attention are known to reduce the threshold for perceiving motion [2,22]. Verbal reports collected systematically after data collection in Experiment 3 are in agreement with this statement; all subjects reported that the displacement of the visual scene was much more ambiguous when unexpected than when actively triggered, both in the active and active-unspecific conditions. Therefore, if the visual flow due to the displacement of the scene can be implicitly or explicitly attributed to object motion instead of self motion, there is no need for the visuo-motor system to initiate a postural re-adjustment. Accordingly, this is what was found in the active and expected conditions in Experiments 1–3.

In our study subjects swayed most, and had an ambiguous perception of self versus object-motion, when the visual stimuli were unexpected. However, it would be hazardous to say categorically whether sway was suppressed because perception was certain or whether little sway facilitated accurate perception since the threshold for object-motion perception has been shown to be raised by concurrent head motion [5].

Previous reports also favour an effect of high level processes on visual control of posture. Lestienne et al. [18,19] reported that subjects who were insensitive to linear visual flow became sensitized when performing a concurrent arithmetic task (dual task). More recently, using the moving room paradigm, Bronstein [6] showed that prior exposure to visual stimulus induces adaptation of the visually evoked response from the first to the second trials. Interestingly, the reduction of the postural readjustment (anterior–posterior direction of sway) was accompanied with a reduction in EMG responses. These data indicate that the reduction of the visually induced postural response observed there was not due to an increased stiffness of leg muscles to counteract the disturbance but was more likely due to down-regulation of irrelevant visual inputs. Therefore, in light of Bronstein’s results [6] it is reasonable to assume that the inhibition of inappropriate postural responses was not the consequence of an increased stiffness of leg muscles. Unfortunately, in contrast to the anterior–posterior direction of sway [6,18], EMG activity is not sensitive enough to detect the rather small visually evoked body sway in the lateral direction.

The latencies of visually induced body sway reported in the literature vary greatly. The short latencies we observed are similar to those reported previously for low stimulus velocities [7]. They are also closer to the latencies at which vision contributes to rapid automatic postural responses (EMG activity around 100 ms) following the displacement of the support surface [4,24]. In contrast latencies as long as 1s [18] or even more [9] have been reported. Differences in the dynamics of the various transduction devices used would not account for the large variations in response latency. The more likely factor being that these latter studies used high velocity visual stimuli which would give an unambiguous percept of object motion when the stimulus started to move.

In conclusion, it appears that although vision is of primary importance in the control of postural orientation, high level processes such as expectation can modulate its impact by providing decisive cues as to whether the visual flow is the consequence of self-motion or object motion.

Acknowledgements

We thank Dr Brian Day and Dr Mary Faldon for their advice on the manuscript and David Buckwell and Bill Cameron for their technical support.

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Visual Control of Postural Orientation and Equilibrium in Congenital Nystagmus

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Purpose. To investigate how humans with congenital nystagmus (CN) use visual information to stabilize and orient their bodies in space.

Methods. Center of foot pressure (COP) and head displacements in the lateral plane were recorded using a sway platform and Schottky barrier photodetector, respectively. In experiment 1, a comparison was made of the oscillatory characteristics of body sway with eyes open compared with eyes closed. Experiment 2 studied the postural readjustments made in response to absolute or relative motion (motion parallax) of objects in the visual scene, generated by lateral displacement of background scenery.

Results. Experiment 1 revealed that subjects with CN were not able to use visual information to stabilize COP but were able to stabilize the head at frequencies lower than 1 Hz. Experiment 2 showed that in response to the displacement of a visual display, for both absolute motion and motion parallax, subjects with CN reoriented their body in space in a manner similar to control subjects.

Conclusions. The results suggest that despite involuntary eye movements, subjects with CN use orientation cues to control their posture, but not dynamic cues useful to control the rapid oscillations that are particularly important at the level of COP. These findings suggest that in CN, visual control of posture is restricted by low-frequency sampling of the visual scene. (Invest Ophthalmol Vis Sci. 2000;41:3798-3804)

Congenital nystagmus (CN) is an ocular motor disorder characterized by involuntary oscillatory eye movements that disrupt foveal target fixation. The onset of nystagmus occurs during the first 6 months of life. Typically, the nystagmus is in the horizontal plane, and each cycle is initiated by slow phases with exponentially increasing velocity, taking the eyes off the target. A fast phase returns the eyes to the object of regard, at which time there is usually a period of transient stability: a foveation period of 10 to more than 100 msec duration within which the target is visually sampled. Despite almost constant eye movement, oscillopsia, or impairment of visuomotor coordination is rare.

Visual information is an essential factor in the multisensory control of movement and balance. Unlike vestibular information, visual motion signals are relativistic: that is, a displacement of the subject or an external object can yield similar patterns of retinal motion stimuli. Therefore, visual control of posture depends on the ability to differentiate optical flow due to self-motion from that due to object motion. Such a differentiation could be compromised in individuals with involuntary eye movements such as CN. Accordingly, in addition to increased thresholds for motion detection, individuals with CN make less use of visual information to control stance, measured as center of foot pressure (COP), than do control subjects.

