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RESEARCH ARTICLE

# The effect of altered gravity states on the perception of orientation

**Richard T. Dyde · Michael R. Jenkin · Heather L. Jenkin · James E. Zacher · Laurence R. Harris**

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**Abstract** We measured the effect of the orientation of the visual background on the perceptual upright (PU) under different levels of gravity. Brief periods of micro- and hypergravity conditions were created using two series of parabolic flights. Control measures were taken in the laboratory under normal gravity with subjects upright, right side down and supine. Participants viewed a polarized, natural scene presented at various orientations on a laptop viewed through a hood which occluded all other visual cues. Superimposed on the screen was a character the identity of which depended on its orientation. The orientations at which the character was maximally ambiguous were measured and the perceptual upright was defined as half way between these orientations. The visual background affected the orientation of the PU less when in microgravity than when upright in normal gravity and more when supine than when upright in normal gravity. A weighted vector sum model was used to quantify the relative influence of the orientations of gravity, vision and the body in determining the perceptual upright.

R. T. Dyde (✉) · M. R. Jenkin · H. L. Jenkin · J. E. Zacher · L. R. Harris
Centre for Vision Research, York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada
e-mail: dyde@hpl.cvr.yorku.ca

H. L. Jenkin · L. R. Harris
Department of Psychology, York University, Toronto, ON M3J 1P3, Canada

M. R. Jenkin
Department of Computer Science and Engineering, York University, Toronto, ON M3J 1P3, Canada

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## Introduction

The perception of self- and object-orientation is fundamental to many aspects of visual, auditory and proprioceptive perception. One measure of perceived orientation is the perceptual upright (PU)—the orientation at which objects are most easily and speedily recognized (Jolicoeur 1985). The orientation of the perceptual upright is determined by a combination of information from different sources especially from vision and the otolithic division of the vestibular system which, often in collaboration with somatosensory pressure cues, indicates the direction of gravity. An internal representation of the axis of the body—sometimes referred to as the idiotropic vector (Mittelstaedt 1983a, 1986)—also makes an important contribution. In extraordinary environments where some of this information is missing or distorted, such as in space or when diving underwater, these cues can become ambigious or misleading, potentially resulting in incorrect perceptions of the direction of up. The diving and aerospace accident literature abounds with examples of divers and pilots who have become disoriented in this way and suffered fatal or near-fatal accidents (see Previc and Ercoline 2004 for a comprehensive review). Here we look at the effect of removing gravity on the perceptual upright with a view to assessing how a multisensory system responds to the loss of one of its inputs. We removed the force of gravity by two means, either (1) by lying subjects supine (which diverts the force of gravity away from its accustomed alignment with the long axis of the body), or (2) parabolic flight (which cancels the force of gravity for brief periods of about 22 s).

Exposure to microgravity has widespread perceptual effects (Glasauer and Mittelstaedt 1998; Oman 1998), including distortions of the perception of visual orientation (Kornilova 1997), changes in sensory-motor coordination (Winter et al. 2005) and in perceived self-orientation (Oman 2003). However, the effect of altered gravity states on the perceptual vertical is only now becoming clear (e.g., Jenkin et al. 2004). There is presently no quantitative model available that can anticipate what the perceptual upright will be under microgravity conditions. This paper begins to address these issues.

The experimental investigation of the perceived direction of "up" has a long pedigree stretching back to early studies into the effects of head-and-body tilt on verticality by Aubert (1886) and Müller (1918). Traditionally the perceived direction of up has been measured by asking participants to judge the orientation of a bar relative to the direction of gravity. The chosen orientation is known as the subjective visual vertical (SVV) (Mittelstaedt 1986). As well as being influenced by the orientation of the participant relative to gravity, even minimal visual frame information, such as the orientation of a simple outlined square surrounding the probe bar, influences the SVV (Asch and Witkin 1948). Environments rich in visual polarity cues can shift the SVV more significantly (Morant and Beller 1965; Purcell et al. 1978; Mittelstaedt 1986; Friederici and Levelt 1990). By manipulating the relative directions of the body, gravity, and the orientation of the visual scene, it has been shown that the direction of the SVV can be modelled as the geometric average of the directions provided by each, with each cue weighted in a way that varies from person to person (Mittelstaedt 1983a; Dyde et al. 2006): we refer to this as the vector sum model.

The vector sum model can be used to predict the direction of the SVV for all possible arrangements of the contributing factors. It also makes predictions about what will happen if a person is deprived of one of these sources of information. Testing these predictions of the consequences of removing gravity is not straightforward however: how can a participant "adjust a line to gravitational vertical" when gravity has been removed?

A measure of the perceptual vertical that is not dependent on the presence of gravity as a reference is needed. One method, that was used successfully in microgravity onboard Neurolab to assess self-orientation, involves shape-from-shading (Oman et al. 2003). In this test the perceived curvature of a shaded disc (is it convex or concave?) is determined and from this the perceived direction of the ambient light is estimated. Since humans assume that light comes from above (Ramachandran 1988), this test provides a gravity-independent, albeit indirect, measure of "above" and hence of the perceived vertical (Jenkin et al. 2004). Using this technique in parabolic flight provided the first assessment of the relative roles of the senses contributing to "up" in the absence of gravity. The results hinted surprisingly that visual cues were less significant in defining the direction of "up" under microgravity conditions than they were under normal gravity and that they might also be less significant during hypergravity (Jenkin et al. 2005).

The validity of results from the shape-from-shading test however relies on the assumption that light comes from above (Adams et al. 2004). This assumption is not always valid (Sun and Perona 1998; Mamassian and Goutcher 2001) and may be particularly questioned in unusual or artificial environments. A new test is required that does not rely on external assumptions, one that does not require participants to imagine the direction of gravity, and that can be applied in a brief period of time. Such a probe was devised through utilising the perception of the form of ambiguous figures (Mittelstaedt 1991) to determine the "midline of saliency" (p. 387) between the "princess" and "witch" percepts of the ambiguous "princess/witch" figure. When an observer was tilted 90° rightwards, the midline of saliency between the two percepts was shifted to an orientation which coincided with neither the subjectively percieved axis of gravity nor the axis of the observer's body, but to an intermediate orientation between SVV and the body axis. This same idea has also been applied using the natural ambiguity of a letter character in what has been labelled the oriented character recognition test (OCHART) (Dyde et al. 2006). OCHART uses an ambiguous symbol "ᓇ", the identity of which ("p" or "d") depends on its perceived orientation. The two points of maximum ambiguity (where the participant performs at chance in their letter descriminations) are found. The orientation of minimum ambiguity is defined as being half way between these maximally ambiguous orientations and is called the perceptual upright (c.f. Hock and Tromley 1978).

When the perceived upright is measured with the cues to orientation (body, vision and gravity) misaligned the relative contribution of each cue can be quantified (Dyde et al. 2006). Although there is considerable individual variability in the relative strength of these cues, in a normal 1 g environment the cues are typically weighted such that vision is given about 0.5 of the weight assigned to the body and gravity about 0.4: that is the visual cue accounts for about 25% [0.5/(0.5 + 1 + 0.4)] of the perceptual upright.

