RESEARCH ARTICLE

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The subjective visual vertical and the perceptual upright

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Abstract The direction of 'up' has traditionally been measured by setting a line (luminous if necessary) to the apparent vertical, a direction known as the 'subjective visual vertical' (SVV); however for optimum performance in visual skills including reading and facial recognition, an object must to be seen the 'right way up'-a separate direction which we have called the 'perceptual upright' (PU). In order to measure the PU, we exploited the fact that some symbols rely upon their orientation for recognition. Observers indicated whether the symbol 'a' presented in various orientations was identified as either the letter 'p' or the letter 'd'. The average of the transitions between 'p-to-d' and 'd-to-p' interpretations was taken as the PU. We have labelled this new experimental technique the Oriented CHAracter Recognition Test (OCHART). The SVV was measured by estimating whether a line was rotated clockwise or counter-clockwise relative to gravity. We measured the PU and SVV while manipulating the orientation of the visual background in different observer postures: upright, right side down and (for the PU) supine. When the body, gravity and the visual background were aligned, the SVV and the PU were similar, but as the background orientation and observer posture orientations diverged, the two measures varied markedly. The SVV was closely aligned with the direction of gravity whereas the PU was closely aligned with the body axis. Both probes showed influences of all three cues (body orientation, vision and

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Department of Psychology, York University, Toronto, ON, Canada, M3J 1P3 gravity) and these influences could be predicted from a weighted vectorial sum of the directions indicated by these cues. For the SVV, the ratio was 0.2:0.1:1.0 for the body, visual and gravity cues, respectively. For the PU, the ratio was 2.6:1.2:1.0. In the case of the PU, these same weighting values were also predicted by a measure of the reliability of each cue; however, reliability did not predict the weightings for the SVV. This is the first time that maximum likelihood estimation has been demonstrated in combining information between different reference frames. The OCHART technique provides a new, simple and readily applicable method for investigating the PU which complements the SVV. Our findings suggest that OCHART is particularly suitable for investigating the functioning of visual and non-visual systems and their contributions to the perceived upright of novel environments such as high- and low-g environments, and in patient and ageing populations, as well as for normal observers.

Keywords Gravity perception · Multi-sensory integration · Vestibular · Visual perception · Orientation · Perceived vertical

Introduction

The perceived direction of up is a fundamental part of our interpretation of the visual world. Knowing this direction contributes to our speed and precision in recognizing objects, letters, actions and people, which often depend on seeing them 'the right way up' (McMullen and Jolicoeur 1992; Rock and Heimer 1957; Jolicoeur 1985; Maki 1986; Valentine 1988; Edelman and Bulthoff 1992; Rock et al. 1994; Corballis et al. 1978). Faces for example should be perceptually upright for easy recognition and huge distortions can go unnoticed if a face is inverted (Thompson 1980). Investigating how the perceived direction of up is derived from the available sensory cues requires both a definition and a reliable measure of this direction.

For the century and a half since Aubert first experimented with the perceived orientation of a luminous line (Aubert 1861), the perceived direction of up has been assessed by setting a line to appear vertical: a direction referred to as the 'subjective visual vertical' (SVV) (see Howard 1982 for a review of the literature from 1861 to 1982). The SVV, and the contributions of visual and non-visual cues in determining it, has been measured by carrying out these adjustments in the light and dark with observers tilted in various orientations relative to gravity and with various visual cues to vertical (e.g. Asch and Witkin 1948; Witkin 1949; Bischof 1974; Howard and Childerson 1994; Guerraz et al. 1998). Considerable effort has been devoted to modelling the relative strengths of the influences of these cues on the SVV, perhaps most notably by Horst Mittelstaedt (Mittelstaedt 1983), who introduced the idea of using weighted vectors to represent the factors involved. Although the perceived direction of gravity and of the visual scene is derived from sensory information, one of Mittelstaedt's keenest insights was to include the body axis as an additional reference direction that contributes to the SVV; a factor he called the 'idiotropic' vector.

