RESEARCH ARTICLE

A.M. Bronstein · D. Buckwell

Automatic control of postural sway by visual motion parallax

Abstract The purpose of this study was to establish whether visual motion parallax participates in the control of postural sway. Body sway was measured in ten normal subjects by photoelectric recordings of head movements and by force-plate posturography. Subjects viewed a visual display ("background"), which briefly moved (2 s) along the y (horizontal) axis, under three different conditions: (1) direct fixation of the background, (2) fixation of a stationary window frame in the foreground, and (3) fixation of the background in the presence of the window in the foreground ("through the window"). In response to background fixation, subjects swayed in the same direction as stimulus motion, but during foreground (window) fixation they swayed in the opposite direction. The earlier forces observed on the force platform occurred at circa 250 ms in both conditions. The results show that motion parallax generates postural responses. The direction of these parallax-evoked postural responses – opposite to other visually evoked postural responses reported so far – is appropriate for stabilizing posture in natural circumstances. The findings show that motion parallax is an important source of self-motion information and that this information participates in the process of automatic postural control. In the "fixating through the window" condition, which does not mimic visual conditions induced by body sway, no consistent postural responses were elicited. This implies that postural reactions elicited by visual motion are not rigid responses to optokinetic stimulation but responses to visual stimuli signalling self-motion.

Key words Visual motion · Parallax · Posture · Balance · Spatial orientation · Human

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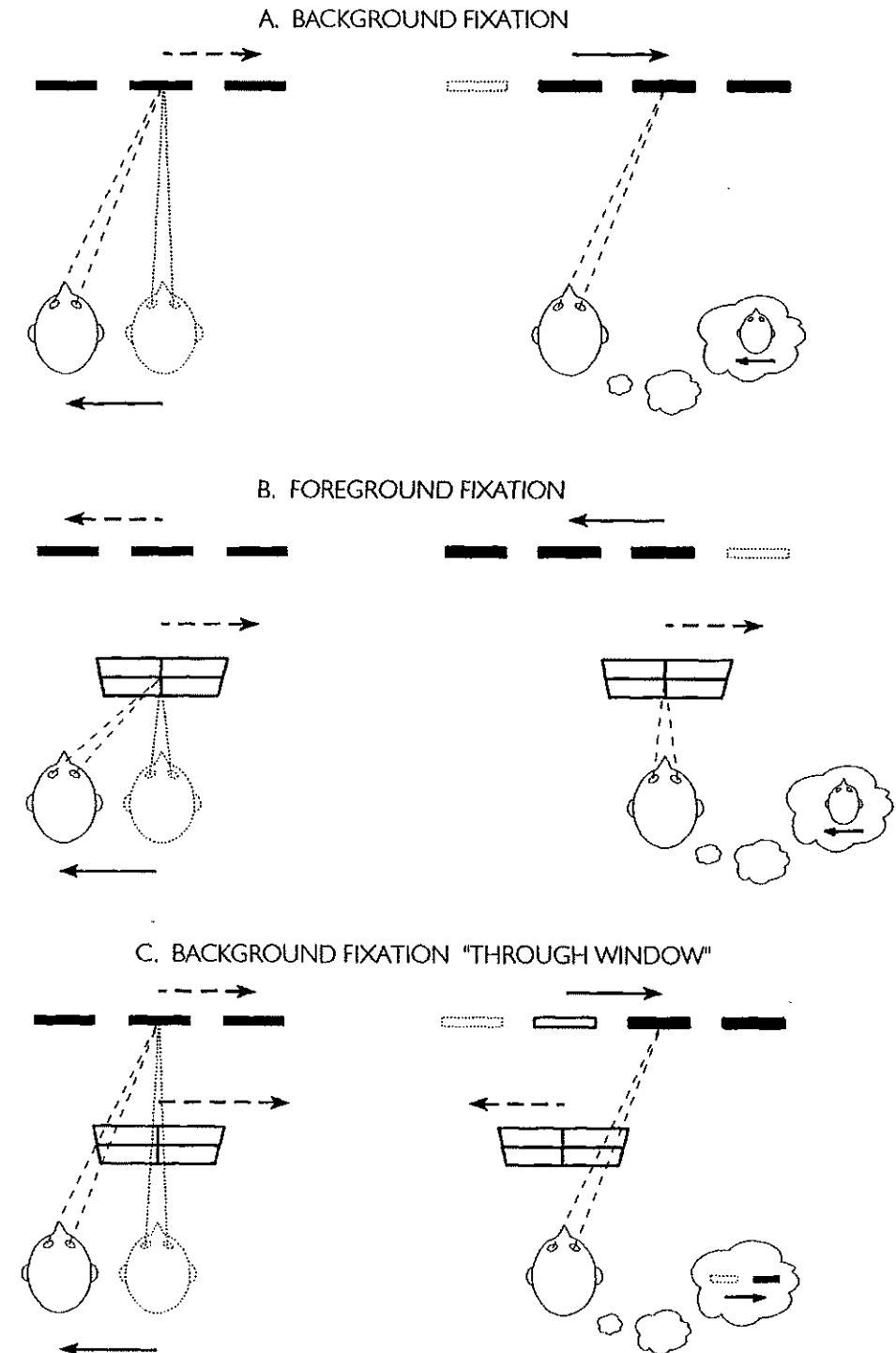Fax: +44-171-837-7281, e-mail: dizzymrc@ion.ucl.ac.uk