We present detailed investigations of the dynamics of visual postural control in subjects with CN. The first experiment sought to identify the frequency bands in which visual control of equilibrium (the oscillatory component of body sway) is disturbed by CN. Because oscillations of the COP have a higher frequency range than upper parts of the body, both COP and head oscillations were recorded. The second experiment determined the extent to which subjects with CN reorient (i.e., tilt or displace in a given direction) their bodies in space in response to visual flow. Normal subjects lean in the direction of motion when viewing a moving background. This postural adjustment reverses in direction when a stationary target providing motion parallax cues is placed between the standing subject and the moving background. Because of the intrinsic visual instability and raised thresholds for motion detection in CN, we hypothesized that these subjects may have disturbed patterns of postural response to such visual motion stimuli.

Materials and Methods

Subjects

Nine adult subjects with horizontal CN and Snellen visual acuity of at least 0.33 in one eye were studied. Six took part in...
experiment 1 (subjects 1-6 in Table 1), and all participated in experiment 2 (subjects 1-9 in Table 1). Fourteen healthy, age-matched subjects participated in experiment 1. Six of these control subjects (mean age, 38.5 years) had their visual acuities artificially reduced to match those of the subjects with CN (acuity control group). These subjects wore spectacles with fogging lenses (<0.1 magnification lenses with ground surfaces) for 15 minutes before the beginning of the experiment. Because two subjects with CN had extremely low vision in one eye (<0.1), two control subjects were tested monocularly in addition to fogging. The other eight subjects (mean age, 40.5 years) were tested with normal vision (normal control group). Fourteen healthy adults, age matched to the subjects with CN (mean age, 38 years) and having normal Snellen acuity, took part in experiment 2. Written informed consent was obtained according to the Declaration of Helsinki.

Postural Recordings

The studies focus on postural adjustments in the lateral plane in response to lateral movements of both the visual scene and the eyes, because a number of published studies as well as our pilot studies have shown that postural responses are coplanar with the visual motion stimuli deployed.\(^{12,16-18}\) Postural movements in other directions are uncorrelated. In both experiments, subjects stood barefoot on a rigid board placed on top of a slab of foam rubber (height, 5 cm; specific weight, 50 g/dm\(^3\)) resting on a sway platform that transduced postural sway as displacement of COP in the lateral direction. Feet were splayed at 30° with heels together. The foam increased the instability of the subjects so that the effect of vision on sway was enhanced.\(^{19,20}\) Subjects also wore a lightweight helmet, on top of which was mounted an infrared light-emitting diode. Displacements of the light were transduced by imaging a top view (subject) onto a two-dimensional Schottky barrier photodetector (United Detector Technologies, Hawthorne, CA) situated 40 cm above the head. Light from the diode was projected onto the detector surface through a Mamiya medium format lens (45-mm focal length, f 2.8; Mamiya America Corporation, Elmsford, NY) mounted on the front of the photodetector. Use of this technique to record complex human movements has been described previously.\(^21\) One axis of the detector was oriented in the lateral plane to transduce lateral head sway. The resolution of the detector in the configuration deployed was of 0.1 mm, linear up to ±8 cm. Head sway values were normalized for each subjects’ height (signal × mean height of group/individual’s height). All signals were filtered with a band-pass filter of less than 30 Hz and thereafter digitally sampled at 125 Hz.

Eye Movement Recording

Bitemporal, direct coupled, electro-oculographic recordings of horizontal eye movements were performed on all subjects with CN during experiments 1 and 2, to monitor the predominant fast phase direction and the frequency of the nystagmus.

Experiment 1: Visual Control of Equilibrium

Subjects were tested under two conditions: eyes open and eyes closed. In both conditions, subjects were instructed to stand still and relax with hands at the sides. With eyes open, subjects were asked to fixate a small cross (1 × 1 cm) placed at the center of an earth-fixed window frame (30 × 24 cm) at a distance of 50 cm from the eyes. The room was normally illuminated. The order of presentation of the eyes-open, eyes-closed conditions was counterbalanced. Each condition was presented for 1 minute, from which the last 50 seconds were analyzed.

Postural equilibrium in the lateral direction was evaluated as sway path and also in the frequency domain. The sway path is the length of the path described by the COP or the head and is defined as the sum of the distances between sequential points sampled during the analysis period (50 seconds). To calculate power spectra, the 50-second epochs were detrended using a line of best fit and then windowed with a Hanning function. A fast Fourier transform algorithm was then applied to the entire 6250-point signal (Matlab; The Mathworks, Natick, MA). The resultant power spectrum had a frequency resolution of 0.02 Hz and bandwidth from 0 to 62.5 Hz. For subsequent analysis, only the 0- to 5-Hz range was considered. For statistical analysis the frequency components from 0.02 to 5 Hz were grouped into 20 bands, each spanning 0.25 Hz with 12 or 13 (alternating) discrete frequency components per band. The power in each of these bands was then calculated by summing the frequency components.

Analysis of variance (ANOVA) was used to investigate the effects of vision in the three subject groups. A two-factor design was used for sway path analysis (3 × 2) with group as the between-subject factor (CN, acuity controls, and normal controls) and vision as the within-subject factor (eyes closed versus eyes open). The Tukey test was used for post hoc comparison. A three-factor design was used for spectral analy-
sis (3 × 2 × 20), with frequency (0 - 0.25 Hz to 4.75 - 5 Hz) as a second within-subject factor.

**Experiment 2: Visually Induced Body Sway**

Postural reorientation was provoked by moving background visual scenery. The scenery was a flat board (2 × 3 m) subtending 67° height × 90° width of visual angle, oriented in the transverse plane, 150 cm from the subject. Photoluminescent yellow-green stripes fixed to the board defined the outline of a house (Fig. 3) in an otherwise dark room. The board was mounted on a motorized wheeled chassis running on a linear track. For background motion, the board first accelerated for 1.25 seconds, rightward or leftward, and then maintained a constant velocity of 6 cm/sec for 8.5 seconds. The overall displacement was 58 cm, subtending 21° from the subject’s viewing position.