Unfortunately, the SVV does not necessarily reflect the orientation of objects that is important for perceptual recognition tasks. Tasks such as the perception of 3D shape-from-shading (Jenkin et al. 2004) and ambiguous figures (Rock 1973; Rock et al. 1994; Rock and Heimer 1957; Jenkin and Howard 1998) show a marked effect of the up direction on observer performance-but the 'up' that underlies these tests is not always the up direction as defined by the SVV. This suggests that at least two uprights can be defined: one aligned with the perceived direction of gravity (the SVV) and another that corresponds to the orientation that defines the up direction most relevant for perceptual tasks that are sensitive to orientation such as object recognition and reading. Ian Howard and others developed a probe which exploited the fact that shape-from-shading assumes that light comes from above (Howard et al. 1990; Ramachandran 1988; Mamassian and Kersten 1996; Wenderoth and Hickey 1993). Under this assumption perceived concavity and convexity indicate the direction from which light appears to come and this is inferred to be the perceptual 'above'. Although this probe has proven to be effective (e.g. Wenderoth and Hickey 1993; Jenkin et al. 2004), it is predicated on the assumption that the direction of incident light defines 'above.' Unfortunately, the direction of the assumed light source is neither strictly equivalent to 'above' (Mamassian and Goutcher 2001) nor fixed (Adams et al. 2004). It would appear that a new experimental probe of perceived upright is required. Here we introduce a new probe which relies upon the fact that the perceived identity of some objects depends solely on their orientation. This probe is the ambiguous symbol ' Ω '. Since the distinction between a 'p' and a 'd' derives exclusively from its orientation, by measuring the orientation at the transition points between these 'p' and 'd' percepts we can measure the direction most influential in this perceptual task. We have labelled this new technique the Oriented CHAracter Recognition Test (OCHART) and use the term 'perceptual upright' (PU) to describe the orientation that it measures.

Here we examine how both the SVV and the PU vary with the relative orientations of the visual background, the posture of the observer, and gravity. Some of these results have been presented in abstract form elsewhere (Dyde et al. 2004; Harris et al. 2004).

Methods

Overview

A simple line probe was used to monitor the SVV using a psychometric variant of the 'luminous line' technique. The 'a' symbol was used to monitor the PU direction using the OCHART technique.¹ All stimuli were presented on a laptop computer screen held rigidly within a specially constructed frame and both techniques (luminous line and OCHART) were run using the same apparatus. In both the techniques, the appropriate test probe was superimposed on a 42° circular background picture which was either rich in visual cues for up (see Fig. 1) or a neutral grey background of the same mean luminance as the polarized display. Peripheral vision was masked off using an obscuring circular shroud. The visually polarized background picture's orientation could be varied. For the OCHART, stimuli were viewed in one of three body postures: upright, right side down and supine (see Fig. 2). The luminous line test was only executed for the upright and right-side-down postures.² Using these combinations of conditions the directions of gravity, the body and the visual background were varied systematically relative to one another and their relative influence on the perceived orientation of the probes assessed.

Observers

Eleven observers between the ages of 22 and 51 (six male and five female) took part in the OCHART test. A partially over-lapping group of 12 observers with the same age range (seven male and five female) performed the luminous line task in an upright posture. Ten of these observers (seven male and three female) also took part in the luminous line task in the right-side-down posture. All observers had normal or corrected to normal vision, and reported no history of vestibular dysfunction. All observers gave their informed consent as required by the Ethics Guidelines of York University which complies with the 1964 Declaration of Helsinki.

¹ The actual font used was sans serif and is illustrated in Fig. 1d.

 $^{^2}$ The luminous line relies on a judgement relative to the axis of gravity. When supine, this is orthogonal to the computer screen which could, therefore, not be measured by this paradigm.

Fig. 1 This figure illustrates how the subjective visual vertical (SVV) (left) and PU (right) were measured. The highly polarized visual backgrounds (a, d) were viewed either with a superimposed line (a) or symbol (d) (see insets). The line projected from the fixation point, the symbol rotated around this same point. Observers chose whether the line was tilted left or right of vertical (a) or whether they thought the symbol was a 'p' or 'd' (d). b, e show typical psychometric functions obtained from such responses. The 50% point was taken as the SVV for the line judgements (b) or the two 50% points were averaged to give the PU (e). The polar plots (\mathbf{c}, \mathbf{f}) show the same psychometric functions (closed circles) but with the complementary data (open circles) to show the percentage of time the opposite choices were made



Convention

The orientation of stimuli, unless otherwise stated, is defined with respect to the body mid-line of the observer. 0° refers to the orientation of the body axis. Positive orientations are clockwise ('rightwards') of this reference point, negative orientations are counter-clockwise ('leftwards') of it, as seen by the observer. For the luminous line, 0° is defined as when the line points straight up relative to the body axis. The ' Ω ' symbol is described as being 0° when the vertical shaft of the symbol is aligned with the body axis with the letter bowl to the right (i.e. the symbol appears as an upright 'p'). Test for subjective visual vertical (luminous line probe)

To measure the SVV, observers were shown a line and asked whether it was tilted counter-clockwise or clockwise from gravitational vertical: 'the direction an object would fall if dropped'. The line stimulus subtended approximately $3.1^{\circ}\times0.45^{\circ}$ of visual arc when upright. The line probe rotated around one endpoint which coincided with the inter-trial fixation point and the origin for rotation of the polarized visual display. The inter-trial circular fixation spot subtended approximately 0.45° of visual arc. Stimuli were presented for 500 ms after which the stimulus was replaced with a grey screen of equal



