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RESEARCH ARTICLE

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Perceiving a stable world during active rotational and translational head movements

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Abstract When a person moves through the world, the associated visual displacement of the environment in the opposite direction is not usually seen as external movement but rather as a changing view of a stable world. We measured the amount of visual motion that can be tolerated as compatible with the perception of moving within a stable world during active, sinusoidal, translational and rotational head movement. Head movements were monitored by means of a low-latency, mechanical head tracker and the information was used to update a helmet-mounted visual display. A variable gain was introduced between the head tracker and the display. Ten subjects adjusted this gain until the visual display appeared stable during sinusoidal yaw, pitch and roll head rotations and naso-occipital, inter-aural and dorso-ventral translations at 0.5 Hz. Each head movement was tested with movement either orthogonal to or parallel with gravity. A wide spread of gains was accepted as stable (0.8 to 1.4 for rotation and 1.1 to 1.8 for translation). The gain most likely to be perceived as stable was greater than that required by the geometry (1.2 for rotation; 1.4 for translation). For rotational motion, the mean gains were the same for all axes. For translation there was no effect of whether the movement was inter-aural (mean gain 1.6) or dorso-ventral (mean gain 1.5) and no effect of the relative orientation of the translation direction relative to gravity. However translation in the naso-occipital direction was associated with more closely veridical settings (mean gain 1.1) and narrower standard deviations than in other directions. These findings are discussed in terms of visual and non-visual contributions to the perception of an earth-stable environment during active head movement.

Keywords Oscillopsia · Head movement · Gravity · Perception · Stable world · Rotation · Translation

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Introduction

How it is that the visual motion associated with self motion does not produce a sensation of the world moving has long been the source of debate (Wallach 1985, 1987; Grüsser 1986; Wertheim 1994; van der Steen 1998). How much does the visual world actually have to move before it is perceived as world movement during a head movement? Differences in the tolerance to the visual correlates of head rotation and translation under different conditions might reveal some of the sensory processes involved. For example, comparing movements with and without changes in orientation with respect to gravity could reveal a role of gravity.

When the head moves both the visual and vestibular systems are stimulated. The displacement of all points of the visual field generates an optic flow which can be used to inform about the movement (Redlick et al. 2001; Vaina et al. 2004; Lappe et al. 1999). The canals and otoliths of the vestibular system transduce information about rotation and translation respectively (Benson 1982; Wilson and Jones 1979). The task of assessing world stability during head movements requires a comparison of the information arising primarily from these sources. Eye movements, generated by either visual or vestibular cues, closely match the geometric requirements for maintaining fixation during active head movements (Tomlinson et al. 1980) but what the eyes do is not a reliable guide to the perception (Stone et al. 2003).

Surprisingly there have been no comprehensive measurements of perceptual stability during translation and rotational head movements in all directions. Furthermore, previous attempts to measure such tolerances have often confused relative and absolute motion (e.g. Wallach 1985, 1987). When objects at different distances from the observer are in view, parallax, or relative retinal motion results (Harris 1994). The perception of relative visual movement between objects in the environment has a much lower threshold (0.03° s^{-1}; Johnston and Wright 1985) than the detection of absolute motion (motion relative only to the observer), in which the entire retinal image moves as a whole (0.1–0.4° s^{-1}; Harris and Lott 1995; Choudhury and Crossley 1981; Johnson and Scobey 1982; Snowden 1992). Measurements of the perception of world motion under conditions in which parallax was present have suggested that a mismatch of as little as 3% between expected and actual motion could be detected (Wallach 1985, 1987). The visual signal of self motion, however, is integrated over a large area of the visual world (Allison et al. 1999) and so, although relative motion can be used to infer self motion (Howard and Howard 1994), it is not the source of visual information that induces the sensation of self motion (Henn et al. 1974).

Our hypotheses were that the responses to rotation and translation should show similar trends but that there would be variations amongst axes and directions. We expected the more "natural" motions such as yaw rotation and naso-occipital translation would be associated with more veridical perceptions of world stability. Similarly we expected motions associated with less sensory information, especially rotations orthogonal to gravity, to be associated with less precision. To make fair comparisons between movements in different directions and with different rotational and translational components, and to force subjects to use full-field motion cues only, we used a visual display that presented visual motion with minimal parallax. Using a head-mounted display, subjects viewed a virtual reality simulation of being inside a sphere. This completely removed motion parallax associated with rotation and very much reduced that associated with translation.

We measured the motion of the visual world that was regarded as perceptually stable during head rotations and translations actively performed by our subjects. Rotations were around the yaw, pitch, and roll axes and translations were in the naso-occipital, inter-aural, and dorso-ventral directions. All motions were carried out both orthogonal to and parallel with the direction of gravity. Our previous study (Jaekl and Jenkin 2003) showed no overall effect of gravity, here we examine this possibility for each axis and direction of motion. Some of these results have already been published in preliminary form (Jaekl et al. 2002a, b, c, d, 2003; Harris et al. 2002a, b).

Methods

Overview

Subjects viewed an immersive virtual reality simulation in a head-mounted display driven by active head movements that were monitored by a low-latency head tracker. The normal linkage between movement of the visual world and of the head was severed by varying the gain of the head movement signal that was used to generate the visual motion viewed in the helmet. Subjects adjusted the magnitude of this gain until the visual scene appeared earth-stable during their head movement.

Subjects

Ten subjects participated in these experiments (six males aged 22 to 48, four females aged 21 to 32). Subjects had normal or corrected-to-normal visual acuity and reported no history of vestibular or balance problems. Subjects read and understood an informed consent form. The York University Ethics Approval Committee approved the experiments. Subjects were paid above the standard York University subject rates.

Visual simulation and head tracking

An immersive visual world was presented using a Virtual Research V8 stereoscopic head-mounted display (HMD) with a focal length of approximately 75 cm. Two displays, one for each eye, presented the same, full-color, 640 by 480 pixel images at 60 Hz with a diagonal field of view of 60°. The rest of the subject's field visual was obscured by the HMD. Sounds were presented used to cue the subject through stereo headphones.