**Test conditions:** In condition 1, subjects were asked to keep looking straight ahead at the background, which was the only object in the visual scene, and not to follow any particular point (absolute motion, Fig. 3A). In condition 2, subjects fixated a cross (1 × 1 cm) in the center of a foreground target consisting of a photoluminescent rectangular window frame lattice (30 cm wide, 24 cm high). This window was located straight ahead of the subject, 50 cm from the eyes and 100 cm in front of the visual background. The background was visible through the window panes (motion parallax, Fig. 3B). Under each condition, subjects underwent 15 pseudorandomized trials: 5 with background motion to the right, 5 with motion to the left, and 5 control trials with the background stationary.

Postural reorientation in the lateral direction was evaluated as the shift in the average position of the COP and of the head during the constant-velocity part of stimulus motion, relative to a 4-second baseline preceding background motion. Trials were averaged for each subject and visual condition. Student’s t-tests were used to compare CN with control subject data.

**RESULTS**

**Experiment 1**

The sway path data measured from COP and head recordings for CN and the two control groups are given in Table 2.

| TABLE 2. Mean Sway Path Length and SD of Both the COP and the Head for the Eyes-Closed and Eyes-Open Conditions in CN and Acuity and Normal Control Groups |
|---------------------------------|-----------------|-----------------|-----------------|-----------------|
|                                 | Eyes Closed     | Eyes Open       | Eyes Closed     | Eyes Open       |
|                                 | M               | SD              | M               | SD              |
| Head                            |                 |                 |                 |                 |
| CN                              | 67.8            | 13.2            | 49.1            | 12.1            |
| Acuity control                  | 56.5            | 12.2            | 35.9            | 9.5             |
| Normal control                  | 53.2            | 17.5            | 31.9            | 13.3            |
| COP                             |                 |                 |                 |                 |
| CN                              | 115.1           | 15.6            | 92.4            | 23.1            |
| Acuity control                  | 111.3           | 23.9            | 45.8            | 10.1            |
| Normal control                  | 128.1           | 55.1            | 50.3            | 11.5            |

Data are in centimeters.

**Effect of Vision on COP**

Comparisons between the sway path lengths measured in the eyes-open and eyes-closed conditions indicated that visual stabilization of the COP was more effective in the two control groups than in the subjects with CN. The sway path of the COP with eyes open was reduced only by 19% in the subjects with CN compared with 59% and 57% in the acuity control and normal control subjects, respectively. Figure 1A illustrates the improvement of stability (%) with vision for each individual CN and acuity control subject. The significant interaction between the group factor (CN, acuity control and normal control groups) and the vision factor (eyes closed versus eyes open) confirmed that vision was more stabilizing in the two controls groups compared with the CN group (ANOVA: P < 0.05). Post hoc comparison indicated that there was no difference among the three groups with eyes closed (P > 0.05). In the eyes-open condition, the sway path was longer in subjects with CN than in the other two control groups (P < 0.01). No differences of any kind were observed between the acuity control and normal control subjects (P > 0.05).

Spectral analysis of COP for the CN and the acuity control subjects is shown in Figure 2. The frequency characteristics of the visual effect on COP displacements can be inferred from a comparison of the spectra of sway obtained with eyes closed versus eyes open. In CN, visual stabilization of the COP was restricted to frequencies lower than 1 Hz (Fig. 2A). In contrast, for acuity control subjects (and normal control subjects), vision had an effective stabilizing influence on COP throughout the frequency range 0 to 5 Hz (Fig. 2B for acuity control subjects). Visual stabilization of the COP was significantly more effective in the control subjects (acuity control and normal control subjects) than in the subjects with CN, reflected by the significant interaction between the group factor and the vision factor (ANOVA: P < 0.05). ANOVAs examining for within group effects indicated that the effect of vision in the subjects with CN failed to reach significance either as a main effect (P = 0.11) or in interaction with the frequency factor (P = 0.58). The effect of vision was similar in the two control groups with a significant main effect of vision (P < 0.05) and no interaction with the frequency factor (P > 0.05).

**Effect of Vision on Head Sway**

Comparisons between the eyes-open and the eyes-closed conditions indicated that the sway path length was shorter in the three groups of subjects when their eyes were open than when eyes were closed (see Table 2). The sway path length with vision was reduced by 27% in the subjects with CN, 34% in the acuity control subjects, and 38% in the normal control subjects, compared with eyes closed. As can be seen in Figure 1B, the improvement in stability with vision was similar to that of acuity control subjects in five of the six subjects with CN. Statistical analysis (ANOVA) confirmed that the reduction of the sway path length with vision was similar in the three groups of subjects. Post hoc comparisons indicated that there was no difference among the three groups in the eyes-closed condition (P > 0.05). With eyes open a significant difference between the CN and the normal control subjects was observed (P < 0.05), but no other comparison reached significance.