Our hypothesis was that if gravity were removed vision would increase its relative contribution to the perception of up. That is, the perceptual upright would tend to line up more with the orientation of the visual background. Dyde et al. (2006) examined this hypothesis by testing participants lying on their backs. The results showed that the contribution of vision was indeed increased with supine observers. Our hypothesis for the effect of hypergravity was that the weightings should remain unchanged since all that gravity is providing is a direction. This direction should be available as long as gravity is above threshold. To test these hypotheses we applied the OCHART technique to a group of participants to measure their relative sensory weightings while upright and supine while on-earth, and then again during transient periods of micro- and hypergravity created by parabolic flight.

## General methods

### Identifying the perceptual upright

Using the method of constant stimuli, the OCHART method presents the ambiguous symbol "ᓄ" in various orientations and scores the number of times it is identified as a "p". At least five orientations are required to obtain a psychometric function from which the points of maximum ambiguity can be identified. Examples of such functions are shown in Fig. 1. The challenge of applying this technique during parabolic flight is to collect adequate data to test the hypotheses within the constraints of the short duration exposure to microgravity associated with each parabola. To maximize the efficiency of data collection we "bracketed" the expected orientations of maximum ambiguity during ground-based testing and used this to define test brackets during parabolic flight. These ambiguity points varied widely between participants; therefore the tested character orientations were tailored to each participant. Ten values were chosen (five for each point of maximum ambiguity) based on pilot studies performed in the laboratory using orientations taken around the clock taken in 15 deg steps. These brackets varied widely across the participant group as shown in Fig. 2. Although there were between-subject differences in terms of the stimuli presented, this does not influence the within-subject comparisons which formed the basis of all our data analyses.

### Apparatus

The OCHART characters were presented on an Apple iBook laptop computer with a resolution of 48 pixels/cm (21 pixels/deg: the characters were approximately $3° \times 2°$). The computer screen was masked to a circle subtending 35° when viewed at 25 cm through a black circular shrouding tube that obscured all peripheral vision (see Fig. 3). The opening to the shroud was shaped to act as a semi-rigid, padded, head restraint to control both the viewing distance and the orientation of the participant's

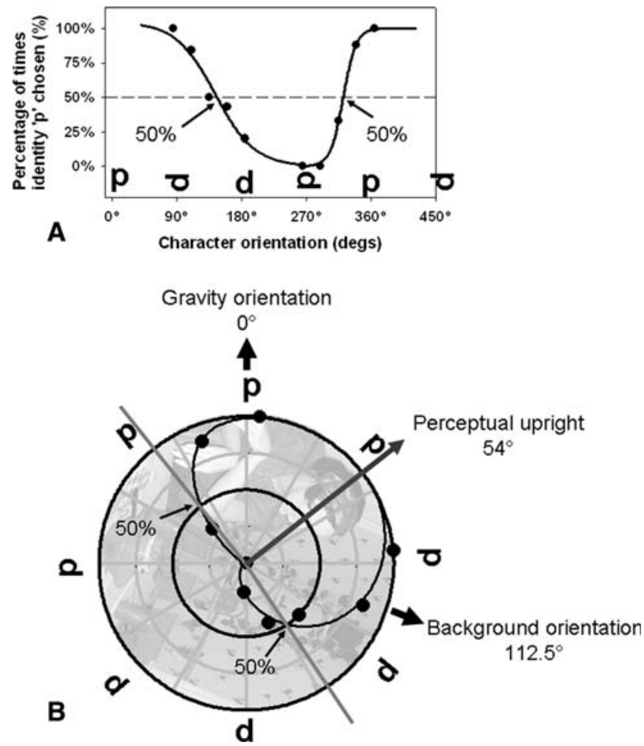



**Fig. 1** The oriented character recognition test: OCHART method for determining the perceptual upright. A constant stimuli design was used in which a character was presented at one of several pre-selected orientations and the participant identified it as a '*p*' or a '*d*'. Illustrated here are example data from one participant ('hj') collected whilst experiencing microgravity (~0.08 g) in Series I, with the background picture oriented at 112.5°. The percentage of times the character was identified as a '*p*' is plotted as a function of the orientation of the character in linear (**a**) and polar (**b**) coordinates. Best fit cumulative Gaussians are plotted through the data. From these curves the orientation of the character at which it is equally likely to be identified as a '*p*' or a '*d*' can be identified. The perceptual upright is defined as the midway between these two transitions

head relative to the screen. The laptop was mounted in an aluminium frame to maintain the screen at a fixed angle and to hold the shroud in place.

Each microcomputer used in both flight series was connected via USB cable to a ADXL311 dual axis digital accelerometer (supplied by Phidgits Inc.) which was held in a rigid plastic casing which was in turn fixed to the aluminium frame holding the microcomputer and shroud. *X* and *Y* accelerations in the plane of the testing screen were recorded at stimulus onset and at the point of the participant's response. These readings were inserted directly into the computer data file which recorded the stimuli presented and the participant's responses.

Data were collected in two series of parabolic flights. In Series I, conducted using NRC's Falcon 20 aircraft, participants remained in a seated position such that their body aligned with the gravity vector (when present). In Series II, conducted using Novespace's Airbus 300 aircraft,

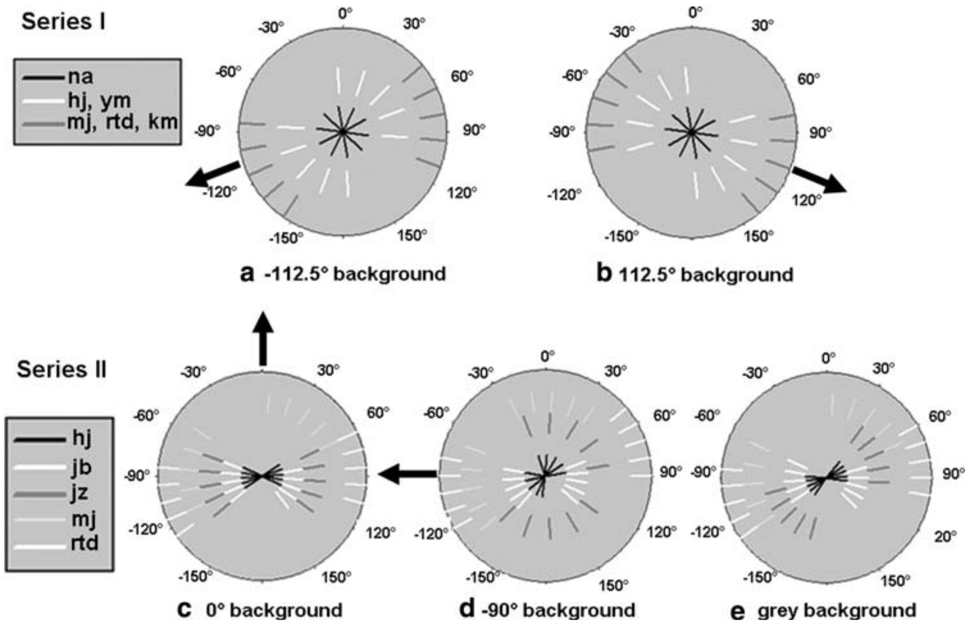



**Fig. 2** Detailed here are the orientations of the p/d character that were presented to each of the participants for each of the backgrounds over experimental Series I (*a*, *b*) and Series II (*c*, *d*, *e*). The selected character orientations were chosen to bracket the expected estimates of the 'orientations of maximum ambiguity' based on more complete tests on the ground for each subject individually (see text). Bracketing was made necessary by the brief periods of time available for data collection on parabolic flights. The same set of brackets was used for a given participant for all data collection conditions. The *dark arrows* indicate the orientation of the backgrounds. N.B. 0° was always aligned with the top of the observer's head (see conventions)