A Puppetworks six-degree-of-freedom, mechanical head tracker monitored the position and orientation of the head. One end of the mechanical tracker was earth-fixed and the other end was fixed rigidly to a custom mount on the HMD. The tracker was counterbalanced to reduce the load on the user (Fig. 1). The counterweight was adjusted for each subject in each condition so they could move comfortably within the apparatus. Subjects felt comfortable and could move freely while wearing the HMD which felt similar to a light motorcycle helmet. The orientations of the seven joints between the rigid links that make up the head tracker were monitored and transmitted via a serial link to an SGI O2 computer that rendered the display. The head tracker was stowed in a calibration rig which defined a six degree-of-freedom fixed reference position in space. Head position and orientation were then calculated from the known kinematics of the tracker and this information was used to drive the visual simulation. The total lag of the system between making a movement and the corresponding updating of the display (end-to-end lag) was 122 ± 4 ms (Allison et al. 2001).

The virtual environment was created using custom code and Open-GL graphics. The visual display was a textured sphere similar to that used earlier in a study of display lag (Allison et al. 2001) and was updated at 30 Hz. The visual simulated sphere was 2 m in diameter

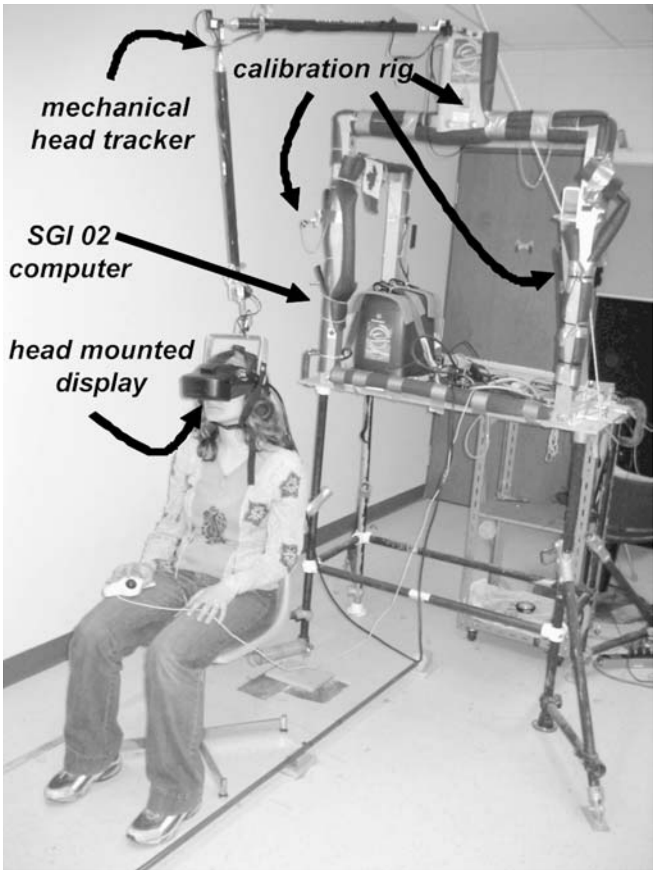

Fig. 1 Experimental setup. A Puppetworks mechanical head tracker was used to track head position while subjects viewed a virtual sphere in a Virtual V8 head mounted display. The simulation was run by an SGI 02 computer

and was centered on the subject's head at the start of each trial. The sphere was patterned with a grid lattice with twelve equally spaced lines of longitude and latitude that converged to points above and below the subject. Alternate squares of the lattice were colored red and white. Before each trial the sphere was positioned so that the same portion of the sphere—that section away from the poles where the texture patterns converged—was in front of the subject. The sphere was illuminated by a single, virtual light source located at its centre. The visual display was generated using a projection whose nodal point was located at the centre of the head for the rotation conditions and between the eyes for the translation conditions.

A controllable gain was introduced between the monitored head motion and the corresponding signal used to generate the visual display. For translation conditions, translational motions were multiplied by this gain. For rotation conditions a quaternion was constructed that represented the monitored head rotation, and the angular part of the quaternion was multiplied by this gain. Because the display was updated in response to movements of the head, the effect of variations in the amplitude of head movement was minimized.

Procedure: rotation

In the rotation experiment, subjects voluntarily rotated their heads around the roll, pitch, or yaw axes with the axis of rotation either orthogonal to or parallel with the direction of gravity, resulting in six conditions. Subjects moved their heads in time to the beats of a metronome played at 1 Hz through the headphones of the HMD. Subjects timed their reversals to correspond to each click and therefore made head movements at 0.5 Hz. During a training session subjects were directed to move their heads approximately 22.5° with corresponding peak velocities around 75° s^{-1}, and peak acceleration around 235° s^{-2}.

Rotations about different axes were run in separate, counterbalanced blocks during which the experimenter continuously monitored their performance by eye. If subjects deviated from the desired movement, the experimenter instructed them to correct their actions. Pitch and roll rotations around axes parallel with the direction of gravity were accomplished by having subjects move their heads while lying in prone (roll) or left-side-down (pitch) body postures while making the appropriate rotations. Yaw rotation with the axis parallel with gravity and pitch and roll rotations around axes orthogonal to the direction of gravity were made while subjects sat upright. For yaw rotation around an axis orthogonal to gravity, subjects were placed in a left-side-down posture. These configurations and motions are shown in cartoon form on the left of Fig. 2. After a training session subjects had no difficulty in making these movements around the intended axes.

As subjects performed these rotations, they pressed the left and right buttons of a standard three-button computer mouse to increase or decrease the gain between the amount of visual motion in the display and their head motion (the gain) in steps of 0.05. When subjects judged the display to be earth-stable, they indicated this by pressing the central mouse button. Each condition was repeated eight times by each of the ten subjects resulting in total sampling of 80 points for each condition. Each condition took about 15–20 min with subjects encouraged to take frequent breaks if they felt uncomfortable or tired. Initial gains were varied pseudo-randomly, with half the trials beginning at a gain of 0.5 and the other half starting at a gain of 2.0.