Spectral analysis showed that visual stabilization of the head in the three groups primarily affected low frequencies of
head movement. In the subjects with CN (Fig. 2C) visual stabilization of the head was restricted to less than 1 Hz, whereas in the two control groups, visual stabilization of the head was apparent up to 2 to 3 Hz (Fig. 2D for acuity-control subjects). Although visual stabilization of the head appeared to have a higher frequency dynamic in the acuity control and normal control groups, the magnitude of visual stabilization of head sway was similar in the three groups. This was shown by the absence of significant interactions in ANOVAs examining interactions among group, vision, and frequency factors ($P > 0.05$). The stabilizing effect of vision was significant in the three groups of subjects, as a main effect or in interaction with the factor frequency ($P < 0.05$).

**Experiment 2**

Postural responses to leftward and rightward stimuli were always of similar amplitude, and thus the data were combined (Table 3). Figure 3 shows sample records of head displacements for a subject with CN during background motion, with both absolute motion and motion parallax. With absolute motion, the displacement of the background induced a displacement of the head (and COP) in the same direction as the background, followed by a return to baseline posture on cessation of the stimulus. In both the CN-affected and control subjects, a postural adjustment in the direction of motion was observed in response to absolute motion, with a similar amplitude in the two groups, both for the COP ($t = 0.15, P > 0.05$) and for the head ($t = 0.21, P > 0.05$).

With a foreground target (i.e., motion parallax) a shift of head position (and COP) in the direction opposite to stimulus motion was induced (Fig. 3). These postural adjustments in the direction opposite to background motion were significant departures from baseline and were of similar amplitude in the two subject groups (COP: $t = 0.27, P > 0.05$; head: $t = 0.38, P > 0.05$).

An additional analysis was made of the results from the seven subjects with CN who had sustained, unidirectionally beating nystagmus (Table 1) to test whether the direction of nystagmus affected the postural readjustment to leftward and rightward stimuli. The postural responses were inverted in the two subjects with CN with right-beating nystagmus to make their data comparable with that of the other five subjects with CN with left-beating nystagmus. Student’s $t$-tests comparing response amplitudes in the same versus opposite direction to the nystagmus fast phase showed that the nystagmus direction

**Figure 1.** Percentage improvement of stability with vision calculated for each subject with CN (○) and acuity control (●) subject for both the COP (A) and the head (B) in experiment 1. This index of performance was computed as: \(((\text{eyes-closed score} - \text{eyes-open score}) / \text{eyes-closed score}) \times 100\).

**Figure 2.** Average power spectra of displacement of the COP (A, B) and the head (C, D) in CN and acuity control subjects in experiment 1. Power spectral density is in log$_{10}$ (in square centimeters with a frequency resolution of 0.02 Hz). Error bars are the SD for each frequency band. Note that the decay in power with increasing frequency for oscillatory head movement (C, D) was greater than for oscillations of the COP.
TABLE 3. Average Position and SD of the COP and the Head under Conditions of Absolute Motion and Motion Parallax, with Moving or Stationary Background in Subjects with CN and Control Subjects

<table>
<thead>
<tr>
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<th>Moving Background</th>
<th>Stationary Background</th>
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<tr>
<td></td>
<td>Absolute Motion</td>
<td>Motion Parallax</td>
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<td></td>
<td>M</td>
<td>SD</td>
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<tr>
<td>Head</td>
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<tr>
<td>Control</td>
<td>3.90</td>
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<tr>
<td>CN</td>
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<tr>
<td>COP</td>
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<tr>
<td>Control</td>
<td>2.92</td>
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<tr>
<td>CN</td>
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Data are expressed in millimeters.

had no effect on COP and head data, either for absolute motion or motion parallax ($P > 0.05$).

**DISCUSSION**

Experiment 1 showed that visual control of equilibrium in the lateral direction in subjects with CN appears to have greatest efficacy for low-frequency components of sway ($<1$ Hz). However, visual control of equilibrium was less effective in subjects with CN than in control subjects. We could detect a marginal loss of visual stabilization of high-frequency head movements in subjects with CN compared with control subjects. However, high-frequency components to head movement were minimal in both the CN-affected and the control subjects (acuity and normal controls) and thus had little implication for postural stability as measured. COP had more power at high frequencies than head movement. The reduction of COP instability due to vision, was smaller in subjects with CN than in control subjects across all frequencies, but particularly at frequencies of more than 1 Hz. No difference was observed between the two control groups tested (acuity controls and normal controls), indicating that the differences between the subjects with CN and the control subjects was not a consequence of the slightly reduced visual acuity of the subjects with CN included in experiment 1. With eyes closed, COP and head stability were similar in the subjects with CN and the control subjects. These results are consistent with previous observations, which support the thesis that somatosensory and vestibular controls of posture in subjects with CN are normal.

Experiment 2 showed that the use of visual information to control body orientation in space (i.e., overall tilt) was normal in CN. Visually induced body sway under conditions of absolute motion and motion parallax did not differ among subject groups. Consistent with reports in the literature, absolute motion induced ipsidirectional body sway, whereas juxtaposing a stationary target between subject and background pro-

![Figure 3](image-url)
voked sway contradirectional to background motion.\textsuperscript{13,14} Thus, despite their nystagmus, subjects with CN made normal use of visual motion cues, including motion parallax, to control postural orientation.