Fig. 2 The three body postures used in these experiments: upright (a), right side down (b) or supine (c). Subjects viewed the display through a shroud to obscure all peripheral vision. Viewed through the shroud, the screen subtended a 42° diameter circle at a distance of 25 cm

average luminance to the stimulus scene containing a central, circular fixation spot. During stimulus presentation, the controlling software precluded any observer response. Observers responded using the buttons on a game pad. The method of constant stimuli was used. A range of orientations for the probe was selected that spanned the likely SVV and these orientations were each presented ten times. Orientations used were from -25° to 25° in 5° steps for the upright observer and from -100° to -50° for the right-side-down observer, where 0° corresponds to an orientation aligned with the observer's body axis and +ve angles to clockwise rotation. Thus, 90° corresponds to the observer's right and -90° to the observer's left. The probes were superimposed on either a background picture rich in polarized cues (Fig. 1a) which was presented at 18 orientations spaced equally around the clock (i.e. rotated in steps of 22.5° about a point coincident with the point of rotation for the line probe) or a neutral grey background. Thus, there were 190 (10×19) stimulus combinations for the SVV probe and background and each combination was repeated ten times resulting in a total of 1,900 trials for each body orientation. Trials were conducted in two blocks of 950 trials. The presentation of stimuli was randomized within each block. No feedback as to observer performance was given.

For each condition, the percentage of 'counterclockwise' responses was plotted as a function of the orientation of the line and the 50% point obtained from a sigmoid fit to the data (see Fig. 1b). Sigmoids were defined as

$$y = \frac{100}{1 + e^{-((x - x_0)/b)}}\%,$$
(1)

where x_0 corresponds to the 50% point and b is the standard deviation (so that b^2 is the variance). A smaller variance corresponds to a steeper slope of the sigmoid

which indicates an easier, more reliable discrimination by the observer.

Test for perceptual upright (OCHART probe)

To measure the PU, observers were shown the symbol 'and asked whether it was a 'p' or a 'd'. The symbol rotated around its geometric centre which coincided with the inter-trial fixation point. When presented as a 'p' the symbol subtended approximately 3.1°×1.9° of visual arc. The inter-trial circular fixation spot subtended approximately 0.45° of visual arc. Stimuli were presented for 500 ms after which they were replaced with a blank screen of the same mean luminance. Observers responded using the buttons on a game pad after stimulus offset. The method of constant stimuli was used to find the two orientations where the 'a' symbol was equally likely to be perceived as a 'p' or a 'd'. The percentage of times the symbol was identified as a 'p' was plotted as a function of the background orientation (Fig. 1). Two sigmoidal functions (see Eq. 1) were fitted to the observers' responses to determine each of the p-to-d and d-to-p transitions. The average of the two angles at which these two transitions occur was taken as the PU (Fig. 1e). The 'a' symbol was presented at a range of orientations that spanned the likely range of values obtained from pilot studies. This range was in 15° intervals from 30° to 150° and in 15° intervals from -30° to -150° . This set of stimuli was used for all observer postures. The probe was superimposed on a background picture rich in polarized cues (Fig. 1d) which was presented at 18 orientations spaced equally around the clock (i.e. in steps of 22.5°) plus a neutral grey background. Thus, there were 342 (18×19) character/background combinations which were each presented seven times in a random order resulting in a total of 2,394 (342×7) presentations. These were completed in two blocks of 1,197 trials each. The presentation of stimuli was randomized within each block. No feedback as to observer performance was given.

The mean of the standard deviations of each of the two sigmoidal fits used to generate the PU ('b' in Eq. 1) was taken as the standard deviation of the observer's response. Variance is the square of the standard deviation. A smaller variance corresponds to a steeper slope of the sigmoid which corresponds to an easier, more reliable discrimination by the observer.

Stimulus presentation

The stimuli were presented on an Apple iBook laptop computer with a resolution of 48 pixels/cm (21 pixels/ deg). The screen was masked to a circle subtending 42° of visual arc when viewed at 25 cm through a black circular shrouding tube that obscured all peripheral vision (Fig. 2). The laptop was mounted within an aluminium frame to maintain the screen at a fixed angle and to hold the shroud.

Observers viewed the screen either sitting upright on a chair (Fig. 2a), lying right side down on a foam mattress with their head supported by foam blocks to ensure that their head was orthogonal to gravity (Fig. 2b) or lying on their back (supine) with the laptop mounted directly above them with the screen orthogonal to gravity and in their fronto-parallel plane (Fig. 2c).