Procedure: translation

In the translation condition subjects followed instructions to make oscillatory movements in the naso-occipital, inter-aural or dorso-ventral directions. Subjects were arranged so that their movements were either parallel with or orthogonal to the direction of gravity. Head translations in the naso-occipital and inter-aural directions parallel with the direction of gravity were accomplished by having subjects standing, leaning over, and supporting themselves by holding on to a crossbar while

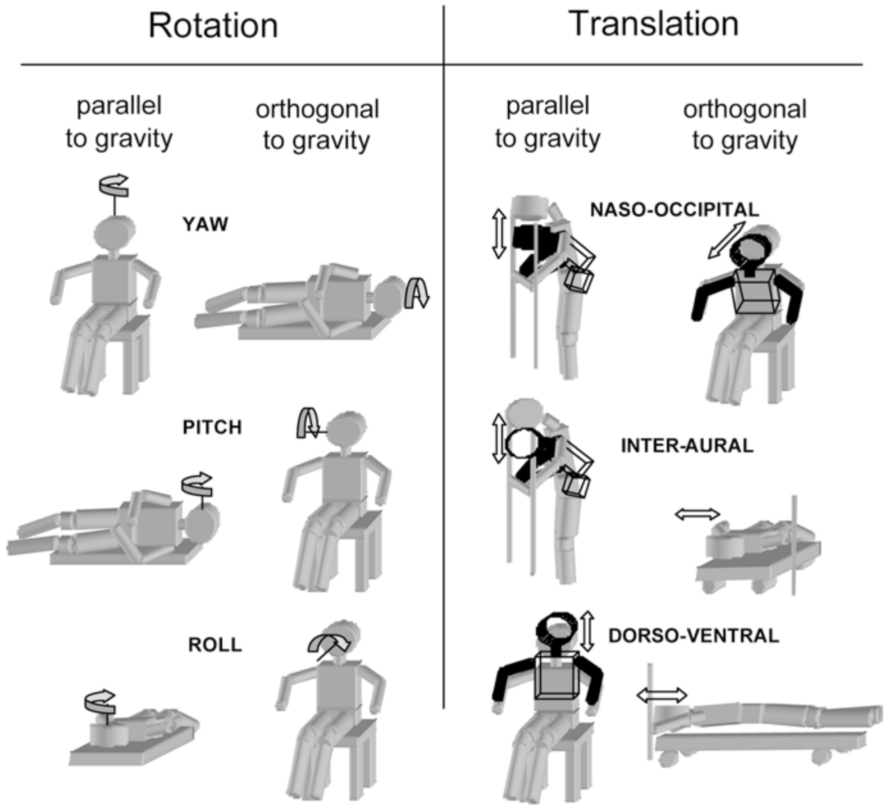

Fig. 2 How the rotation and translation movements were made. Rotation: subjects actively made approximately $\pm 25°$ sinusoidal roll, pitch, and yaw, head movements along axes (i) parallel with gravity or (ii) orthogonal to gravity. Movements were made while sitting upright or lying in a left-side-down position. Translation: Oscillatory movements of about ± 17 cm were made in the naso-occipital, inter-aural or dorso-ventral directions either (iii) parallel with gravity or (iv) orthogonal to gravity. Movements were made sitting upright, while on a cart or while standing and leaning on a crossbeam for support as shown (see text for details)

pushing up and down with their arms and legs with their heads pointing downwards (naso-occipital) or sideways (inter-aural; see Fig. 2). Parallel-with-gravity translations in the dorso-ventral direction were carried out while subjects sat in a chair and moved their head up and down. Orthogonal-to-gravity translations in the inter-aural and dorso-ventral directions were made while subjects held on to a pole and pushed and pulled themselves while lying in a prone body posture on a garage creeper. Subjects were either lying along the creeper (dorso-ventral) or across the creeper (inter-aural). Movements orthogonal to the direction of gravity in the naso-occipital direction were carried out while subjects sat in a chair and moved their heads back and forth.

During a training session the experimenter monitored the subject's head movements using a ruler, and corrected the subjects until they were able to make movements consistently of approximately ± 17 cm which corresponded to a peak velocity of around 53 cm s^{-1}, and a peak acceleration of around 168 cm s^{-2}. The set of configurations and motions is shown in cartoon form in Fig. 2. As with the rotation experiments, subjects moved their heads in time to the beats of a metronome played at 1 Hz through the headphones of the HMD. Subjects timed their reversals to correspond to each click and therefore made head movements at 0.5 Hz.

During their translations, subjects adjusted the gain between the visual and head translation in steps of 0.04 using the mouse. When they felt the display appeared earth-stable they indicated this by pressing the central button. Each condition was repeated eight times by each of the ten subjects resulting in a total sampling of 80 points for each condition. The starting gain varied pseudo-randomly in the range 0.5 and 2.0. Each condition took about 15–20 min with subjects encouraged to take frequent breaks if they felt uncomfortable or tired.

Data analysis

Data were expressed as a visual gain defined as the ratio of the visual motion to the head movement that created it. The distribution of visual gain values reported as stable had a normal distribution when plotted on a log scale and was fitted with a Gaussian.

$$\text{Frequency} = a \times \exp\left(-0.5 \times (\log(x/x_0)/b)^2\right)$$

where x_0 is the visual gain value at the peak of the Gaussian, b is an estimate of the width, and a is the height of the peak of the Gaussian

To test for any differences across axes of rotation, directions of translation or any effects of gravity, a within-subjects ANOVA was used in conjunction with multiple pair-wise comparisons to determine individual effects.

Results

Rotation

Figure 3a shows how often each value of log visual gain (log ratio of visual rotation to head rotation) was judged