Insight into the impairment of visual control of high-frequency postural instability in CN is given by the behavior of normal subjects in stroboscopic light, when the flashes are presented at a strob ing frequency of 3 to 5 Hz.\textsuperscript{22-27} This frequency range is similar to the nystagmus frequency in this sample of subjects with CN (see Table 1). Isableu et al.\textsuperscript{22} showed that subjects with normal vision, standing in front of a tilted frame, leaned in the direction of tilt under normal or stroboscopic lighting (2.8 Hz). Displacement of an oscillating background under strob ed light also causes a continuous modulation of low-frequency postural sway.\textsuperscript{25} These results indicate that discrete visual sampling is sufficient for controlling body orientation. However, unlike body orientation, normal equilibrium appears to be degraded under stroboscopic vision at frequencies lower than 6 Hz.\textsuperscript{24-26} Measured at different levels, from ankle to head, the destabilizing effect of such discrete visual sampling principally affects the lower parts of the body.\textsuperscript{27} The latter investigators concluded that discrete visual information (static cues) were sufficient to control the upper part of the body, which has predominantly low-frequency dynamics. Visual motion cues (dynamic cues) control oscillations of the lower part of the body, which extend through a higher frequency range. Thus, subjects with CN appear to be similar to normal subjects in stroboscopic light, in that they share some ability to orient and control low-frequency head instability but are less able to control the higher frequency instabilities of the COP with the visual cues available. Dynamic visual cues, requiring continuous visual feedback, appear to be particularly crucial for fast stabilization of the COP.

The similarity between normal subjects in stroboscopic light and subjects with CN is consistent with the concept that the waveform of CN affords intermittent, low-frequency visual sampling at the time of the foveation periods. Subjects with CN do not behave as though they were exposed to continuous visual motion because of their nystagmus, and this intermittent sampling of vision to control posture may be related to the mechanism whereby they suppress oscillopsia.

The mechanisms proposed for suppressing oscillopsia in CN include a reduced sensitivity to retinal image motion\textsuperscript{5,6,28}, an ability to extract visual information during foveation periods (the parts of the nystagmus waveform when the eyes are quiescent and images are most stable on the fovea) and to ignore the smeared vision during high-velocity slow phases\textsuperscript{29,30}, and the use of extraretinal signals—i.e., efference copy of the CN waveform—to negate the visual effects of the oscillation.\textsuperscript{4,31,32} Of these, the most recent evidence suggests that the efference copy of the CN waveform is the major factor in oscillopsia suppression.\textsuperscript{4,9} Although foveation periods may not be primarily responsible for oscillopsia suppression, they are important for visual acuity,\textsuperscript{29} and they may be responsible for the discrete sampling of visual cues to postural orientation in CN.

\textbf{Acknowledgments}

The authors thank the volunteers who enthusiastically participated in this project.

\textbf{References}


Appendix F

Visual-vestibular control of posture and gait: physiological mechanisms and disorders
Adolfo M. Bronstein and Michel Guerraz

The scientific analysis of clinical disorders of posture and gait is an emerging field. Precise definition of the forces and postural movements involved has been pivotal to understanding many aspects of the visual and vestibular contributions to balance. However, a great deal of argument still surrounds the question of how much gait and posture laboratories actually contribute to improve the clinical management of individual patients. One of the reasons why gait analysis techniques have not penetrated rehabilitation clinics may be that the research questions asked have been aimed at understanding mechanisms rather than at quantifying disability. The condition known as primary orthostatic tremor, which is not too well known to many neuro-otologists and posturographists, is briefly reviewed here. We propose that posturography could be the easiest way to diagnose this treatable condition. Curr. Opin. Neurol. 12:5-11 © 1999 Lippincott Williams & Wilkins

Introduction

This review covers approximately the period between August 1997 and July 1998. Occasionally, earlier articles have been included if they provided the basis for more recent work published within the review period. The topics covered have been grouped as vestibular and visual mechanisms in postural balance, clinical applications of posturography, orthostatic tremor, psychophysiological unsteadiness and gait analysis, particularly applied to Parkinsonian gait.

Vestibular mechanisms in postural balance

Low intensity galvanic vestibular stimulation (0.5 mA) induces postural responses in humans, in the form of leaning and bending of the body towards the anodal [1]. Stance widening and sitting reduced or eliminated the galvanic-induced electromyogram activity in the hip and ankle muscles, and the amount of head tilt relative to the pelvis. This suggests that the initial posture of the body modifies the vestibularly evoked drive to muscles at a premotoneuronal stage and that the response to the galvanic stimulus is organized to stabilize the body in space instead of the head. Apparently the central nervous system interprets the galvanic input as roll-tilt of the supporting surface, a concept that is in agreement with the predominantly torsional eye movements evoked at low [2] or high [3] current intensities. Although most studies use bipolar galvanic stimulation (across mastoids) Severeac-Cauquil et al. [4] have shown that this response is essentially a linear summation of a cathodal vestibular excitation on one side with anodal inhibition on the opposite side.

Bilateral vestibular patients may sway more than normal individuals in response to moving visual stimuli. Loughlin et al. [5] described a new technique to analyze sway signals dynamically over time and found that patients, unlike control individuals, do not adapt to continuous visual motion. These results indicate that vestibular information is used to attenuate visually induced sway by participating in an adaptive process over time. A similar difficulty in suppressing visually induced sway was observed in an astronaut after anodal inhibition on the opposite side.

A puzzling feature of balance disorders is the large variability in recovery that can occur after a vestibular lesion. Lacour et al. [6] studied the influence of vision on
postural control before and after unilateral vestibular surgery in patients with Menière’s disease. Visual influence was quantified as the mean percentage change in sway with eyes open and eyes closed. Surprisingly, patients who relied heavily on vision before surgery showed a reduction in sway with eyes closed as early as a week after surgery (i.e. became less reliant on vision for balance). Patients who did not rely on vision before surgery were particularly unstable with eyes closed compared with eyes open even 1 year after surgery (i.e. became reliant on vision). Why patients with Menière’s disease ‘switch strategies’ after surgery is not clear, but the authors suggest it may be a fast adaptive response to the lesion-induced postural instability.