Introduction

Vision controls balance and walking in at least two ways. Visual targets, from prey to bus stops, initiate and guide locomotion. Much more automatically, vision also controls postural sway, by generating postural reactions that tend to stabilize the subject with respect to the visual world. The simplest demonstration that retinal input is important in the control of posture is that the amount of body sway with eyes open is approximately 40–50% less than that with eyes closed (e.g., Diener et al. 1984; Paulus et al. 1984). Since postural sway is controlled by a complex process involving proprioceptive and vestibular inputs, the specific role of vision required experiments with isolated visual motion stimuli. These experiments showed that movement of the visual surroundings induces body displacements in the same direction as that of the visual stimulus (Dichgans et al. 1972; Lee and Lishman 1975; Lestienne et al. 1977; Bles et al. 1980; Bronstein 1986), thus provided evidence that vision plays a direction-specific role in postural control.

It is important to note that such visuo-postural reactions are evoked, in normal circumstances, in response to our own head/body sway. Head displacement, say to the left, produces visual motion to the left (Fig. 1, top left, "Real life"). In turn, rightwards visual motion is known to produce a corrective postural adjustment to the left bringing the head/body back towards the starting position (Dichgans et al. 1972; Bronstein 1986), presumably because the visual stimulus is interpreted as leftwards head sway (Fig. 1, top right, "Experiment"). Flat, depthless visual surfaces are, however, the exception rather than the rule in the visual world. In any natural or urban environment, side to side head sway induces complex parallax motion patterns to the eye of an observer (see Rogers 1993 for review). The reader can experience this by standing near a window, whilst optically fixating on some of its features such as a window catch, and exaggerating his/her normal lateral sway. It will then be noticed than on swaying, say to the right, the distant background, for instance buildings across the road, appears to

Fig. 1A–C Schematic diagram showing a subject swaying from right to left in the "real world" (*left*) and the experiments conducted with motion of the background (*right*). The subject is fixating: **A** on a flat background (*top*), **B** on an earth-fixed window in the foreground viewed against the background (*middle*), or **C** on the background viewed through the window in the foreground (*bottom*). The experiment in **A** reproduces the visual conditions produced by sway in the real world. Experimental background motion in **B**, which provokes induced motion of the window in the foreground, also mimicks visual conditions induced by sway in the real world – albeit no eye movement is necessary to maintain fixation on the window in the experiment. Note that in **C**, leftwards sway of the subject induces rightwards visual motion of both background and foreground, whereas experimental rightwards background motion induces leftwards visual motion of the foreground window (compare *bottom left-right*). Also note that the experiments **B** "window fixation" (*right*) and **C** "fixation of the background through the window" (*right*) induce visual motion with opposing foreground-background directions but that these two experiments provide different vergence, accommodative and retinal-disparity cues. *Solid arrows* indicate translation in space, either of the head or of the projected visual background. *Dashed arrows* indicate visual motion with respect to the subject produced by head or eye movements and induced movement (the illusion that a small stationary object moves in the opposite direction to that of a large background motion; Wallach 1959)