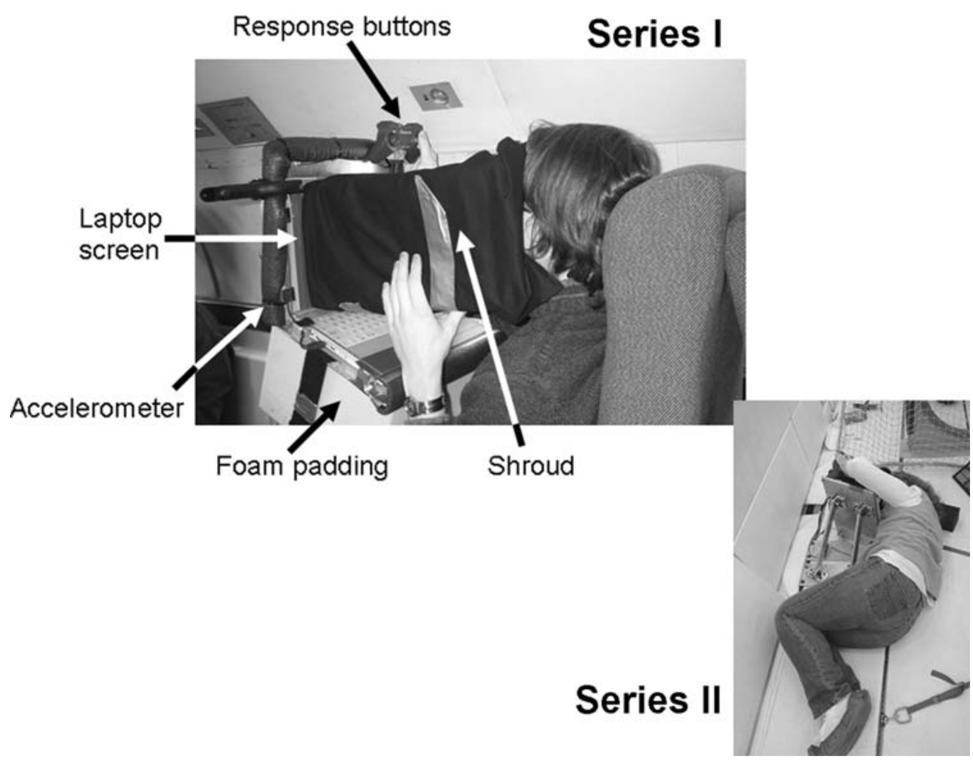
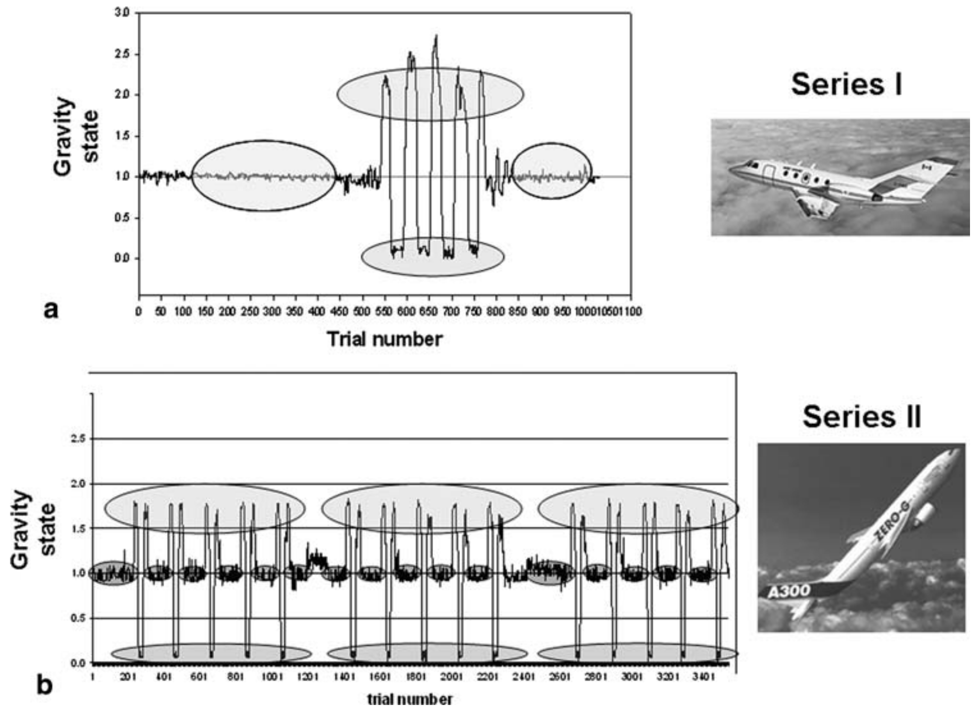



**Fig. 3** Participant orientation. Stimuli were presented on a laptop screen viewed through a shroud that obscured peripheral vision and created a circular aperture. For Series I participants sat upright in their seats; for Series II they lay on their right sides. Examples of the presented stimuli (a character on a highly polarized background) are shown in Fig. 5

participants lay right side down relative to the gravity vector (when present). Typical gravity states recorded during Series I and Series II flights are shown in Fig. 4.

For the upright posture of Series I, both for pre-flight laboratory testing and for in flight testing, the aluminium frame holding the laptop was fixed to a semi-rigid foam

**Fig. 4** Typical acceleration profiles for the Series I and II parabolic flights. Periods of increased, normal and reduced gravity are shaded during typical flights for Series I (*top panel* **a**) and Series II (*lower panel* **b**). Gravity state is plotted as a function of trial number where each trial took approximately 800 ms to complete




wedge that was strapped to the participants' knees (Fig. 3 Series I). The wedge was tailored individually for each participant to ensure that the laptop screen was in the fronto-parallel plane of the participant. For the pre-flight laboratory based, supine posture data collection sessions, the aluminium frame with the laptop was fixed to an outer frame which held the screen above the participant and ensured that the screen was in the fronto-parallel plane of the participant and orthogonal to gravity. In Series II, participants lay on their right hand side (Fig. 3 Series II). During all parabolic flights the participants were loosely secured to the seat (Series I) or the floor (Series II) of the aircraft.

## Conventions

All conventions for orientation are with respect to the participant's body/head. In all these experiments the head was kept aligned with the torso and the head-and-body were treated as one vector. When describing the orientation of the background, the letter probe, or gravity we use the same convention in which 0° corresponds to the top of the head. A positive angle (e.g., of +45°) corresponds to a tilt to the right (clockwise) and a negative angle indicates a tilt to the left (counter-clockwise) relative to the top of the head.

