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RESEARCH ARTICLE

A. Thurrell · P. Bertholon · A.M. Bronstein

Reorientation of a visually evoked postural response during passive whole body rotation

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Abstract Visually evoked postural responses (VEPR) to a roll-motion rotating disk were recorded from normal subjects standing on a yaw axis motorised rotating platform. The disk was fluorescent so that subjects could be tested in an otherwise dark room. Movements of the head and centre of foot pressure were measured while subjects looked at the disk with their eyes and head in the primary position and while the rotating platform moved the subjects randomly to 0, +/–45° and +/–90° angles from the visual stimulus. Subjects were instructed to maintain fixation on the centre of the rotating disk but the amount of horizontal eye and head movement used was not specified. Platform rotational velocity was set near threshold values for perception of self-rotation (~2°/s) so that subjects would find it difficult to reconstruct the angle travelled. The data showed that the VEPR occurred in the plane of disk rotation, regardless of body position with respect to the disk, and despite the subjective spatial disorientation induced by the experiment. Averages of the response revealed a good match (gain=0.95) between disk orientation and sway direction. The horizontal gaze deviation required to fixate the centre of the disk was largely achieved by head motion (head 95%, eye 5%). The results confirm previous results that VEPRs are reoriented according to horizontal gaze angle. In addition, we show that the postural reorientation is independent of cognitively or visually mediated knowledge of the geometry of the experimental conditions. In the current experiments, the main source of gaze position input required for VEPR reorientation was likely to be provided by neck afferents. The results support the notion that vision controls posture effectively at any gaze angle and that this is achieved by combining visual input with proprioceptively mediated gaze-angle signals.

Key words Vestibular · Posture · Visual motion · Proprioception · Human

A. Thurrell · P. Bertholon · A.M. Bronstein (✉)
MRC Human Movement and Balance Unit,
8–11 Queen Square, London, WC1 N 3BG, UK

Introduction

Vision is used in conjunction with proprioceptive and vestibular signals for spatial orientation and balance control. If a subject, standing upright and looking straight ahead in a room, spontaneously starts to fall to the right, the optic flow will be to his/her left. The correct righting response for the subject in this case is to increase the pressure on the right foot and decrease it on the left, such that the change in forces acts to rotate the subject's body leftwards. The usual cause of large-field visual motion is the movement of the retina in space; therefore large-field motion is treated as if it was due to self-motion by the subject. If this retinal motion is simulated by a visual scene moving to the left when the subject is in fact upright, then the change in pressures at the feet will act to destabilise the subject to the left, i.e. in the same direction as the visual motion. The response to a large-field moving stimulus is therefore to sway in the same direction in space as the visual motion (Dichgans et al. 1975; Clément et al. 1985; Bronstein 1986).

A common feature of many previous experiments is the use of visual motion stimuli that are viewed by the subject looking straight ahead, i.e. with both the eyes centrally placed in the orbits and the head centrally placed on the shoulders (Dichgans et al. 1975; Clément et al. 1985; Bronstein 1986). However, Wolsley et al. (1996) investigated the effect of supplying identical retinal inputs with the eyes and head at different positions in the yaw plane. It was found that subjects reoriented the main direction of sway, so as to match the direction of the visual stimulus, for a variety of combinations of head-on-trunk and eye-in-orbit positions. However, this experiment was run in a well-lit visual environment, with subjects instructed to position themselves actively. Thus subjects may have been able to determine their orientation, and that of the visual stimulus, visually and cognitively. Here we examine whether accurate reorientation of visually evoked postural responses (VEPR) still occurs during passive body rotation and with diminished visual and cognitive cues.

Methods

Eight normal subjects aged between 21 and 33 years of age were instructed to stand relaxed, with arms at their sides, fixating the centre of a visual display. The visual display consisted of a large disk of diameter 0.9 m positioned 40 cm from the subject's nasion at eye level, such that it covered a large area of the subject's visual field (97°). This disk was covered in randomly distributed fluorescent circles of 2 cm diameter with an average density of 320 m^{-2} and could be rotated around the visual axis at an angular velocity of 40 /s either clockwise or anti-clockwise. Acceleration and deceleration of the disk took less than 2 s. The visual environment was otherwise dark.

The subjects stood on a posturography platform (internal malleoli 3 cm apart), which measured the position of the centre of foot pressure (COP) in the anterior–posterior and lateral directions. A 3-D magnetic search coil system (Polhemus 3space fastrack) measured head position in anterior–posterior, right–left directions and yaw. Horizontal DC electro-oculography was used to check that subjects fixated the centre of the disk and to reveal the relative extent of the head-on-trunk and eye-in-orbit rotations. The posturography platform was mounted on an externally controlled rotating platform moving smoothly about a vertical axis at 2°/s. This is near the reported values for perception of rotation (Hulk and Jongkees 1948; for review see Jongkees 1974); pilot studies indicated that most subjects could not perceive being rotated when their eyes were closed. Thus the visual stimulus could appear between –90° (left) and +90° (right) relative to the subjects' trunk mid-sagittal plane.