REAL LIFE:
Sway (self) generated visual motion

EXPERIMENT:
Visual background motion stimuli

A. BACKGROUND FIXATION

B. FOREGROUND FIXATION

C. BACKGROUND FIXATION "THROUGH WINDOW"

move to the right, i.e. in the *same* direction of body sway (Fig. 1, middle left, "Real life"). Although neurons in the cerebral cortex suited to code motion parallax have been identified (Roy and Wurtz 1990), it is not known whether such visual information contributes to the automatic process of postural control.

Materials and methods

Ten normal subjects gave their informed consent to participate in these experiments (age range 24–49 years, weight range 55–80 kg). With the exception that one of the authors (D.B.) was tested, subjects were naive as to the purpose of the experiment.
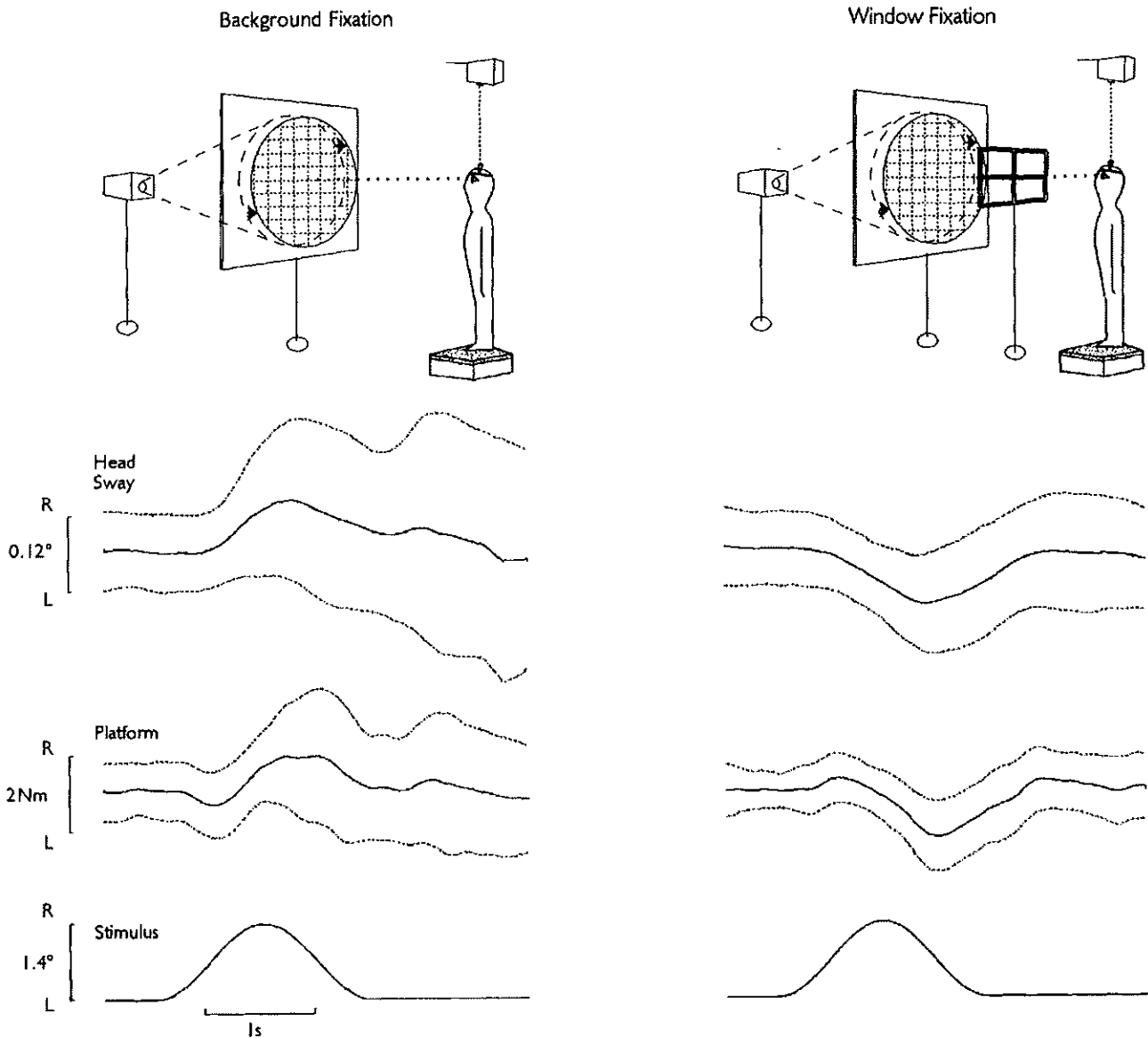
Background Fixation　　　　　　　　　　　　　　　Window Fixation