Although well-compensated vestibular patients perform fairly normally in the range of behavioural tasks, an inability to process unusual sensory inputs remains. For instance, dorsal neck vibration induced different postural responses in normal and labyrinthine-defective individuals [8,9]. Although forward body sway is induced in normal individuals, backward tilt restricted to the head is observed in labyrinthine defective persons. These results illustrate the importance of vestibular–cervical interaction in postural control.

Visual mechanisms in posture
Vision contributes to postural balance and this is the basis of the Romberg test. Previous studies defined characteristics of the visual input controlling balance such as luminance, distance eye-object, contrast and size. During the period covered by this review it was found that spatial frequency [10] and motion parallax [11] are also contributory. The role of central versus peripheral vision was re-examined by Nougier et al. [12].

A prerequisite to the visual control of posture or locomotion, is the visual perception of motion, and particularly self-motion. Patients with congenital nystagmus have reduced object motion perception [13,14] but, in spite of this, self-motion perception (measured as time to onset of self-motion perception (circularvection)) and visual control of posture are close to normal [15]. The differences between object motion and self-motion perception or visual control of posture in congenital nystagmus cannot be explained in terms of a primary deterioration of visual motion signals. Dissociation between object perception and self-perception or posture can also be observed in patients with vestibular lesions. Ipsilesional tilts of the subjective visual vertical in acute unilateral vestibular patients are the rule, although patients did not show a bias in their ability to adjust their body vertical in a flight simulator [16]. In addition, in normal individuals the level of visual field dependency in a perceptual task, the rod and frame test, did not predict the level of visual field dependency for posture [17]. Thus, different mechanisms and pathways subserving perceptive and postural tasks should be assumed.

As in the field of perception, a hemispheric dominance in the visual contribution to postural control has been put forward [18]. In an experiment in which individuals were seated on a rocking chair, head stabilization in space was better with left visual field viewing (right hemisphere) than with right visual field viewing. Interestingly, more severe impairment of body stability was observed in left hemiparetic patients than in right hemiparetic patients [19,20]. Furthermore, a functional magnetic resonance imaging study in normal individuals showed a right predominance for cortical activation by visual-optokinetic stimuli [21].

A parallel between the effect of visual and somatosensory cues via hand and fingertips on balance has recently been drawn. In essence, gentle contact of a finger with a stationary object (through a cane or not) reduced body sway as effectively as mechanical contact that is forceful and supportive (in normal vestibular and blind subjects) (for review [22*]) and as effectively as sight of the surroundings [22*,23]. Furthermore, when the contact surface moved rhythmically, a clear displacement of the entire body to the frequency of touch surface movement was observed [24]. These studies suggest an equivalence between information about body orientation registered visually and haptically [22]. Interestingly, auditory information from a stable environment also improves stability significantly in normal and blind individuals, but to a lesser extent than visual and haptic cues [25].

Clinical applications of posturography
Most neurologists are peacefully unaware of the ongoing, sometimes vitriolic, argument about the clinical usefulness of posturography [26**,27–29]. Probably the first article to appear in a neurological journal (Neurology) with potential to attract the general neurological readership [30] conveyed the Report on the Therapeutics and Technology Assessment Subcommittee of the American Academy of Neurology. The specialist panel concluded in 1993 that dynamic posturography had a promising role in the assessment of balance disorder-patients, but the ensuing discussion 5 years later testifies that such potential has not been fully developed. No one questions that platforms and other sway recording devices have been and will continue to be vital in better defining patient groups or abnormal balance mechanisms. The centre of the debate is whether posturography can improve the diagnosis or management of an individual patient. An incisive ‘against’ article by Dobie [26**], along with several ‘for’ replies published in the American Journal of Otolaryngology [26**,27] will be of value for those interested in this discussion.
The difficulties are illustrated in a recent paper by Baloh et al. [31] who compared dynamic posturography in patients with peripheral bilateral vestibulopathy and cerebellar patients. Although both groups swayed significantly more than normal control individuals, no testing condition or parameter measured could reliably distinguish between the two groups, except for the presence of an anteroposterior body tremor in the cerebellar patients. The tremor, measured by Fourier analysis of the sway signals, was clinically observed anyhow. In view of these findings the authors' answer to their own question 'Does posturography have a role in the clinical diagnosis of patients with balance disorders?' was, not surprisingly, 'no'. Other recent studies have again shown the value of posturography in group assessment, e.g. to indicate progression of disease in polynuropathy [32] or to detect subclinical balance deficits in patients with benign positional vertigo after treatment [33]. The study by Burgnezay and Munro [34] on 200 patients with a balance disorder reported that 50% of the 129 patients with a single diagnosis had normal results on dynamic posturography. Discrepancies with other series in the literature showing higher hit rates were not discussed in depth.