During a trial, each subject started facing the disk at one of five platform positions: –90, –45, 0, +45, +90. The stimulus sequence was as follows (see Fig. 1, bottom panel): 1) stationary platform, stationary disk (15 s), 2) stationary platform, rotating disk (30 s), 3) rotating platform, rotating disk (22.5–90 s, depending on amplitude of platform rotation), 4) stationary platform, rotating disk (30 s) and 5)stationary platform and disk (15 s). These periods were contiguous. There were 40 different possible trials: two disk rotation directions vs five positions for the start-point and four positions for the end-point of platform rotation. Each subject experienced ten different trials in a Latin-square paradigm, the first trial starting and the last trial ending with the disk straight ahead. Subjects remained in the dark between trials to prevent use of visual cues to determine their orientation.

All signals were sampled at 125 Hz and analysed offline. COP was arithmetically normalised to represent the signal given by a 70 kg mass. Five seconds of the onset response (average position between 25 and 30 s of disk rotation) were measured, relative to the average position during the 15 s before disk rotation. For the offset response, 1 s was measured (between 1 and 2 s after cessation of disk rotation), relative to the average position during the last 15 s of disk rotation. Based on these position measurements, the average orientation of the VEPR was then calculated for all subjects at each onset or offset condition, e.g. clockwise disk rotation at +45˚ platform position. In order to control for the effects of platform rotation in isolation, four subjects were rotated six times each between –45˚ and +45˚ and vice versa at 2°/s while fixating the stationary visual display. This control experiment showed that subjects' COP shifted by a mean of 1.05 cm, SD 0.88 cm, in the direction of body rotation; due to the randomisation process for disk and platform rotational direction this bias would be cancelled out.

Results

Signals of head yaw and horizontal eye positions showed that the steady-state reorientation of gaze for all subjects was mainly due to rotation of the head on the trunk (95%, SD 5%), with the remaining 5% performed by the eyes. During subject rotation, the proportion of movement carried out by the eyes sometimes exceeded this until further rotation of the head occurred. Subjectively, subjects were unsure of the relative position between themselves and the visual stimulus; some reported disorientation.

Figure 1shows raw sway platform traces from one subject (JB) during the condition where the disk started

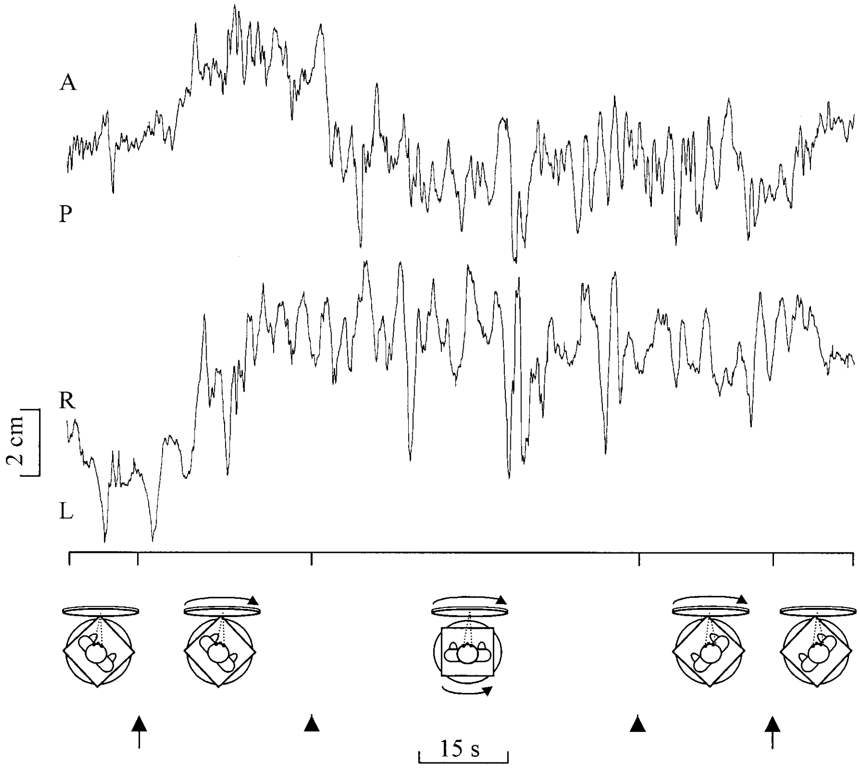

Fig. 1 Raw platform traces from subject JB for the condition with clockwise disk rotation: starting condition at –45° (left), ending at +45° (right) relative to the subject. The two traces show the anterior (*A*)–posterior (*P*) and right (*R*)–left (*L*) movements of the centre of foot pressure. The period of disk rotation is shown between the *arrows* and platform rotation between the *arrowheads*. The sequence of events is also represented by the *icons* below