Head
Sway

R

0.12°

L

Platform

R

2 Nm

L

R

Stimulus

1.4°

L

Is

Fig. 2 *Top* Schematic diagram showing the experimental situation. *Bottom* Sway responses to visual motion of the background, during background or foreground (window) fixation. Upwards deflections indicate rightwards motion. The grand mean and standard deviation of ten normal subjects are shown. Note reversal of sway direction when parallax effect is introduced by window fixation. There is good agreement between head sway and platform signals, except for an early foot torque component in the direction opposite to the ensuing sway

Two of them had participated in a pilot study several months earlier (see Footnote 3). Subjects stood barefoot on a 5-cm-thick piece of rubber foam (density 30 g/dm³) placed on a force platform.[1] The room was dimly lit and subjects faced a checkerboard pattern, 80 cm in diameter, back-projected by a grating generator onto a translucent screen. The image was moved linearly in the horizontal plane by the grating generator under computer control, to and fro from the centre, with a raised cosine trajectory. The image moved for 2 s, amplitude 25 mm (corresponding to 1.4° of hori-

zontal visual angle) at a peak velocity of 40 mm/s. A trial comprised 30 pseudo-randomized stimuli, 10 to the right, 10 to the left motion and 10 sham (no motion). Postural sway was recorded with a photo-detecting system (Schottky camera, resolution 0.10 mm, linear up to ±10 cm), placed 27 cm above the head, whilst subjects wore a helmet carrying a light source on the top, and with the torque-calibrated signals from the platform. The sway signals were displayed on-line so that the experimenter could deliver the stimuli at the points of maximal stability.

Subjects were exposed to three visual conditions presented in a latin-square design: (1) fixating one of the central squares of the checkerboard pattern (Fig. 1, "background fixation"), (2) fixating an LED attached to a bar placed in the centre of a purpose-built, self-illuminating, earth-fixed window frame (27×19 cm; Fig. 1, "foreground fixation"); the arrangement allowed vision of the background through and around the window frame. In condition 3, subjects fixated the background display through the earth-fixed window present in the foreground (Fig. 1, "background fixation through the window"). Eye-background distance was 100 cm and eye-window distance 50 cm. The experimental arrangement can be seen at the top of Fig. 2. Before being exposed to each of the three visual motion-stimuli, subjects were asked to remain as steady as possible for 30 s, with identical optic fixation to that they would be requested to maintain in the experimental trials to follow, so that they experienced visual motion generated by their own body

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[1] Standing on foam reduces the accuracy of lower limb proprioceptive signals so enhancing the influence of vision on sway control (Bles et al. 1980; Bronstein 1986).

Table 1 Spontaneous and visually evoked sway during background and foreground fixation

	Background fixation					Foreground fixation				
	Spontaneous		Visual response[1]			Spontaneous		Visual response[1]		
	Mean	SD	Mean	SD	%	Mean	SD	Mean	SD	%
Head sway (mm)	3.3	2.15	1.35	2.14	41	2.18	0.38	1.48	1.48	69
Foot torque (Nm)	2.15	1.24	0.88	1.66	41	1.28	0.46	1.26	1.09	97

[1] Percentages represent the amplitude of the visual response with respect to that of the spontaneous sway

sway.[2] Sway responses were averaged, aligned by stimulus onset, in order to cancel the spontaneous sway and therefore allow the specific component of sway due to the visual stimuli to emerge.