A positive way forwards in the question of what is the actual value added by posturography is to compare balance and gait performance clinically and by posturography. El-Kashlan et al. [35] compared results from a clinical battery known as the 'clinical test of sensory integration and balance' with those of dynamic posturography. Many interesting aspects stem from this paper, not least the finding that customized vestibular exercises were found to be superior to routine rehabilitation. A highly significant correlation of the clinical and posturography version of the balance assessment was also evident. Lower sensitivity (false negatives) in the clinical assessment was reported, but the finding could equally be interpreted as a false positivity in dynamic posturography. Tang et al. [36] also compared dynamic posturography in normal elderly individuals with a well developed clinical assessment of balance and mobility that mimics real-life activities. These authors found that the results of dynamic posturography correlated mostly with posturographic conditions using all sensory systems available, i.e. eyes open with stable supporting platform. The results are useful but, at the same time, puzzling. They could be interpreted as if a simple static posturography assessment could be as good a predictor of an elderly person's overall mobility as an expensive dynamic posturography test.

Other studies investigating balance in the elderly have appeared. In healthy elderly individuals up to the age of 80 years, minimal change in equilibrium was observed during quiet standing. Balance decline became evident when multiple sensory inputs were disrupted (both visual and proprioceptive information). Individuals older than 80 years are more susceptible to proprioceptive disturbances and are less able to compensate with visual information [37]. Thus, important changes occur before age 80 years, but a deficit in central processing after age 80 years further compromises balance. On a large sample of ambulatory elderly individuals (approximately 500), a relationship was found between balance problems and cerebral atrophy investigated by magnetic resonance imaging [38]. The strongest association with balance performance was white matter disease and ventricular size.

**Primary orthostatic tremor**

Patients with orthostatic tremor are well known to the neurologist specializing in movement disorders. However, these patients often 'slip through the net' and turn up in neuro-otology clinics. This is not surprising because the chief symptoms in these patients are discomfort while standing up, unsteadiness and 'shakiness' during upright stance due to the leg-trunk tremor. The neuro-otologist should not expect overt signs in these patients. The standing tremor may just be visible and there are no 'central' vestibulo-oculomotor signs. Keeping this diagnosis in mind is, however, most rewarding for the clinician, because conventional surface electromyogram recordings easily identify the pathognomonic high-frequency tremor (12-20 Hz, typically 16 Hz). In neuro-otological practice the diagnosis can be made with...
The posturography platform, which shows the high frequency tremor peak. This latter use of the posturography platform may turn out to be one of its few disease-specific practical applications (Fig. 1).

For a review of orthostatic tremor see Thompson [39]. No definitive aetiology for this condition has been identified and some overlap with essential tremor has been suggested. Alcohol and β-blockers, however, are usually ineffective, whereas primidone and clonazepam can be helpful treatments. A review of the efficiency of the various drug treatments, diagnostic limitations of accelerometric recordings and 10 new cases have just appeared in the French language literature [40]. These authors conclude that orthostatic tremor deserves to be investigated in all patients with unexplained instability or postural phobia. In the past year controversy on orthostatic tremor centred on whether the leg tremor can [41] or cannot [42] be reset by transcranial cortical stimulation. Although there is agreement that the tremor has a central origin, central resetting by cortical stimulation would provide more direct evidence in this direction. Cases of orthostatic tremor with additional neurological findings are beginning to be reported (e.g. with progressive instability of stance and gait and lower limb hypertrophy [43]). Two cases of symptomatic orthostatic tremor secondary to lesions in the pontine area have been reported [44], supporting the view that cerebellar–brainstem loops are involved in this syndrome [45].

**Psychophysiological unsteadiness**

Anxiety can create dizziness and vice versa. Almost all clinicians will share this view, but no one would claim to have an easy solution to the dizziness–anxiety problem. A recent paper by Andersson et al. [46*] is exemplary in its multidisciplinary approach to the problem. A group of 16 patients with defined vestibular disorders and normal control individuals were compared with regard to objective unsteadiness (posturography) during specific and nonspecific balance perturbations (calf and arm muscle vibration, respectively). Subjective unsteadiness (self-rating) as well as levels of worry, discomfort and anxiety and arousal (blood pressure and heart rate) were also measured. There was good agreement between subjective and objective unsteadiness and, as expected, the patients had increased levels of coping difficulty, less positive thoughts and increased sensitivity to somatic symptoms. It is difficult to interpret the findings fully but, in this group of patients, no evidence of undifferentiated postural responses or disproportionate levels of subjective reporting of unsteadiness was found, in spite of the increased psychological difficulties. This suggests that the psychological findings were genuinely secondary to the vestibular disorder.

One of the diagnoses raised in the context of psychogenic unsteadiness is the hyperventilation syndrome. Remarkably, very little is known on the effects of hyperventilation on the balance system and, vice versa, the effects of vestibular stimuli on the respiratory system. Sakellari and coworkers [47*48] have shown that voluntary hyperventilation caused a measurable increase in body sway, both in normal individuals and in patients with unilateral and bilateral vestibular disease. This raises the possibility that, at least partly, the unsteadiness reported by hyperventilators may be secondary to veridical detection of increased sway. Similarly, hyperventilation induced significant nystagmus in well compensated vestibular patients. On the basis of neurophysiological studies, the authors concluded that the effects of hyperventilation on postural mechanisms are in the main due to interference with the somatosensory system and with the processes mediating vestibular compensation.