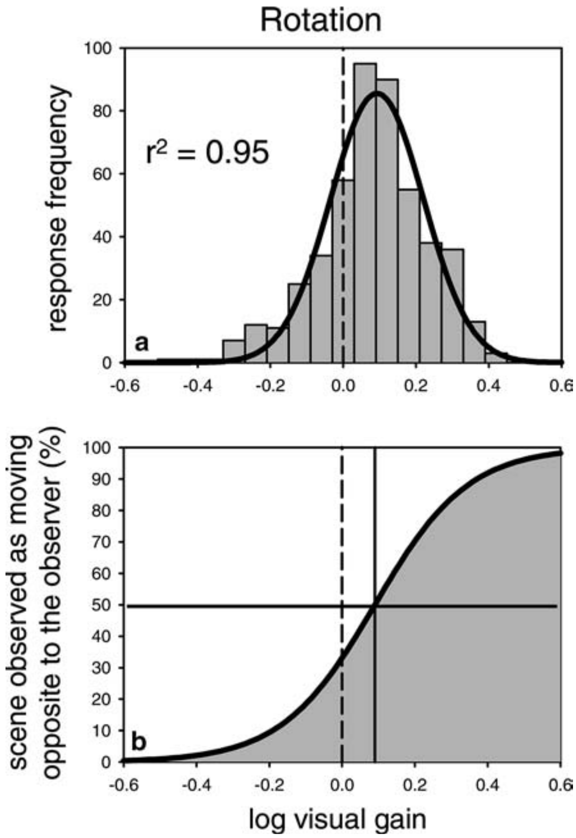

Fig. 3 (**a**) Frequencies at which gains of visual rotation to head rotation (visual gain) were judged stable during head rotation. The *dashed line* corresponds to the point of "natural stimulation" at which the image was rotated by an equal and opposite amount to the head rotation. The *solid line* is a best-fit Gaussian. Note the logged horizontal axis. (**b**) The best-fit Gaussian through the data shown in (**a**) was transformed into a sigmoid indicating the frequency at which head movements would be judged as moving "too much" for a given head rotation. The *solid horizontal line* indicates the 50% (chance) level and the *solid vertical* where the sigmoid crosses this line indicates the corresponding point of equality (0.08 ± 0.03 on the log scale i.e. a gain of 1.2)

as stable for all six conditions (three axes, each in two body positions) pooled together. On the logarithmic scale of Fig. 3, zero on the abscissa corresponds with image rotation that is equal to and opposite to head rotation. A best-fit Gaussian was fitted through the logarithmically transformed data (peak = 0.10; std deviation = 0.13; $r^2 = 0.95$). The peak, which is an approximation of the mean of the subject's means pooled across conditions, was significantly above zero (which, on a log scale, corresponds to a gain of 1, i.e. the geometrically expected value) ($t = 4.169$, $P < .01$, $df = 9$). Subjects were most likely to report the display as stable when it was in fact rotating in the direction opposite to the head relative to a stable world (log gain > 0). The peak of the Gaussian fit indicates that the visual gain most likely to be chosen as stable during head rotation was when the visual movement was 1.26 times the amount geometrically required. Adding and subtracting one standard deviation from this peak shows that visual gains between 0.84 and 1.41 account for 68% of the "stable" measurements (Table 1). Figure 3b shows the integral of the best-fit Gaussian of Fig. 3a to form a more conventional sigmoidal psychophysical function. The ordinate represents the estimated probability that the display would be judged as having *too much* visual motion than expected for the head rotation.

Comparison between axes and orientations

Figure 4 shows the number of times that each gain was chosen as stable, broken down into the six conditions tested. The gains and standard deviations of the best-fit Gaussians to these distributions are given in Table 1. The distributions in Fig. 4a depicts the responses to pitch, roll, and yaw movements with the axes parallel with gravity. Fig. 4b depicts the judgments of perceptual stability when each type of movement was made with the axis of rotation orthogonal to gravity. A within-subjects ANOVA using a Greenhouse–Geisser adjusted F (to control for unequal variances) showed that there was no significant difference between parallel and orthogonal orientations ($F = 3.25$, $P > .05$, $df = 1, 9$) and no differences between the three axes ($F = 1.62$, $P > .05$, $df = 1.5, 13.5$). Multiple pairwise comparisons, using Bonferroni, revealed no significant differences between orientations relative to gravity for any axis ($P > .05$, $df = 9$).

The mean gains regarded as stable for roll, pitch, and yaw are compared in Fig. 5a along with their standard errors for movements orthogonal to and parallel with gravity

All means, except for yaw movements around an axis parallel with the direction of gravity (i.e. in the normal upright body position) were significantly greater than 1 ($P < .05$ one-sample t-tests, using Bonferroni adjustment).

Figure 5b depicts the range of visual movement tolerated as appearing earth-stable for each condition, quantified as the mean standard deviations across subjects. A within-subjects ANOVA, using a Greenhouse–Geisser adjusted F, indicates there were no significant differences between movements orthogonal to and parallel with gravity ($P > .05$, $df = 1,9$) and no differences between axes ($P > .05$, $df = 1,11.6$).

Translation

Figure 6 shows the number of times that each gain of visual translation to head translation was judged as stable, pooled across all directions of movement and orientations relative to gravity. The visual gains chosen were normally distributed on a logarithmic plot (peak = 0.18; std deviation = 0.15; $r^2 = 0.97$). The gain at the peak of the Gaussian shows that the visual movement most likely to be judged as stable was 1.5 times the amount geometrically required by the head movement. The peak as approximated by the subject's

Table 1 The antilogged mean of each Gaussian fit to the histograms of visual gains regarded as stable during roll, pitch and yaw rotations both parallel with and orthogonal to gravity (Figs. 3 and 4). The standard deviation of the Gaussian was added to and subtracted from each mean and then antilogged to indicate the amount of visual motion bracketing 68% of all the settings regarded as stable

Visual gains most likely to be judged stable during rotation					
Rotation axis	log mean	log standard deviation	Mean	antilog of (log mean−log standard deviation)	antilog of (log mean + log standard deviation)
Parallel					
Roll	0.07	0.092	1.16	0.94	1.43
Pitch	0.11	0.091	1.30	0.11	1.16
Yaw	0.03	0.090	1.09	0.88	1.33
Orthogonal					
Roll	0.06	0.079	1.15	0.96	1.39
Pitch	0.13	0.083	1.35	1.12	1.64
Yaw	0.10	0.080	1.27	1.05	1.53
Mean	0.08	0.08	1.22	0.84	1.41

means pooled across conditions was significantly greater than unity ($t = 9.43$, $P < .001$, $df = 9$) which means that subjects were most likely to report the visual scene as earth-stable when it was in fact moving in the opposite direction to the head relative to a stable world. Adding and subtracting one standard deviation to and from the peak indicates that the range of gains between 1.07 and 2.14 account for 68% of the ''stable'' measurements. Figure 6b shows the integral of the best-fit Gaussian, which represents a hypothetical psychometric function. The ordinate represents the estimated probability that the display would be judged as having ''too much'' visual motion than was expected for the head translation.