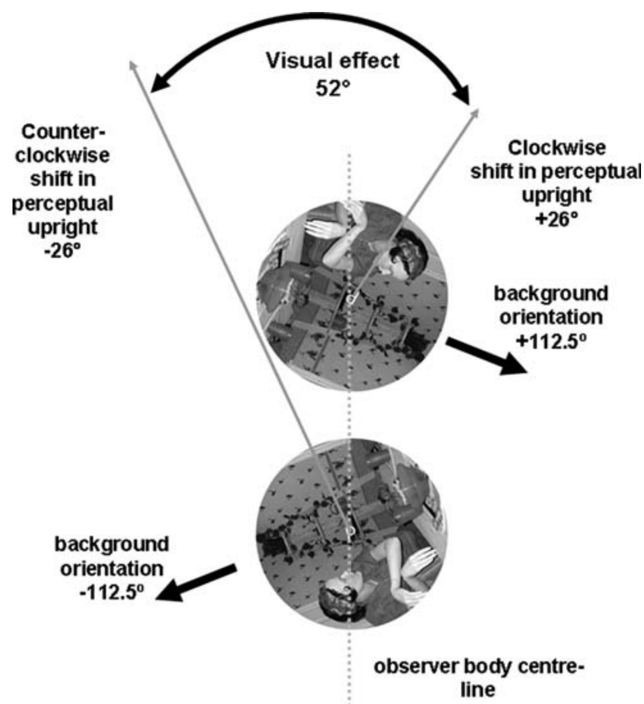



**Fig. 5** Definition of the 'visual effect' for Series I. The visual effect is the angle between the perceptual upright measured against the background orientated at 112.5° clockwise and at 112.5° counter-clockwise

## Procedure

All trials consisted of a stimulus formed by the p/d character superimposed on a visual background (see Fig. 5 for examples). Each stimulus was presented for 500 ms after which the image was replaced by a blank screen of the same mean luminance, containing a centrally positioned fixation point. Participants made to a two-alternative forced choice between the "p" or "d" letter percepts by pressing a key on a gamepad (Gravis Gamepad Pro) input device. The participant's response was blocked by the controlling software until stimulus offset and appearance of the fixation point. Once the response was made, the next trial was initiated after an approximately 150 ms delay. Each trial took less than a second. Participants continued the sequence of trials until instructed to stop.

### Data analysis

Flight trials data were first pooled by gravity level: 1 g, hypergravity, and microgravity. Laboratory data were divided into two conditions, upright and supine. For each condition and background a psychometric function was created of the percentage of time one identity of the character was chosen as a function of character orientation. Two cumulative Gaussian sigmoids were fitted to each data set using:

$$p = \frac{100}{1 + e^{\frac{-(x - x_0)}{b}}} \qquad (1)$$

where $p$ is the percentage of times the character is identified as a "p", $x$ is the orientation of the character, $x_0$ is the orientation at the point of subjective equality (PSE), i.e., the orientation at which either identity of the character was equally likely to be chosen (50%) and b is the standard deviation. The mean of the two PSEs (see Fig. 5) was taken as the perceptual upright. The square of the mean of the two slopes' standard deviations was taken as the intra-observer response variance.

## Series I

Series I consisted of two experiments: a lab-based experiment comparing the effects of sitting upright versus lying supine; and a flight-based experiment where the same participants were tested in normal gravity, microgravity and hypergravity (while in an upright position) in a Falcon 20 aircraft flying out of NRC's Ottawa-based microgravity flight facility.

### Methods

#### *Participants*

Six participants (4 males, 2 females, aged between 22 and 45 years) took part in these experiments. All participants had normal or corrected-to-normal vision and reported no history of vestibular dysfunction. Each completed informed consent agreements which conformed to the ethical guidelines of York University, the Canadian National Research Centre, and the Treaty of Helsinki. Three participants (hj, mj and rtd) had prior experience of parabolic flight, three participants (na, ym and km) did not.

#### *Bracketing*

Pilot experiments were run with each of the six participants using character orientations round the clock. From this a subset of ten character orientations was chosen to be used in the limited testing time available during parabolic flight. The values selected are shown in Fig. 2a, b for the 112.5° and −112.5° background orientations respectively: participants fell into three groups (in terms of the brackets used) as shown. For each participant and background the same set of character orientations were used for all five conditions (lab upright, lab supine, microgravity flight, 1 g flight, hypergravity flight).

#### *Laboratory testing*

Participants were tested upright and supine, before and after parabolic flight to balance order effects across conditions. The results for the laboratory based data are formed from the average of before- and after-flight data collection sessions.

#### *Parabolic flight testing*

The aircraft used was a Falcon 20 modified for parabolic flight, based at the National Research Centre of Canada, Ottawa. This aircraft performed four parabolas per flight. Three participants sat facing forward, three facing aft each with a laptop computer fixed semi-rigidly in front of them (Fig. 3 Series I). For safety reasons all participants were loosely restrained by seat belts throughout the flight.

Four separate flights took place over 4 days of testing. Each flight consisted of a period of 1 g level flight, followed by four parabolas, and ending with a second level flight period. Data collection started soon after take off and continued until the second period of level flight. On reaching the required altitude and location, equipment was deployed and participants started viewing their screen and making responses. The set of ten character orientations were shown against four backgrounds: a polarized image aligned with the body axis; polarized images tilted either 112.5° or −112.5°; and a grey screen of the same mean luminance as the polarized image. There were thus 40 combinations of character orientations and backgrounds. These were presented in pseudorandom order so that a complete set of the 40 combinations was completed before the next sequence was run. With a trial duration of about 800 ms, there were about 200 trials during the parabolic phase of each flight. Over four flights responses to about eight repetitions of stimuli combination were accumulated for both microgravity and hypergravity phases.

*Data analysis*

Data were collected continuously throughout the flight. Responses were pooled according to the values recorded by the accelerometers. The recorded average value of g (across the participant group) for the data used to represent the in-flight 1 g phase was 1.0 g (SD 0.03). The average value of g for the data used to represent the hypergravity phase was 1.97 g (SD 0.02.). The group average value of g for the data used to represent the microgravity phase of the parabolic arcs was 0.085 g (SD 0.01).

## Results for Series I

The orientation of the perceptual upright was measured for each background tested as described in the general methods. Changes in the strength of the visual background's influence were examined by calculating the "visual effect" defined as the difference in the direction of the perceptual upright when the background was tilted 112.5° counterclockwise compared to when it was tilted 112.5° clockwise. These two backgrounds were chosen because they have been found in previous earth-based studies (Dyde et al. 2006) to be associated with the largest shifts of the perceptual upright. The definition of "visual effect" is illustrated in Fig. 5.

*Comparison of upright and supine conditions in the laboratory*

Figure 6a shows the average direction of the perceptual upright while participants were upright and supine with the background presented in one of three orientations (0°, 112.5° and −112.5°). There was a substantial effect of the orientation of the visual background in both postures. When upright in the laboratory the perceptual upright shifted to 32.3° (SE 17.4°) when measured against the 112.5° background and to −39.4° (SE 13.8°) when measured against the −112.5° background: an average visual effect of 71.7°. When supine the equivalent shifts were to 38.8° (SE 16.8°) and to −39.1° (SE 13.6°); a visual effect of 77.9°. Figure 6d shows the size of the visual effect for each participant measured upright compared to when measured supine. Although there was substantial variability between participants, with visual effect sizes ranging from 7° to 197°, in every case the visual effect was larger when measured supine than when upright, with an average difference of 6.2° (SE 2.5°). The difference in visual effect size between upright and supine postures was statistically significant: $t(5) = 2.64$, $P < 0.05$ (two-tailed), $d = 1.08$, $r^2 = 0.58$, power = 6.8%.