Jacob et al. [49] used dynamic posturography in a group of patients with panic disorder with agoraphobia, on the basis of previous findings that these patients report space and motion discomfort and show occasional vestibular abnormalities. The patients showed diminished postural performance in conditions when lower limb somatosensory information was minimized, a posturography pattern referred to as support surface dependence. This strategy can lead to intolerance in situations when the supporting surface is unstable or unreliable. The authors emphasized the need for a positive search for the presence of this phenomenon in these patients, suggesting that cognitive therapy or rehabilitation should be helpful in resolving them. We wish to point out that cognitive therapies and customized regimens of vestibular rehabilitation have gradually converged. They both aim at identifying specific subsets of symptoms and difficulties upon which the therapist could work. This approach has been taken up by many groups dealing with chronic symptoms in balance disorder patients, regardless of the difficulties encountered in establishing final diagnoses and defining pathophysiological mechanisms [50–52].

**Gait analysis**

Gait analysis techniques experience at least the same difficulties as posturography in finding a way into clinical practice. Commercial pressure by manufacturers, research versus practical management needs, different technical or medical background of the health professionals and different populations of patients assessed guarantee that this debate will continue for some time. A recent paper by Mulder et al. [53*] aimed to clarify some of these issues by reviewing 96 papers in the field of gait analysis and attempting to answer why it is that instrumental techniques of gait analysis are rarely used in the rehabilitation
of tasks adopted during gait measurements and the conclusions are not unexpected; only 15 of the 96 papers reviewed used gait tasks that were aimed at quantifying disability, as opposed to impairment. Be this as it may, researchers have yet to prove – both for posturography and for gait laboratories – that the considerable technical and financial investment required to set up such laboratories can improve the quality of day-to-day patient care.

Of the many clinical topics in the field we have chosen gait in Parkinson's disease, for its clinical importance and fascinating pathophysiology, and because considerable work was published in the past year. Recently, Lyon and Day [54] measured forces and movement trajectories, and modelled the first step in healthy individuals. The conclusion reached was that the observed movement of the centre of mass at 'toe off the ground' is under a ballistic mode of control. Thus, the central nervous system has to compute in advance the required size and direction of what is effectively a 'throw' of the body towards the supporting foot. One could therefore predict that premovement ballistic computations would be abnormal in Parkinson's disease and that this would account for the occasional 'freezing' of gait in this disorder. A study on gait initiation in young, old and Parkinsonian individuals, however, did not produce spectacular results [55]. There were many differences in gait parameters measured amongst these three groups, but the authors found that all these differences could be explained as a function of gait velocity. Bursts of electromyogram activity in tibialis disease patients. A minus in this paper was that, although patients' gait froze before the study, this did not happen during the recording session; it is not clear whether this is just bad luck or yet another mystery of Parkinsonian gait. A plus is that, in addition to the original results, the authors reviewed and table-summarized 22 papers on gait initiation in young, elderly and Parkinson's disease patients.

Gait facilitation by visual stimulation (striped floors) can be striking in some Parkinson's disease patients. Azulay et al [56] quantified walking performance in 13 Parkinson's disease patients and found that only seven improved when they walked on a striped floor. As a group, there was no significant improvement with the visual stimulus. Less well known is the fact that Parkinsonian gait can also improve with rhythmic auditory stimuli. McIntosh et al. [57] quantified gait performance of patients under different conditions, including rhythmic auditory stimulation at a rate 10% faster than the spontaneous baseline cadence. The results confirmed previously observed gait improvements, which opens up the possibility of using rhythmic auditory stimulation as a rehabilitation tool in Parkinson's disease. Voluntary and sensory-mediated modulation of gait in patients with Parkinson's disease was also documented in two studies that used the relationship between walking cadence (stepping frequency) and stride length to express gait performance [58,59]. Interestingly, the slope of this cadence/length function was the same in normal control individuals and in patients on and off medication, but the intercept (i.e. stride length) was reduced in patients, particularly those who were off medication. Morris et al. [58] concluded that the basic abnormality in Parkinson's disease is defective step scaling and not a timing disorder. The study of Zijlstra et al. [59] reached similar conclusions and also observed that the addition of visual cues allows considerable improvement in step length. It is interesting that both in normal individuals [60] and in Parkinson's disease patients [59] visual manipulation affected mostly space-related gait parameters (stride length) but not temporal parameters (stride frequency), whereas vestibular caloric stimulation in normal individuals affected both [61]. A review on recent advances in the control of locomotion by vision has recently been published [62].

Conclusions

No agreement has been reached as to whether gait and posturography techniques are of immediate practical value to patient management. These techniques continue to provide, however, a great deal of understanding of normal and abnormal physiological mechanisms in gait and posture control. We suspect that primary orthostatic tremor, which causes sometimes ill-defined stance discomfort with few clinical signs, may be one of the few diagnostic applications with high specificity in posturography.

References and recommended reading

Papers of particular interest, published within the annual period of review, are highlighted as:

* of special interest
** of outstanding interest

Provocative arguments on whether posturography is of practical clinical use are presented. A puzzling change was observed in visual dependence for posture after vestibular neurectomy.


A puzzling change was observed in visual dependence for posture after vestibular neurectomy.


Jeka JJ. Light touch contact as a balance aid. Phys Ther 1997; 77:476-487.

This is an interesting review on the role of light touch for postural control.


This is a good study with a multidisciplinary approach to balance disorders.


This is a posturographic, neuropsychological and oculographic investigation into the mechanisms mediating postural imbalance in response to hyperventilation.


Visual-vestibular control of posture and gait Bronstein and Guerraz


53 Muller T, Nienhuis B, Pauwels J. Clinical gait analysis in a rehabilitation context: some controversial issues. Clin Rehab 1998; 12:99–106. This is a review of the literature concluding that gait analysis techniques could find their way into the clinic if the research questions were disability-orientated.