Results

Figure 2 shows the results of the experiment as a grand mean of the 10 subjects, combining rightwards and leftwards stimuli, in the visual conditions examined. Scatter in the grand mean is represented as ±1 SD of the sway responses. It can be seen that visually elicited postural sway was in the same direction to that of the stimulus when fixating directly on the moving pattern (Fig. 2, "Background fixation"). When subjects fixated on the window in the foreground, the visually elicited postural reaction was reversed in direction (Fig. 2, "Window fixation"). Although interfered with by the spontaneous body sway, this pattern could be observed in approximately 70% of the individual means.

Latencies of the head sway responses were of circa 300 ms from stimulus onset in both conditions (Fig. 2); recordings from the sway platform showed an earlier component in the opposite direction of the main direction of sway which represents the foot torque responsible for the ensuing sway (latency circa 250 ms).

The peak amplitude of the head sway response was approximately 1 mm (0.06° horizontally at screen level) and 1 Nm of foot torque in both conditions (Fig. 2, Table 1). There was a statistically significant difference (one-tailed Student's t-test for independent samples) between the peak response magnitude in background fixation and window fixation (head: $t=3.44$, $P<0.01$; torque: $t=3.00$, $P<0.01$) as well as during window fixation and its corresponding "no stimulus" condition (head: $t=1.81$, $P<0.05$; torque: $t=2.12$, $P<0.02$). The difference between the response during background fixation and its corresponding no stimulus control approched $P<0.05$ significance for the head ($t=1.57$) but not for torque date ($t=0.86$).

Collectively, the amplitude of the response to the motion stimuli represented approximately half of that of the

spontaneous, background sway (Table 1). The table shows lateral, baseline head sway and foot torque during the initial 30 s prior to visual stimulation. The values shown represent the mean sway amplitude, measured as the mean deviation of head position (or foot torque) from the normalized, mean head position (or foot torque) values. Since baseline sway was smaller during window fixation that during background fixation, the relative amplitude of the response elicited by the visual motion stimulus was larger during window fixation (69% of head sway and 97% of foot torque) than during background fixation (41% for both measurements; Table 1).

Means of trials during fixation of the moving background in the presence of the stationary window in the foreground (Fig. 3, "Background fixation through window") showed no consistent postural sway response. Sham, no stimulus trials produced stable, flat means in all conditions of optic fixation (Fig. 3, "No stimulus").[3]

Discussion

The main result in these experiments is that the direction of visually induced body sway can be reversed if subjects fixate an object in the foreground during visual background motion stimulation. In this and all previous studies, visually induced sway was in the same direction as the motion stimuli in the absence of a foreground. We now show that that if subjects fixate a stationary object in the foreground, sway in the opposite direction to background motion is induced. This is what would be expected if the visuo-postural system were sensitive to motion parallax cues, and the results therefore indicate that motion parallax has a profound influence on the direction of visually mediated postural responses.

Motion parallax produced by head movements is widely used in the animal kingdom to gain depth and distance information for the programming of goal-oriented movements (Ellard et al. 1986; Sobel 1990). The head movements occurring during spontaneous body sway, however, can hardly be regarded as purposeful. Instead

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[2] The dynamic characteristics of the projected visual stimulus were chosen to be within the range of those present in spontaneous body sway, so that subjects would find it difficult to know if the visual motion observed was generated by their own sway or by the experimenter. Most subjects, however, were, able to detect the experimental motion of the background.