Comparison between directions and orientations

Translations were made in three different directions: naso-occipital, inter-aural, and dorso-ventral (see Methods and Fig. 2). Figure 7a plots the distribution of visual gains judged as earth-stable when the translation was parallel with gravity; Fig. 7b shows the distributions when they were orthogonal to gravity. The mean and standard deviation of each Gaussian fit to these distributions is shown in Table 2.

A within-subjects ANOVA, using a Greenhouse–Geisser adjusted F, determined that there were significant differences between the distributions of visual gains regarded as stable for different paths of translation ($F = 26.5$, $P < .001$, $df = 1.21,10.9$). There was, however, no effect of the orientation of the movement relative to gravity ($P > .05$, $df = 1,9$). The mean gains regarded as stable for each condition are compared in Fig. 8a for movements both orthogonal to and parallel with gravity. The means for inter-aural and dorso-ventral translations, both orthogonal to and parallel with gravity, were significantly greater than required geometrically ($P < .05$, $df = 9$, one-sample t-tests using Bonferroni adjustment). The means for naso-occipital translation were not significantly different from veridical.

Figure 8b depicts the ranges of visual motion tolerated as appearing earth-stable for each condition, quantified as the mean standard deviations across subjects. A within-subjects ANOVA, using a Greenhouse–Geisser adjusted F, indicated no effect of direction ($P > .05$, $df = 1.6,14.3$) or orientation relative to gravity ($P > .05$, $df = 1,9$).

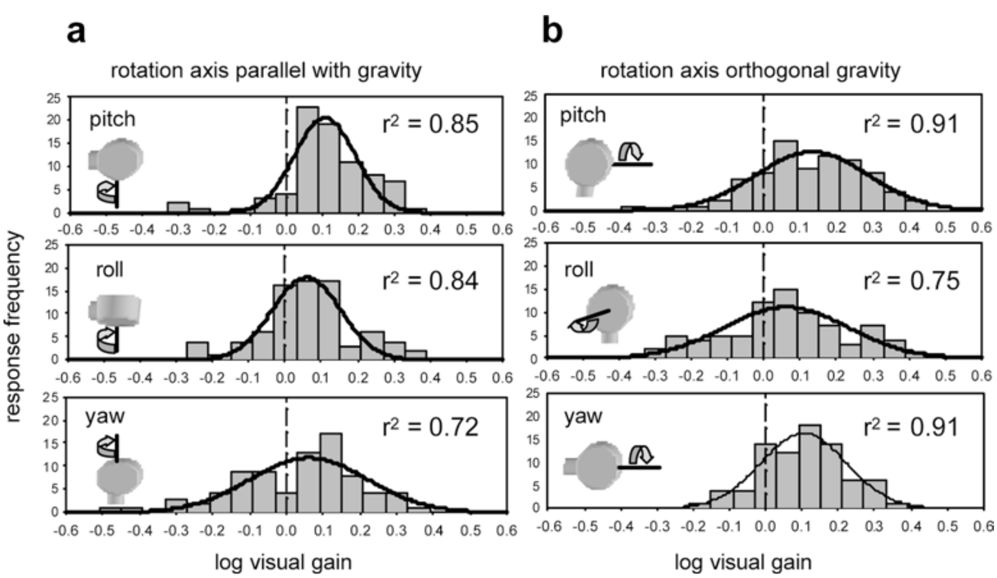

Fig. 4 The frequency at which gains of visual motion to head rotation were judged as earth-stable during head rotation around axes (**a**) parallel with gravity and (**b**) orthogonal to gravity. Judgments during pitch, roll, and yaw are shown separately as indicated by the cartoon inserts. The regression coefficients for each Gaussian fit are shown by each curve. Conventions as for Fig. 3a

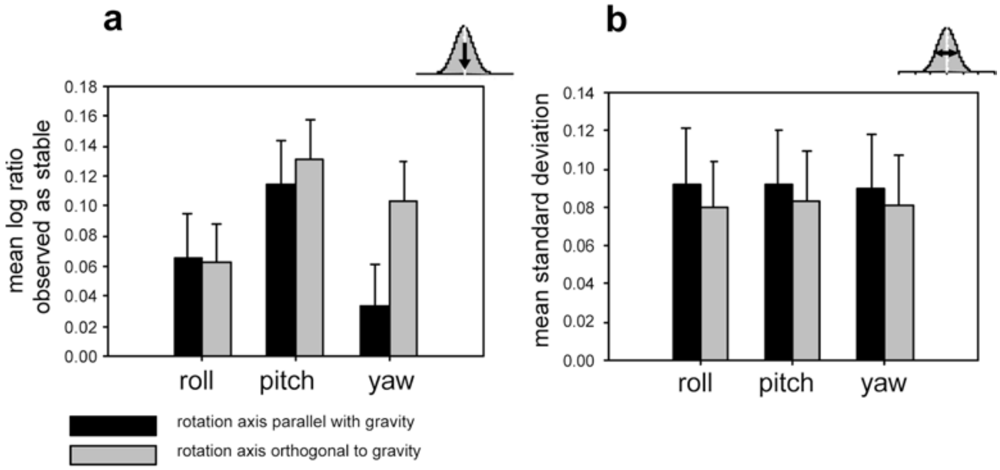

Fig. 5 (**a**) Mean log gains of visual motion to head rotation that were judged stable for roll, pitch, and yaw rotations parallel with (*black bars*) and orthogonal to (*grey bars*) the direction of gravity. *Error bars* indicate standard errors between subjects. There were no significant main effects between orientations or axes ($P > .05$). All conditions except for yaw rotation parallel with gravity required significantly more visual rotation than geometrically necessary (visual gain > 1) for the image to appear stable ($t = 4.3$, $P < .01$, $df = 1.5,13.5$). (**b**) Mean standard deviations represent the tolerance of visual motion during roll, pitch, and yaw rotation both parallel with (*black bars*) and orthogonal to (*grey bars*) gravity. *Error bars* indicate standard errors between subjects. There were no significant main effects between orientations or axes ($P > .05$)

Discussion

These experiments have shown several unexpected features of the judgment of perceptual stability during active, sinusoidal, 0.5 Hz head movements. The amount of visual movement most likely to be judged as stable during either rotational or translational head movements was more than geometrically required: a condition sometimes referred to as "overconstancy" (Bridgeman 1999). The most stable perception of moving in a stable world was found when the world was in fact moving backwards relative to the geometrically earth-stable position. Furthermore, there was a substantial variation in the amount of visual motion that was accepted as consistent with a stable environment: the system did not seem to be at all precisely tuned to a particular match between visual and non-visual cues to movement. Because the peak of the distribution of settings regarded as stable was above unity, and because the distribution was normal on a log scale, the range of gains accepted as stable was from close to unity to about double the geometrically required amount. Translation in the naso-occipital direction (normal forwards translation) required significantly less visual motion before instability was detected than motion in other directions, such that the amount of motion judged as earth-stable during these movements was not significantly different from the amount geometrically required. Although, in general, there was no effect of the orientation of the movement relative to gravity, the mean for yaw rotation was more veridical when rotation was around a vertical axis.