*Comparison of normal gravity and microgravity in flight*

Figure 6b shows the effect of the orientation of the visual background on the perceptual upright measured in the microgravity phase of parabolic flight compared to level flight. During level flight (1 g) the average perceptual upright was 28.0° (SE 15.9°) when measured against the 112.5° background and −38.1° (SE 13.7°) when measured against the −112.5° background: a visual effect of 66.1°. During microgravity the equivalent orientations for the perceptual upright were 22.9° (SE 14.4°) and −30.6° (SE 12.6°): a visual effect of 53.5°. Figure 6e shows the size of the visual effect in level flight compared to the microgravity phase for each individual. As with the ground-based controls there was substantial variability between participants. For all but one participant the visual effect size was smaller in the microgravity phase than in the 1 g phase of flight, with a mean decrease in visual effect of 12.6° (SE 4.2°). The difference in visual effect size between the 1 g and microgravity conditions was statistically significant: $t(5) = 2.98$, $P < 0.05$ (two-tailed), $d = 1.22$, $r^2 = 0.64$, power = 8.9%.

*Comparison of normal gravity and hypergravity in flight*

Figure 6c shows the effect of the orientation of the visual background on the perceptual upright measured while participants were in the hypergravity phase of parabolic flight. There was a substantial effect of the visual background in which the perceptual upright was 23.7° (SE 14.4°) when measured against the 112.5° background and −32.8° (SE 12.6°) when measured against the −112.5° background: a visual effect of 56.5° during hypergravity. Figure 6f compares the size of the visual effect for each participant during level flight and during the hypergravity phase. For all but one participant the visual effect was smaller in hypergravity than in normal gravity (by 9.6° on average). However the difference in visual effect size between 1 g and hypergravity failed to reach significance: $t(5) = 2.16$; $P = 0.08$ n.s. (two-tailed).

*Comparison between laboratory and flight data*

Comparing the visual effect size across the two baseline conditions (upright in the laboratory versus the 1 g phase in flight) showed no difference between these two conditions: $t(5) = 1.04$; n.s. Comparing the two "microgravity" conditions (supine in the laboratory vs. microgravity in flight) revealed a reliable difference: $t(5) = 2.70$, $P < 0.05$ (two-tailed), $d = 1.10$, $r^2 = 0.59$, power = 7.2%.

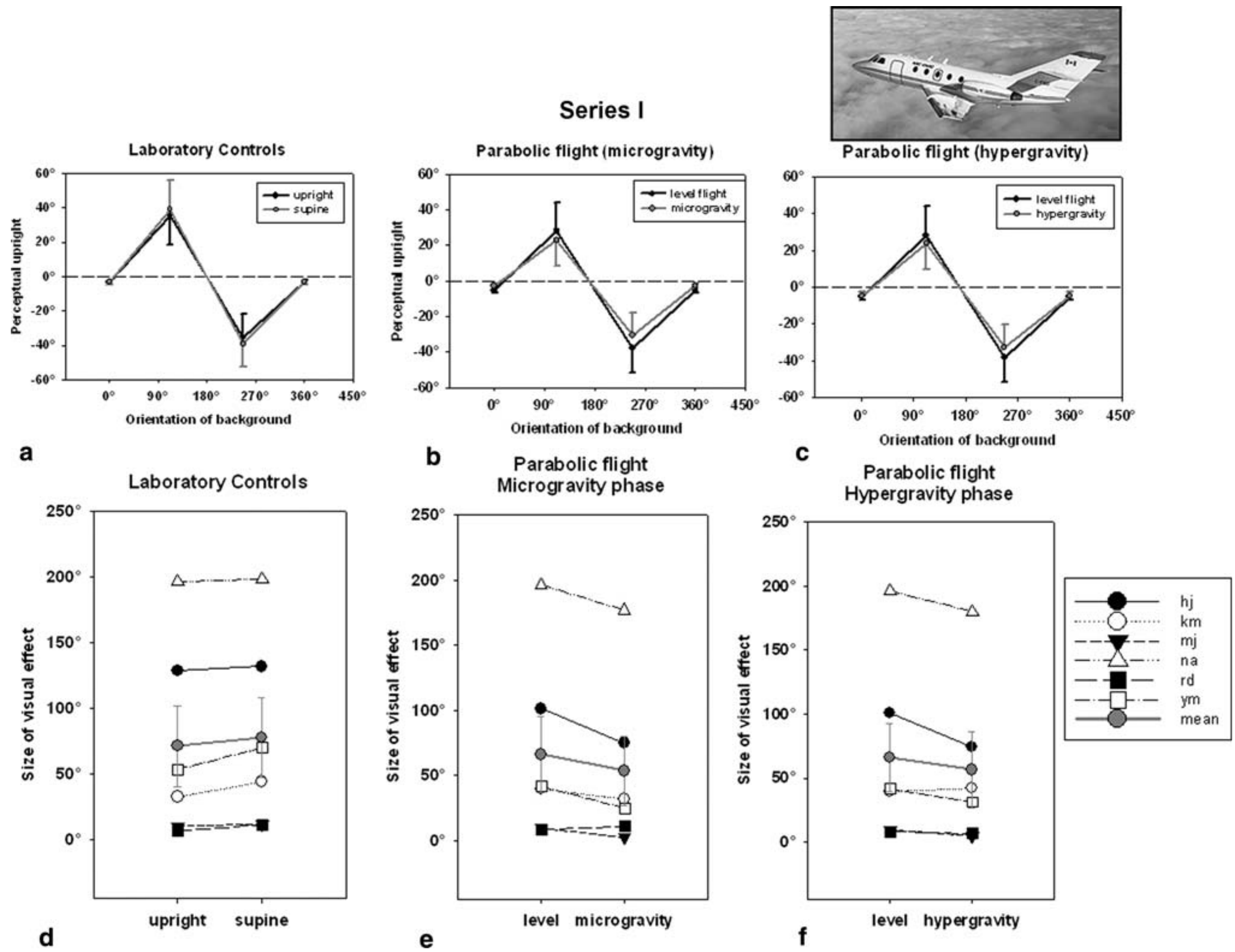



**Fig. 6** Series I data. The *top panels* (**a**, **b**, **c**) show the average orientation (and SE's) of the perceptual upright as a function of background orientation for data collected in (**a**) the laboratory upright compared to supine, (**b**) microgravity compared to level flight and (**c**) hypergravity compared to level flight. The *lower panels* (**d**, **e**, **f**) show the same comparisons for the visual effect (see Fig. 5) for each participant for (**d**) laboratory controls, (**e**) microgravity, and (**f**) hypergravity conditions

### *Comparison of variance across conditions*

We calculated each participant's variances (defined as the square of the standard deviations of the cumulative Gaussians fits: see general methods "Data analysis"). These variances were taken from the data which contributed to the calculated perceptual upright measured in the presence of the 112.5° and −112.5° backgrounds. The variance data can be interpreted as indicating the confidence and/or reliability of each participant in their letter discriminations. The group mean variances were: during microgravity 313 deg$^2$ (SE 141); during 1 g flight 211 deg$^2$ (SE 83); during hypergravity 231 deg$^2$ (SE 84). The equivalent variances from our laboratory testing were: while upright 205 deg$^2$ (SE 86); when supine 197 deg$^2$ (SE 71). There were no reliable differences in the amount of variance between any two conditions. There was no significant increase in the variance of observations between laboratory and flight, or between normal and altered *g* states.