[3] Reproducibility of the results is reinforced by the fact that a pilot experiment in eight subjects (only two of whom participated in the definitive experiment), using only the head recording device, showed identical results during the conditions investigated (foreground fixation, background fixation and no stimulus).
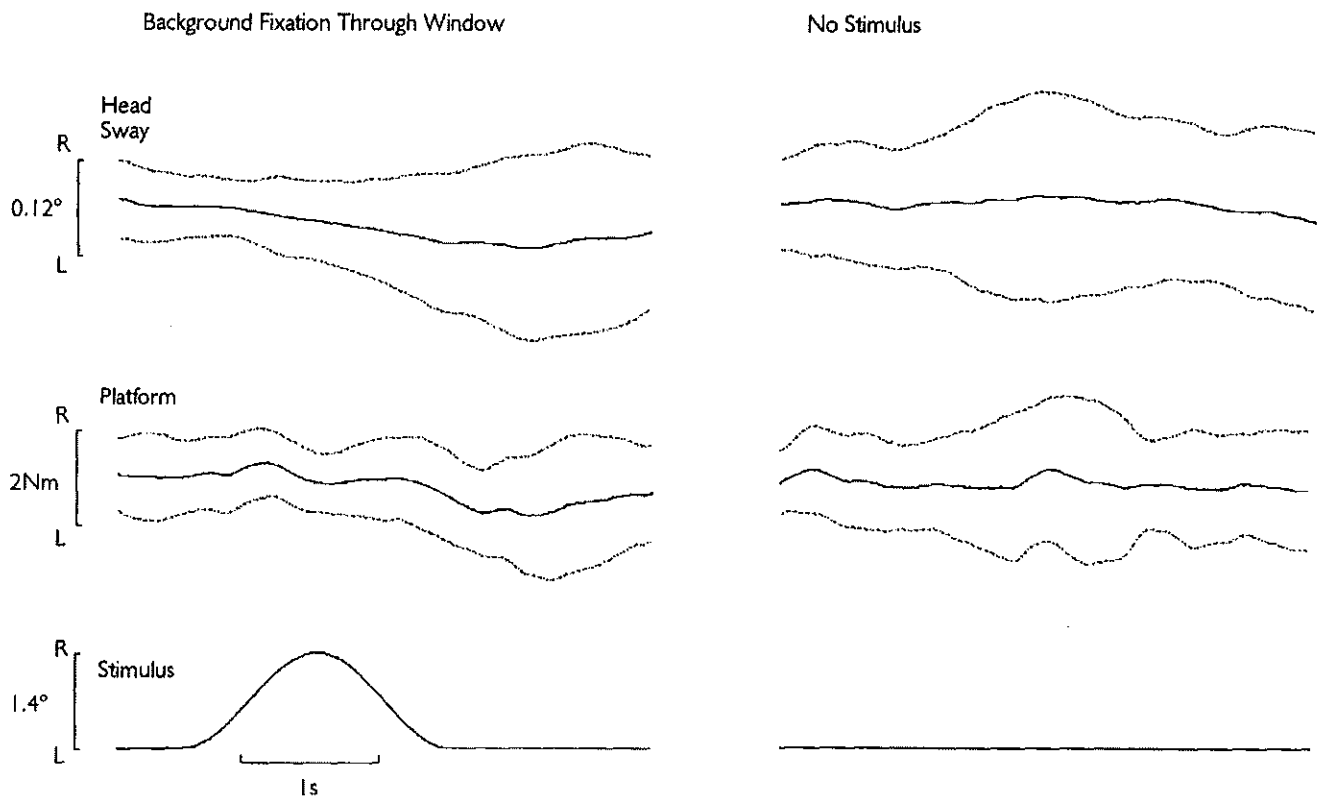
247

Background Fixation Through Window

No Stimulus

Fig. 3 Grand means in the ten subjects during background fixation "through" the window (*left*) and during the sham (no stimulus) trials during background fixation (*right*). In contrast to Fig. 2, no consistent response is seen in either condition

they may be considered as "noise" or imperfections in the postural control system; indeed, intoxication (e.g. alcohol; Woollacott 1983), impairment of the visual (Paulus et al. 1984), vestibular (Keshner et al. 1987) or proprioceptive input (Mauritz and Dietz 1980; Bergin et al. 1995) and central nervous system (CNS) disease (Diener et al. 1984) all increase body sway. In spite of not being purposeful, the parallax cues produced during such "unwanted" body sway are automatically used as feedback by the postural control centres. These experiments provide further evidence that the visual control of sway does not result from a rigidly "wired up", optokinetic reflex: the introduction of parallax cues can reverse the direction of a visually induced sway response. Recent work has shown that the direction of sway in response to rotatory roll-stimuli can be modulated by the angle of the eye in the head and that of the head on the trunk (Bronstein 1994; Wolsley et al. 1996). Furthermore, visually evoked postural reactions can be suppressed altogether if the proprioceptive system signals that no real self-motion has occurred (Bronstein 1986). Thus, parallax cues, inputs specifying eye position relative to the body and central "weighting" of the reliability of the visual input, respectively, all contribute to shape postural responses to visual motion. Such complex processing may underlie the relatively long latencies found in this and most studies of postural responses in response to visual motion stimuli.