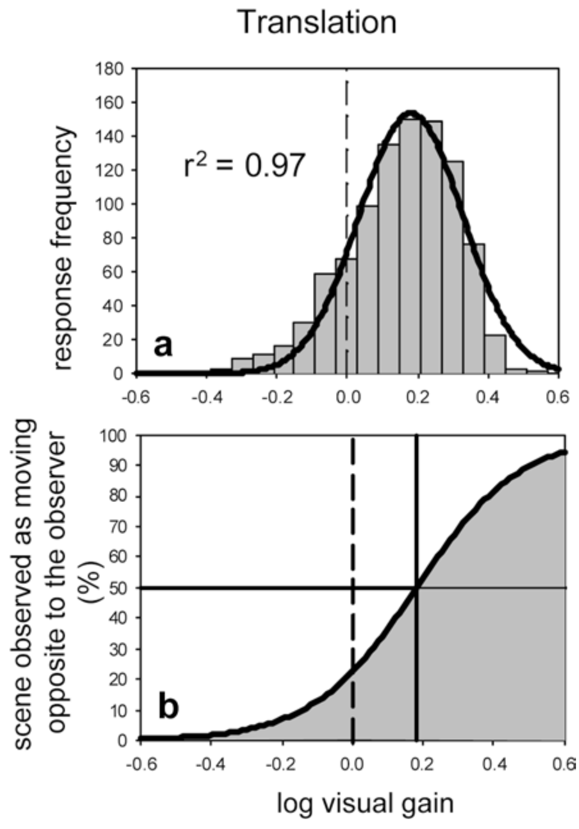

Fig. 6 (**a**) Frequencies at which the log gains of visual movement to head movement were judged as earth-stable during head translation. The *dashed line* at zero on the abscissa corresponds to the "natural stimulation" in which the image was translated by an equal amount and in the opposite direction to the head translation. The *solid line* is the best-fit Gaussian. Note the logged horizontal axis. (**b**) The best-fit Gaussian through the data shown in (**a**) was transformed into a sigmoid indicating the frequency at which head movements would be judged as moving "too much" for a given head translation. *Solid lines* indicate the 50% (chance) level and the corresponding point of equality (0.15 ± 0.03 corresponding to a visual gain of 1.4)

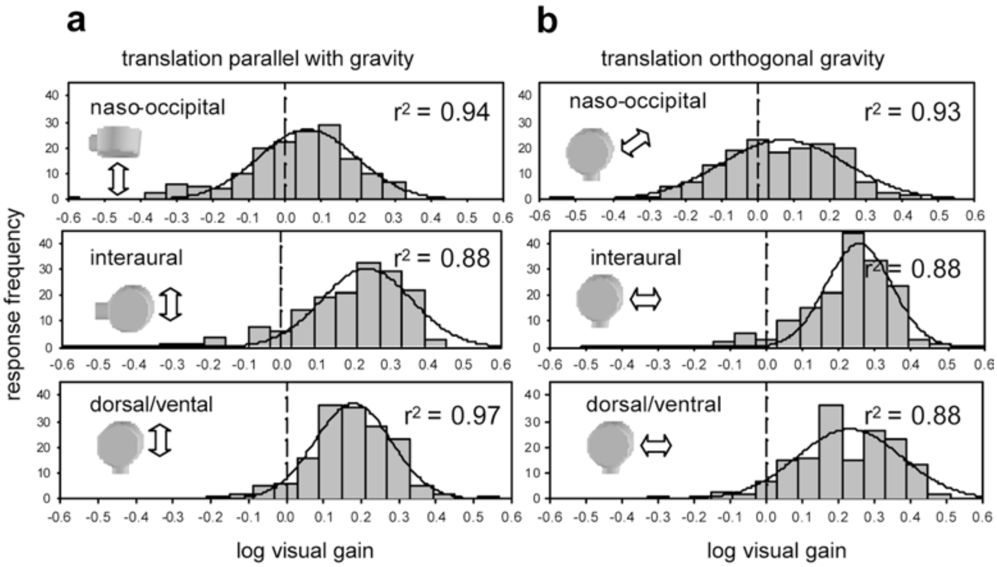

Fig. 7 (**a**) The frequency at which log gains of image translation to head translation were judged as earth-stable during head translations (**a**) parallel with and (**b**) orthogonal to gravity. Judgments during pitch, roll, and yaw are shown separately as indicated by the cartoon inserts. The regression coefficients for each Gaussian fit are shown by each curve. Conventions as for Fig. 3a

Table 2 The antilogged mean of each Gaussian fit to the histograms of visual gains regarded as stable during naso-occipital, inter-aural and dorso-ventral translations both parallel with and orthogonal to gravity (Figs. 7 and 8). The standard deviation of the Gaussian was added to and subtracted from each mean and then antilogged to indicate the amount of visual motion bracketing 68% of all the settings regarded as stable

Visual gains most likely to be judged stable during rotation					
Translation direction	log mean	log standard deviation	Mean	antilog of (log mean−log standard deviation)	antilog of (log mean + log standard deviation)
Parallel					
Naso-occipital	0.02	1.117	1.06	0.81	1.39
Interaural	0.20	0.108	1.57	1.22	2.02
Dorsal/ventral	0.17	0.096	1.49	1.20	1.86
Orthogonal					
Naso-occipital	0.06	0.097	1.16	0.93	1.45
Interaural	0.23	0.095	1.68	1.35	2.09
Dorsal/ventral	0.22	0.091	1.65	1.33	2.03
Mean	0.15	0.10	1.44	1.14	1.81