## Discussion of Series I

The data from our Series I flights shows that the effect of vision on the orientation of the perceptual upright was significantly decreased (relative to 1 g level flight controls) during microgravity. This contrasts with the on-earth data obtained when zero g was crudely simulated by having participants lying on their backs. For supine participants the visual effect was significantly increased (relative to upright controls). Our results also suggested a tendency for the effect of vision to be reduced during the hypergravity phase. The absence of any reliable increase in variances during flight suggests these changes were not related to the stress or unusual nature of parabolic flight itself: observers were equally reliable in their responses in the laboratory and in flight. To further examine these observations we performed a second series of experiments (Series II) where the directions of gravity (normal, microgravity and hypergravity) and body cues could be dissociated by having the participants lying right side down.

## Series II

Series II experiments were performed on the Novespace Airbus 300 aircraft. Participants were tested right side down lying on the floor of the aircraft. This arrangement meant that, unlike for Series I, during the hypergravity and 1 g phases of the flight, the gravity and body vectors were orthogonal rather than aligned. Under these circumstances it is easier to disocciate the effects of gravity (or hypergravity) from the effects of body orientation.

### Methods

#### *Participants*

Five participants (4 male, 1 female, between the ages of 26 and 45 years) took part in the Series II in flight experiments. Three had participated in Series I (mj, rtd, hj). All participants had normal or corrected-to-normal vision and reported no history of vestibular dysfunction. Each completed informed consent agreements which conformed to the ethical guidelines of York University, Novespace, and the Treaty of Helsinki. All participants had extensive previous experience with parabolic flight.

#### *Conditions*

The visual cues were varied by providing the same highly polarized visual background as used in Series I but with the participant lying right side down throughout the flights as shown in Fig. 3 Series II. The laptop and shroud were identical to that of Series I. The background was oriented at either 0° (aligned with the body axis) or −90° (orthogonal to the floor of the plane and aligned with the axis of gravity when gravity was not cancelled). A grey featureless background was used to present a third condition with no visual orientation cues.

#### *Procedure*

Testing for Series II was similar to Series I. Pre-flight testing for Series II identified the appropriate bracketing for each participant for the three backgrounds selected: 0°, −90° and neutral grey. The selected bracketing for each participant and background for Series II is shown in Fig. 2c–e.

The aircraft used for the second series of microgravity experiments was a specially adapted A300 Airbus modified for parabolic flight-based out of Bordeaux, France. Testing took place over four flights conducted over 5 days. Each flight consisted of 31 parabolas of which 30 parabolas were available for data collection. Only one participant at a time could perform the experiment. Each testing session consisted of 15 consecutive parabolas (see Figure 4b). In this way the experiment could be conducted by up to two participants per flight. The microgravity phase of each parabola was similar to that of Series I, with periods of approximately 22 s of microgravity separated by periods of hypergravity. Due to different flight profiles and the different aerodynamic qualities and control systems of this larger aircraft, the hypergravity phases involved lower accelerations of approximately 1.76 g (compared to 1.97 g from Series I).

On reaching the required altitude and location, the participant got into position (right side down, see Fig. 3). Participants lay on the padded floor of the Airbus300 with their head supported by a neck roll and with a loose tether around their legs to prevent uncontrolled movement of the lower limbs. Participants then viewed the screen and made their responses until instructed to stop. Participants responded throughout the hypergravity and microgravity phases of the flight and also during periods of level flight. The gravitational acceleration was recorded at stimulus onset and when the participant responded for each trial. The *g* state for that trial was taken as the average of these two values. There were thirty combinations of character orientation and backgrounds. Similar to Series I, the stimuli were presented in a continuous sequence of pseudo-randomized blocks each of 30 trials.

#### *Data analysis*

The orientation of the perceptual upright was measured for each background tested as described in the general methods ("Data analysis"). Data were pooled by *g* state as described for Series I (see "Parabolic flight testing"). The effects of vision were assessed by comparing the orientation of the perceptual upright with the background either lined up with the body (0°) or at −90° (to the participant's left). The difference in these orientation corresponds to the visual effect in this in flight paradigm. Note that Series I compared the effects of backgrounds that were 135° apart (see Fig. 5) whereas Series II compared backgrounds that were 90° apart. As such the magnitude of the visual effect was expected to be lower in Series II.

## Results of Series II

### *Effects of altered gravity states on the perceptual upright*

Figure 7 summarizes the results for all participants in Series II. The average orientation of the perceptual upright under each condition is shown in Fig. 7a–c. The average visual effect (the difference in the orientation of the perceptual upright measured with the background oriented at 0° and with it oriented at −90°) under the normal gravity of level flight was 29.6° (SE 13.8°). On-ground controls produced an average visual effect of 37.1° (SE 14.9°). During microgravity the visual effect size decreased to 23.8° (SE 13.4°). The reduction in the size of visual effect size in microgravity was significant compared to both level flight (a mean reduction of 5.9°, SE 1.8, $t(4) = 3.18$, $P < 0.05$ (two-tailed), $d = 1.43$, $r^2 = 0.71$, power = 8.9%) and on-ground controls (a mean reduction of 13.4°, SE 4.4, $t(4) = 3.00$, $P < 0.05$ (two-tailed), $d = 1.34$, $r^2 = 0.69$, power = 7.6%).

The visual effect size measured under hypergravity was 27.8° (SE 13.5°) which was not significantly different from the result under 1 g either in level flight [$t(4) = 1.11$; n.s.] or on the ground [$t(4) = 1.54$; n.s.]. As was the case in Series I, the large standard errors of these averaged results is due to the large inter-participant variability of the visual effect. Figure 7d compares the size of the visual effect in normal gravity (level flight) and microgravity for each participant individually. For four of the five participants the size of the visual effect decreased. Figure 7e compares the size of the visual effect in normal gravity (level flight) and hypergravity.

### *Effect of gravity state on response variance*

Extracting the intra-participant variances from the results allowed us to determine whether the change in *g* state influenced the reliability of their responses. The mean of participants' variances were: in 1 g 98.8 deg$^2$ (SE 38.4); in microgravity 126.7 deg$^2$ (SE 46.1); and in hypergravity 83.1 deg$^2$ (SE 36.7). No one condition was significantly different from any other.

## Discussion of Series II

The results of our Series II microgravity flights confirmed the observation made during Series I that the influence of vision on the perceptual upright is significantly reduced during microgravity. The magnitudes of the visual effects obtained in the two series cannot be compared directly because the visual background orientations were different and the observer groups (within which there is considerable inter-participant variability) also differed. The possible reduction of the size of the visual effect in hypergravity suggested in the first series was not supported by the second series where no systematic differences from the normal gravity control condition were found. [1]Residual somatosensory cues provided by the light restraint system used in series II could partially explain why, when in microgravity and with a visual stimulus aligned with the body, there was still a small tilt of the perceptual upright of 7.7° towards the direction in which gravity normally operated.