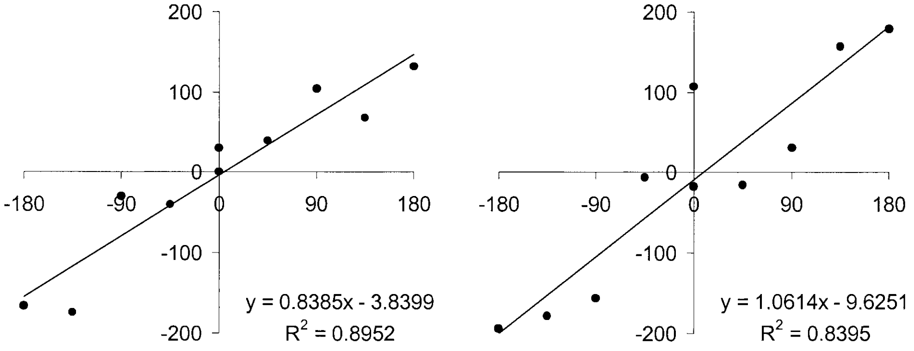

Fig. 2 Direction of sway (*abscissa*), as measured by the position of the centre of foot pressure, plotted against direction of disk upper half motion, i.e. predicted sway direction (*ordinate*). Conditions were onset (left) and offset (right) of disk rotation. All values in degrees, with zero corresponding to the direction of the subject's toes

at a position of –45° before moving (relative to the subject) to +45°. The traces show the onset of the VEPR, with forwards and rightwards sway, at circa 25 s. As the platform rotates rightwards (between arrowheads, Fig. 1) there is a reorientation of the COP from a right anterior to a right posterior position. On cessation of disk rotation (last arrow) the COP moves anteriorly and partly leftwards towards the original baseline position.

Visually evoked postural reponses were normalized with respect to a 15 s period preceding the onset or offset of disk rotation. The orientation of the VEPR after 30 s (onset) or 1 s (offset) was converted into degrees relative to the subjects' trunk mid-sagittal plane for direct comparison with the orientation of the visual display. The reorientation of the VEPR at both the onset and offset of disk rotation, measured for COP signals for all conditions, is summarised graphically in Fig. 2; a strong reorientation of VEPR by relative disk position can be seen. The best-fit curve reveals that the gain of the reorientation response at onset is ~0.82 ($y=0.84x-3.8$, $r^2=0.90$, as measured at the COP, and $y=0.80x+4.61$, $r^2=0.95$ measured at the level of the head, where x and y are visual motion and sway directions respectively). The offset response (at 1 s after the end of disk rotation) had a gain around unity ($y=1.06x-9.63$, $r^2=0.84$ as measured by the COP, or $y=1.05x-7.3$, $r^2=0.96$ as measured at the level of the head).

Discussion

Many previous studies have shown that visual motion is capable of generating postural reactions (e.g. Dichgans et al. 1975; Clément et al. 1985; Bronstein 1986); however, relatively few have investigated the influence of different positions of these stimuli relative to the subject (Stoffregen 1985; Gielen and Asten 1990; Wolsley et al 1996). Wolsley et al. (1996) reported an accurate reorientation of a VEPR during deviation of both the eyes in head and head on trunk. It was reasoned that, since the retinal motion stimulation was the same in the different positions, the postural reorientation must be due to eye-in-orbit and head-on-trunk position signals, possibly proprioceptive in origin. However, their experiment was conducted in a well-lit environment with subjects having prior cognitive knowledge of the position of the visual stimulus and of the relative rotations of the eyes and head. The present experiment was therefore conducted to test whether the reorientation of the VEPR is affected by reduced cognitive and background visual information and by passive positioning of the subjects on a rotating platform.

In the present experiment the directions of VEPRs induced by both the onset and offset of disk rotation were measured. The gain of the reorientation of VEPR was ~0.8 at the onset but ~1.0 during the offset. This slight difference may be explained by the fact that the posturally-relevant sensory cues for vertical realignment of the body during disk rotation are conflicting, but those for realignment after disk rotation has ended are not. A comparison with the data of Wolsley et al. (1996), who found a gain of reorientation of 1.08±0.2 (calculated from published diagrams), suggests that little or no role is played by cognition, background visual structure or active positioning in the reorientation of VEPRs.

The origin of the signals used to determine the direction of gaze for visual control of posture is not yet clear. For the neck, proprioception would seem useful due to the possibility of external forces acting on the head. Neck afferents have been shown to be the main source of information used to estimate head–trunk horizontal angular deviation (Nakamura and Bronstein 1995). In the current experiments, where 95% of gaze deviation was achieved by head-on-trunk deviation, neck proprioceptive information is therefore the most likely source. Neck proprioceptive afferents are also thought to be responsible for the reorientation of vestibularly (galvanic) elicited sway during head turns (Lund and Broberg 1983; Britton et al 1993). External forces do not normally act on the eyes and, therefore, efference copy or a mixture of efference copy and ocular proprioception has been favoured as source of an eye-in-orbit position signal. In pointing and estimation tasks (Bridgeman and Stark 1991) physiological gains of oculomotor efference copy and proprioception were found to be 0.61 and 0.26 respectively. The finding that extra-ocular muscle vibration elicits directional postural responses (Roll et al. 1989) suggests that at least some ocular proprioceptive component influences postural control. The current experiments suggest that visual and proprioceptive signals combine in order to provide effective, gaze angle-independent, visual control of posture. This process appears to be largely independent of cognitive comprehension of the geometry involved.

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