Visual motion most likely to be perceived as stable during a head movement

Judging whether the visual world is stable during a head movement required a comparison of the visually estimated head movement with a non-visual estimate. If these did not match *oscillopsia* resulted, in which the world would appear to move. Deducing self motion from visual cues requires additional information about eye movements and about the 3D geometry of the environment. Errors in any of these factors can affect the judgment of perceptual stability (Mesland and Wertheim 1995). A model of the cross-modal comparison required is illustrated in Fig. 9. This figure makes it clear that the task requires a comparison between the visual and non-visual estimates of self motion. Normally these two would both contribute to a single estimate of self motion probably being combined to form a weighted average (Zupan et al. 2002; Harris et al. 2000). Here we are looking instead at the *difference* between these estimates. The fact that the most stable world was perceived with gains above unity for both rotations and translations indicates that the "visual" estimate was less than the "non-visual" estimate (Fig. 9). However our judgment required only a *relative* comparison and cannot tell which estimate, if either, was veridical: the visual estimate might be too small or the non-visual estimate might be too great, or both.

Visual estimates

During these experiments it is likely that the retinal image was fairly stable, especially at the fovea, because of compensatory eye movements which we expect would have a high gain under these conditions (Tomlinson et al. 1980), although we did not have the technology to measure eye movement within the head-mounted display. To recover the visual motion from the essentially stable retinal image requires knowing how much the eyes have moved. Aubert (1886) established that although visual motion can be reconstructed from eye movement information, perceived speeds are estimated at only about 70% of their actual value. That is, if subjects underestimated visual motion by this amount, they would require $1/0.7 = 1.4$ times as much visual motion to make the match.

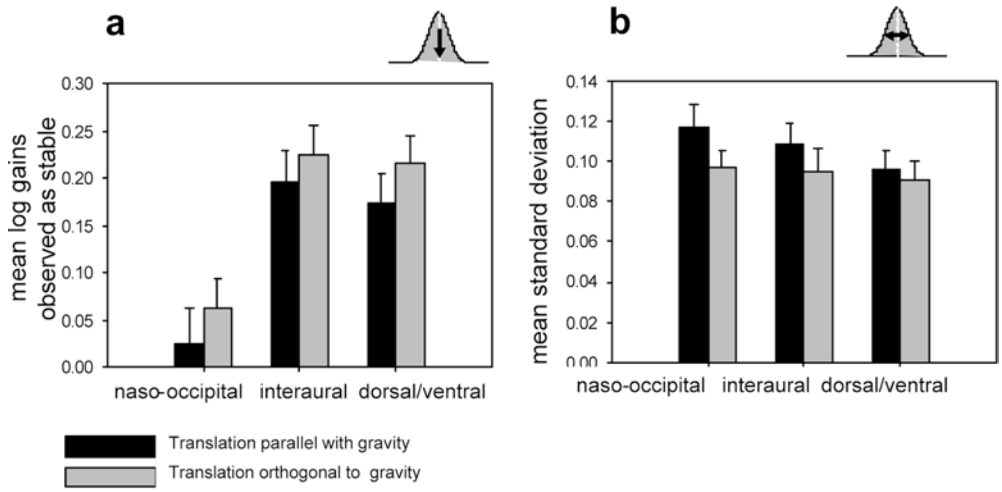

Fig. 8 (**a**) Mean log gains of image translation to head translation that were judged stable for translations parallel with (*black bars*) and orthogonal to (*grey bars*) gravity. *Error bars* indicate standard errors between subjects. (**b**) Mean standard deviations represent the tolerance of visual motion during translations parallel with and orthogonal to the direction of gravity. *Error bars* indicate standard errors between subjects

The Aubert relationship has only been established for smooth pursuit (Wertheim and Van Gelder 1990). The translational vestibulo-ocular reflex shares many of the features of smooth pursuit (Walker et al. 2004) and so this may be a significant factor in the high peak gains for inter-aural and dorso-ventral translations. However, this argument does not apply to forward translational movements where eye movements would be minimally involved and retinal motion would closely approximate the visual motion (Fig. 9c). Indeed, the match of visual movement was much closer to veridical from movements in the forwards/backwards direction (1.18 compared with about 1.66 for other directions of translation).

An additional contributory factor to a visual underestimate of motion during translation could be due to subjects' underestimation of the distance to the "virtual sphere". If the sphere were perceived to be closer than it really was, then higher retinal velocities would be expected. Virtual reality displays are often reported as appearing flatter than the simulation intends (Foley and Held 1972; Morrison and Whiteside 1984) and distances can be systematically underestimated even in the real world (Viguier et al. 2001). The lower gain for naso-occipital translation might reflect more accurate depth estimates available during this direction of motion where optic flow is radial rather than lamellar (Busettini et al. 1997). When subjects were asked informally to report their perceptions they often reported that the sphere appeared "closer" than the simulation specified.

Although our field of view was quite large, it is possible that the lack of peripheral visual cues might have played a role and that a larger field of view might have made subjects feel they were moving more (Allison et al. 1999; Van Veen et al. 1998; Zikovitz et al. 2001).

During rotation, the incidental translation of the eyes may have played a role in producing a visual estimate of head velocity that was too small. During rotation, the simulation accurately rotated the simulated world around the centre of the head. However during a natural head movement the eyes are not only rotated but also