## General discussion

These experiments demonstrate that the orientation of the visual background is significantly less influential in determining the perceptual upright during the microgravity phase of parabolic flight than it is under normal gravity. In contrast, when an observer is supine in a normal gravity environment such that gravity is not in its customary relationship to the long axis of the body, the orientation of the visual background is significantly more influential in determining the perceptual upright. This suggests a dissociation between supine and parabolic methods of simulating the absence of gravity.

The nature of parabolic flight experiments necessitates a relatively small number of subjects and the inter-individual differences were rather large (Figs. 6, 7). These factors influence the power of our comparisons. For each significant result the power was quite low (ranging from 6.8 to 8.9%). Despite this, the visual effect measured in microgravity was significantly different from the 1 g controls for both flight series, and the effect size measured was large based on Cohen's *d* and $r^2$.

The low power however, makes the non-significant effects, especially between the size of the visual effect collected under hypergravity and under 1 g conditions, less easy to interpret. There was some indication of a trend, but further experiments will be required to confirm or disprove any "hypergravity effect".

## Modeling the influence of body, gravity and vision on the perceptual upright

Inspired by the work of Mittelstaedt (1983a, 1986), we modelled the effect of visual cues, the internal representation of the body axis (the idiotropic vector) and gravity in determining the orientation of the perceptual upright as the weighted vector sum of the three directions of upright

[1] The subjective visual vertical is unchanged by hypergravity when the head is upright or close to a roll tilt of 90° (Schone and Parker 1967; Schone et al. 1967). This may reflect a 'normalizing' of the otolith outputs coming from the vestibular system on each side of the head (Mittelstaedt 1983a, b; Mast 2000).

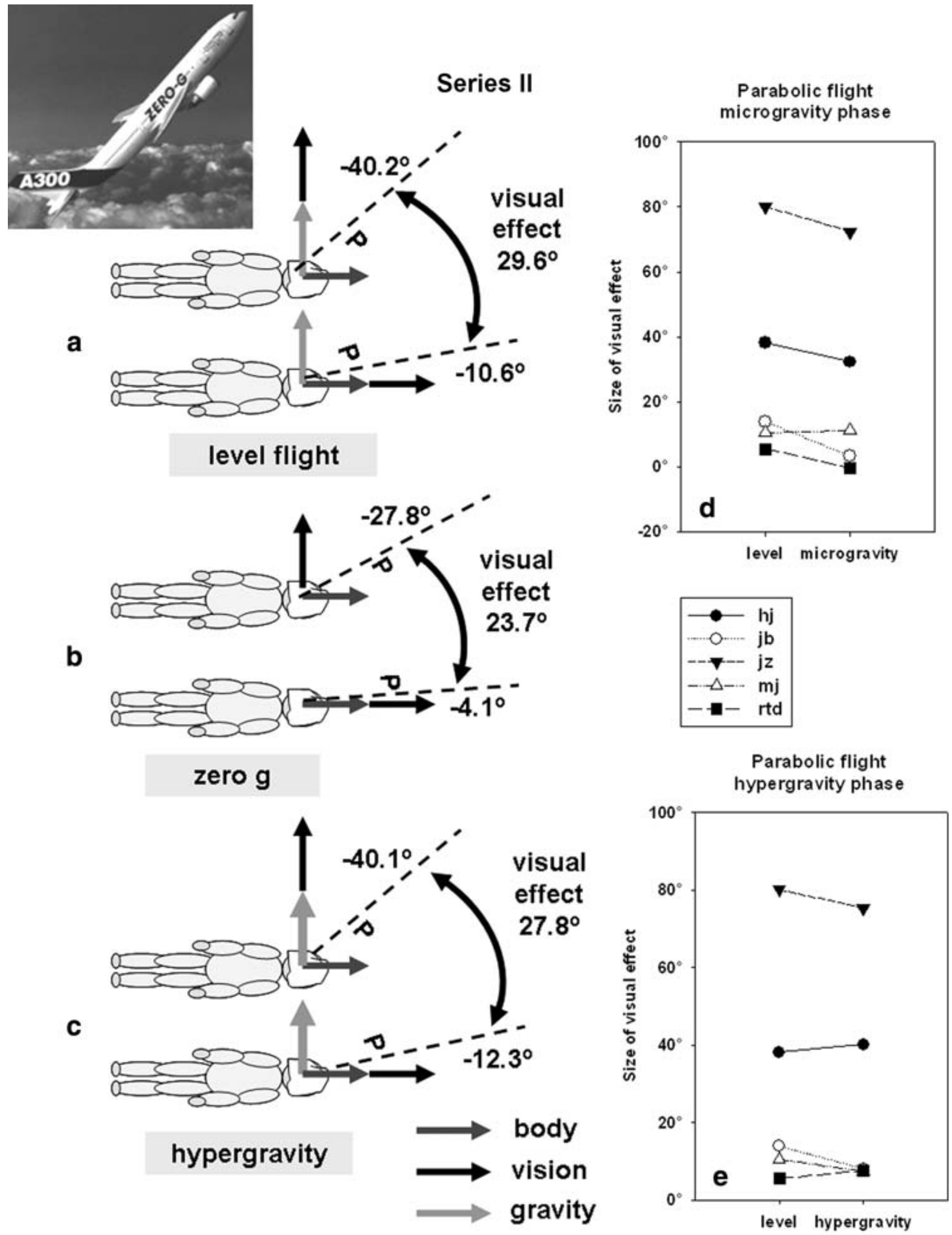



**Fig. 7** Series II data. The perceptual upright measured with subjects right side down (see Fig. 3) viewing backgrounds aligned either with the body (0°) or the axis of gravity if present (−90°). The results are shown by *dotted lines* indicating the angle of the average perceptual upright for the two oriented backgrounds during level flight (**a**), microgravity (**b**) and hypergravity (**c**). **d** Compares the visual effect (difference between perceptual upright for the two backgrounds) for level flight with that obtained under microgravity for each subject. **e** Compares the visual effect for level flight with that obtained under hypergravity conditions

signalled independently by each of these three cues as described in Eq. 2 (Dyde et al. 2006)

$$\overrightarrow{pu} = \vec{v} + \vec{g} + \vec{b} \tag{2}$$

Here $\overrightarrow{pu}$ is in the direction of the perceptual upright and $\vec{v}$ and $\vec{g}$ are vectors describing vision and gravity relative to the unit vector $\vec{b}$ used to represent the body. Because we are only interested in the direction of $\overrightarrow{pu}$ and not its magnitude, the choice of which vector to set to unity is arbitrary.

Although there were substantial individual differences in the average vector lengths (see also Dyde et al. 2006), ratios of the lengths of the vision and gravity vector relative to the body vector for typical subjects are $v{:}b = 0.5$ and $g{:}b = 0.4$. (Here we use the shorthand $v$, $b$ and $g$ to represent the magnitude of the vector $\vec{v}$, $\vec{g}$ and $\vec{b}$ respectively). For the six participants in Series I the ground-based ratios were $v{:}b = 0.7$ and $g{:}b = 0.2$. For the five participants in Series II the ground-based ratios were $v{:}b = 1.5$ and $g{:}b = 0.3$. The values were obtained by fitting Eq. 2 to the measured direction of the $\overrightarrow{pu}$ obtained in the laboratory studies in various body postures. This process is a simplification of Mittelstaedt (1983a, 1986) detailed and sophisticated modelling which attempts to capture the nuances of the variation of the subjective visual vertical with changes in the orientation of the visual background

(Bischof 1974).When using the weighted vector sum model to predict the effect of microgravity (or supine posture), the gravity vector is removed, leaving only the body and visual vectors to predict the direction of the perceptual upright as shown in Eq. 3:

$$\overrightarrow{pu} = \vec{v} + \vec{b} \tag{3}$$

Under the assumption that the remaining weights remain unchanged the prediction is that for Series I the ratio of the length $v{:}b = 0.7$ and that, as a percentage, the predicted influence of vision increases from 37 to 41%. For Series II (using a different set of participants) the ratio $v{:}b = 1.5$ and therefore the predicted increase in the influence of vision increases from 54 to 60%.