Central weighting is the name given to the process which allows successful postural control when the information conveyed by a particular sensory channel is reduced or unreliable. More weight is given to visual information when proprioceptive information is unreliable (e.g. compliant supporting surface or proprioceptive disease) and vice versa (e.g. darkness or movement of the visual surroundings; Bronstein 1986). This weighting is usually thought of as an across-sensory modality process. The experiments reported here, however, provide information on two "intra-visual" aspects of this weighting process. These are the effects of tracking the visual motion and the effects of incoherence (or conflict) within the optic flow field. These two aspects will be discussed in turn.

When subjects fixate on the experimentally moved background, tracking eye movements (pursuit/optokinesis) tend to cancel retinal image motion, whereas fixation on the window suppresses tracking eye movements, which enhances retinal image motion (Fig. 1A,B, right). In spite of this difference, however, both experimental conditions produced postural sway responses of comparable magnitude. It should also be noted that during fixation on an object in the foreground, spontaneous (sway-generated) visual motion will induce tracking eye movements in the opposite direction of head sway, i.e. towards the window (Fig. 1B, left). In contrast, eye movements during foreground fixation with background visual motion are almost totally suppressed (Pola et al. 1995). Here, again, the presence or absence of tracking eye movement in the natural or experimental condition, respectively, did not seem to matter for the postural response. These results agree with previous data indicating

that the illusion of perceived self-motion during optokinetic stimulation is independent of the presence or direction of tracking eye movements (Dichgans and Brandt 1978) and that the direction of self-motion can be correctly estimated with or without pursuit eye movements (Warren and Hannon 1990).

Although at first sight condition 3, background fixation through the window, would also appear to simulate parallax induced by self-motion, this is not the case. Figure 1C (bottom left) illustrates that, if a subject spontaneously sways to the left whilst fixating the background, parallax will make the window in the foreground appear to move further and faster than, but in the same direction as, the background (in the example illustrated, to the right). Therefore, an experiment to mimic this situation should move both foreground and background in the same direction, the former faster than the latter. The lack of a consistent response to movement of the background whilst looking through the stationary window therefore suggests that, unless the visual-motion stimuli mimic those encountered during body sway, visually elicited postural responses are not generated. This condition induced "intra-visual conflict" leading to down-weighting of visuo-postural responses.

This interpretation is supported by single-unit analysis in the medial superior temporal area (MST) in monkeys foveating a stationary target whilst optokinetic stimuli were presented either in front or behind the plane of fixation (Roy et al. 1992). Over 90% of binocular disparity neurons in this area responded to either optokinetic stimuli presented in front of or behind the fixation plane. This effectively codes whether motion occurs in the foreground or the background. Furthermore, some 40% of the neurons responded to one direction of motion in the background and the opposite direction of motion in the foreground. These disparity-dependent, direction-selective neurons are uniquely placed to code the direction and speed of self-motion. Such precise central coding self-motion-induced parallax implies that visual stimuli not mimicking the visual conditions generated by self-motion will not elicit an appropriate response in the visual and, therefore, postural systems. Examination of Fig. 1C (right) illustrated that movement of the background neither reproduces visual conditions generated by body sway whilst fixating through the window (Fig. 1C, left) nor during window fixation (Fig. 1B). It differs from fixation through the window in the direction and relative speed of motion and from window fixation in the convergence and disparity cues.

Postural control relies on multi-sensory processing and motor responses that appears to be automatic and of which we are largely unaware. It can be concluded that these responses are critically dependent on the detection of self-motion by different sensory systems, including congruent visual parallax cues.

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