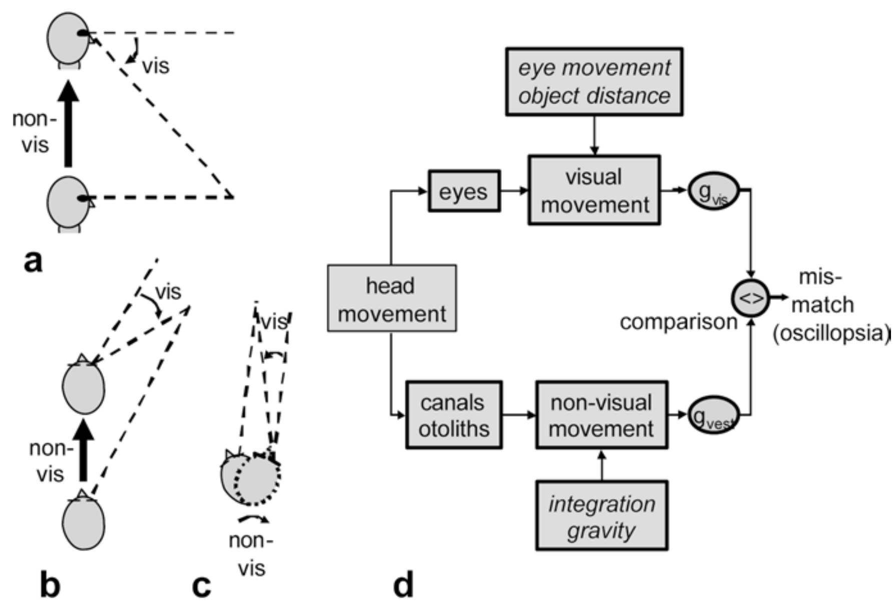

Fig. 9 Diagrammatic representation of the sources of visual and non-visual motion available to the subject for comparison during dorso-ventral translation (**a**), naso-occipital translation (**b**), or yaw rotation (**c**). (**d**) the comparison mechanism. Head movements generate visual and non-visual signals. These signals are multiplied by gains (g_{vis} and g_{vest}) before being compared

translated (Harris et al. 2001) and this translational component was not included in the simulation. If subjects had expected such a component, this may have led to a demand for increased retinal motion. However such incidental translation is greater for yaw and pitch movements than for roll and yet yaw movement (especially for earth-vertical yaw) was accompanied by less additional required movement suggesting this is unlikely to be a major factor.

Non-visual estimates

The high visual gains required for perceptual stability could also reflect non-visual cues to self motion generating an overestimate the magnitude of movement. This has been indicated for translation (Harris et al. 2000; Israël et al. 1993; Golding and Benson 1993; Marlinsky 1999a) and rotation (Marlinsky 1999b). It is unlikely that the increased effort of moving the head because of wearing the helmet contributed (Blouin et al. 1999).

The reason that the preferred gain is typically greater than one when matching visual motion with head movements is probably due to several factors, including underestimation of eye velocity, misperception of distance, allowing for translation of the eyes, and overestimation of non-visual cues to head movement. Naso-occipital translation and yaw rotation may be more veridical because they are more usually experienced and therefore better calibrated. A better calibration for commonly experienced motions has been suggested as the reason why a motion aftereffect is not usually experienced after prolonged forwards motion (Harris et al. 1981).

Tolerance for a range of visual motion during head movement

This study has shown that a large range of visual motion is accepted as compatible with moving in a stationary environment. For example a 10° s^{-1} yaw head rotation could be accompanied by visual motion between 9.3 and 17.1° s^{-1}, all of which would all be regarded as corresponding to earth-stable. Why might such a large range be tolerated?

Natural head movements in a normal, rich visual environment create a complex retinal motion with many different retinal velocities. In particular, a large range of retinal motions is created by translation where retinal velocities depend on the distance of objects from the observer. Even "pure" rotational head movements (were they to occur naturally) are associated with translation of the eyes, since the centre of rotation of the head is behind the eyes (Harris et al. 2001). This incidental translation is also associated with parallax. The motion of an object due to translation varies from zero (requiring a visual gain of unity in our experiment) when the object is infinitely far away, to some high retinal velocity (requiring a high visual gain) when it is close to the viewer As the peaks of our distributions were above unity, the entire range of motions judged as stable was almost completely above unity (Tables 1 and 2), thus including mostly velocities expected to occur during natural movements for objects at various distances.

Detecting a mismatch

A likely reason that a large range of motions is tolerated as corresponding to self motion in a stable world is that, as outlined above, in a visually rich environment, a wide range of visual velocities normally accompanies a given head movement. Only when the velocities are clearly outside the normal range does the perception of instability arise. The detection of a conflict between visual and non-visual cues to self motion indicates a very serious malaise and should not be triggered lightly.

When a conflict or mismatch is detected between visual and non-visual cues to head movement it indicates that the calibration mechanism of the brain is slipping. The consequences of detecting a conflict between visual and non-visual signals are not trivial (Lathan et al. 1995) and involve behavioral strategies, sickness and long-lasting recalibration of brainstem pathways (Tweed 2003). As in the detection of pain (Melzack and Wall 1965), "false positives" are to be avoided. The large tolerance for full-field visual motion during head movements reflects this ecological sense. Previous estimates of a much lower range of tolerance (e.g. 3%, Wallach 1985) are probably because of other aspects of the visual world being visible, such as parallax and body-fixed frame effects. Using the immersive technology of virtual reality enables such cues to be controlled explicitly.

The effect of gravity

For rotation about an axis that is not perfectly vertical, the otoliths signal the changing orientation relative to gravity, and can therefore supplement the rotation information provided by the semi-circular canals (Angelaki 1992). In these circumstances the brain therefore has more information available than it does concerning rotations around a strictly earth-vertical axis (Darlot et al. 1988; Denise et al. 1988). The vestibularly evoked compensatory eye movements are dramatically different when gravity is involved in this way (Harris and Barnes 1985), which will affect the retinal motion and might therefore be expected to affect stability judgments.

Linear accelerations are always confounded by gravity. Detecting linear accelerations requires dissociating imposed accelerations (the movement) from the total acceleration vector that includes a gravity component. When the gravity and motion components are aligned, the resultant motion vector differs from the gravity component only in magnitude whereas linear motions in other directions cause a swing in the direction of the resultant vector relative to the gravity-alone condition. These differences also might be expected to affect stability judgments.

However there was no effect of whether the rotation axis or direction of translation was parallel with or orthogonal to gravity, implying that although gravity plays a major role in eye movement control it may not be involved in perceptual processes such as those measured here.

Predictions for the real world

When comparing visual to non-visual cues to head motion, non-visual cues seem to indicate a faster speed than visual cues. Therefore visual cues arising from the relative motion between earth-stable objects and a moving observer may be incorrectly interpreted as indicating world motion in the same direction as the observer. This tendency might underlie illusory motions such as the oculogyral effect (Graybiel and Hupp 1946) and the common observation that distant objects such as the moon or far-away mountains often appear to move with the observer's motion. It may also play a central role in everyday visual perception during head movements.

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