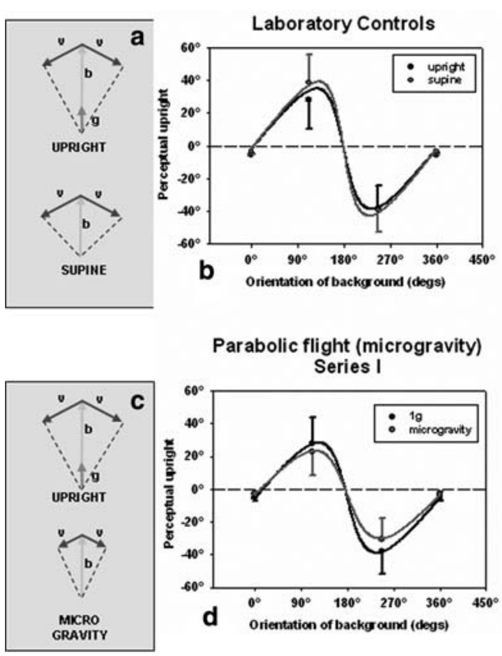
For Series I we tested this prediction under two circumstance, firstly by arranging the body to be supine (to remove $g$ from the plane of the experiment) and secondly by cancelling gravity using parabolic flight. For the supine condition the influence of vision increased in the predicted way and was fitted by substituting the values $v{:}b = 0.7$ and $b = 1$ in Eq. 3. This is shown diagramatically in Fig. 8a and the predicted curves are plotted through the data in Fig. 8b. However the influence of vision was significantly reduced in the microgravity of parabolic flight and the weighting of the model needed to be adjusted downwards to $v{:}b = 0.4$ to fit the data. This is illustrated diagramatically in Fig. 8c and the adjusted model is plotted through the data in Fig. 8d. For Series II the visual effect was likewise reduced which required a reduction of the visual weighting from $v = 1.5$ to $v = 0.8$. All best fit weight values are summarized in the table of Fig. 8d. Why might the visual influence be increased in the circumstance that removes gravity from the coronal plane, but be reduced during the microgravity of parabolic flight?

## Comparison of supine posture and parabolic flight for producing microgravity

Attempts to assess the significance of gravity on perception have used three main methods: lying supine (e.g., bedrest), parabolic flight and, more rarely, spaceflight. The effects of lying supine have been inconsistent. Measurements of the rod-and-frame effect have found an increased effect size when measured supine (Templeton 1973), but this effect disappears (Goodenough et al. 1981) or even reverses (Luyat et al. 1997) depending on the details of the way it is assessed. Some visual illusions decrease in their effect: e.g., the horizontal/vertical effect and the Ponzo illusion (Clement et al. 2007) when measured supine. Results from experiments performed during parabolic flight are more consistent since all visual effects seem to be reduced: rod-and-frame (Villard et al. 2005), horizontal/vertical illusion and Ponzo Illusion (Clement et al. 2007), and influence of a tilted background in shape-from shading (Jenkin et al. 2004). Why might vision have less effect under these circumstances?

## Why might the visual effect be reduced in microgravity?

Since the weighted vector sum model does not predict a reduction in visual weighting, we need to suggest possible explanations of this reduction of the visual effect during parabolic flight. Under microgravity there seems to be a




e

Weightings

| | Series I | | Series 2 | |
|---|---|---|---|---|
| | 1g | 0g | 1g | 0g |
| vision | 0.7 | 0.45 | 1.5 | 0.84 |
| gravity | 0.2 | x | 0.3 | x |
| body | 1 | 1 | 1 | 1 |

**Fig. 8** Modeling the perceptual upright as a vector sum of weighted vectors corresponding to the directions of upright signalled by vision, gravity (when present) and the body. **a** and **b** Model the laboratory based data showing that one set of vector lengths (shown in **a**) model the data for both upright and supine (shown in **b**). Data collected under level flight (**d**) are again fitted by vectors with the same weighting as fitted the laboratory upright data, but the microgravity data required a reduction in the visual vector length as shown diagrammatically in (**c**). All vector lengths are summarized in (**e**)

change in weighting of the visual cue that is not predicted by cue combination, since the variances are not significantly changed: under microgravity the cues do not seem to be combined to produce the lowest variance.

The microgravity periods associated with parabolic flight are very short (22 s) so that a steady state is not really reached. Furthermore the transition into microgravity is from a hypergravity state (see Fig. 4). These transitions are associated with nystagmus (Cheung et al. 1994), torsional effects (Diamond and Markham 1991; Markham and Diamond 1993; Cheung et al. 1994) and asymmetrical vertical displacements of the two eyes (Karmali et al. 2006). These effects render the interpretation of visual effects of parabolic flight challenging. Visual degradation has been shown to reduce the visual effect on the perceptual upright (Dyde et al. 2005) and so it remains possible that our effects are secondary to a degraded retinal image produced by induced eye movements. Experiments with longer periods of microgravity experienced on Neurolab, although possibly associated with eye movement effects of their own (Buckey and Homick 2003), have also suggested reduced visual effects (Buckey and Homick 2003). However, there was no reliable increase in our observers' variance during any of the g-states including microgravity – so even these visual artefacts of parabolic flight remain to be substantiated as an explanation for our results.

An alternative explanation for our finding can be inferred from results found during the sustained microgravity of orbital flight (Glasauer and Mittelstaedt 1998). Observers were denied any visual reference and then passively rotated. When they attempted to point to the perceived (though unseen) "ceiling" of the spacecraft they showed a strong bias towards indicating that the ceiling was positioned at a point consistently above their own (rotated) head—i.e., the body (idiotropic) vector became dominant in their judgements of "above." By flight day 30 the previously strong correlation between actual body position and perceived above had weakened—suggesting that by this time in their exposure to microgravity, observers had experienced some form of adaptive process. It may be the case that during the brief periods of microgravity experienced in parabolic flight some analogous process is engaged in terms of the perceptual upright. In other words the direction of up becomes more strongly driven by and aligned with the body vector, resulting in a proportionally weaker influence of the visual cue.

Experiments in the sustained microgravity of the International Space Station are planned to investigate the effect of longer periods of microgravity on the OCHART protocol; experiments for which the present study forms a necessary pilot.

## Conclusions

The disocciation between the effects of vision producing a larger effect when lying supine and smaller effects when in parabolic flight are significant for two reasons. First, it challenges the equivalence of the two methods which have been widely used to simulate the microgravity conditions of space (bedrest and parabolic flight). Second, it suggests a non-linearity in the way multimodal sensory information is combined when one source is removed.

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