Results

The effect of visual background orientation and body orientation on the subjective visual vertical

The orientation of the line probe where it was equally likely to be judged tilted clockwise or counter-clockwise from gravitational vertical was taken as the SVV. The SVV is plotted as open symbols in Fig. 3 as a function of the orientation of the visual background for two body orientations: upright (open circles) and right side down (open squares). Figure 3a shows the SVV relative to the observer and Fig. 3b shows the SVV relative to gravity. The SVV was strongly influenced by the orientation of gravity, remaining within 25° of the true direction of gravity at all times. When lying right side down (open squares), the SVV was pulled slightly in the direction of the body (by 11° on average). This shift away from the gravitational 'up' was significant [t(16) = 7.6; P < 0.0001] and can be seen most clearly in Fig. 3b. When the probe was superimposed on the unpolarized background the mean setting when upright was $0.2 \pm 0.6^{\circ}$ and when lying right side down was shifted by $8.4 \pm 2.5^{\circ}$ from the true direction of the gravity towards the body axis [t(20) = 3.6; P < 0.01). This value is plotted as a horizontal dashed line in Fig. 3.

The effect of visual background orientation and body orientation on the perceptual upright

The PU is plotted (filled symbols) as a function of the orientation of the visual background with observers either upright (filled circles), lying on their right side (filled squares) or on their back (filled diamonds) in Fig. 3. Figure 3a shows the orientation of the PU relative to the observer and Fig. 3b shows the orientation relative to gravity. The supine data are plotted only relative to the body. The PU was strongly influenced by the orientation of the visual background, varying by more than $\pm 20^{\circ}$ with the background orientation for each condition.

The PU stayed within 36° of alignment with the body's orientation, even in response to a 90° body tilt. There was, however, a consistent pull towards the direction of gravity in response to lying on the right side,



Fig. 3 The effect of visual background orientation on the SVV measured by the luminous line (*open symbols*) and the PU measured by the OCHART (*closed symbols*) for upright (*circles*), supine (*diamonds*) and right side down (*squares*). The *horizontal dashed grey bars* show the PU and SVV measured with an

unpolarized grey background. **a** The settings are plotted relative to the observer: negative means to the left (counter-clockwise) as indicated by the inset cartoons. *Error bars* represent ± 1 SE of the mean. **b** is a re-plotting of the data from (**a**) reframed to be relative to gravity

with the data shifting by 17° towards the gravitational axis [t(16) = 7.8; P < 0.00001]. With the unpolarized background the mean orientation of the PU was 4.1° $(\pm 1.6^{\circ})$ to the left when the observer was upright. When lying right-side-down, this was shifted further to 12° $(\pm 2.3^{\circ})$ left, i.e. towards the direction of gravity. The difference between the upright and right side down conditions was reliably different [t(5) = 5.2; P < 0.005]. This is plotted as a horizontal dashed line in Fig. 3. Note that it is not possible to compare SVV and PU for the supine condition as SVV was not measurable with the luminous line probe in this posture (see Methods).

Variances of the estimates of PU and SVV

The technique used for obtaining PU and SVV generated psychometric functions of the type shown in Fig. 1. As well as providing points of subjective equality, the slopes of these functions also provide a measure, for each observer, of their within-subject variance of these judgements under each condition. We compared conditions in which one, two or all three of the body, gravity and visual factors were available to determine 'up' in order to deduce the variance associated with each cue alone (see Discussion). Table 1 shows the variances obtained for PU estimates under the following four conditions, and for the SVV under conditions (1) and (3) only.

- 1. Head and body gravitationally vertical, with a gravitationally vertical, polarized, visual background (the conditions shown as '0' in Fig. 3). Here all three factors (body, gravity and vision) can contribute to the judgement of 'up'.
- 2. Lying supine with the polarized visual background aligned with the body axis. Here only body and visual cues can contribute to judgements made in the fron-to-parallel plane as this plane is now orthogonal to gravity.

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- 3. Head and body gravitationally vertical with a featureless grey background. Here only body and gravity cues can contribute.
- 4. Lying supine with a featureless grey background. Here only body cues can contribute.

For PU, the variance was largest when only the body cue was available $(72 \pm 23 \text{ deg}^2)$ and smallest when all three cues were available $(39.2 \pm 11 \text{ deg}^2)$. When only two cues were available (vision and body or body and gravity), intermediate values were found $(49.1 \pm 15 \text{ deg}^2)$ and $49.3 \pm 16 \text{ deg}^2$, respectively). For the SVV, the deviation was much lower than for the PU. The addition of vision reduced the variance from $2.9 \pm 1.1 \text{ deg}^2$ when body and gravity cues were available alone to $0.13 \pm 0.09 \text{ deg}^2$.

Discussion

The SVV as measured by the luminous line test has been used as a measure of up for centuries (for a review, see Bischof 1974). But what is this 'up'? The SVV is explicitly defined in terms of gravity, but is this the direction that influences perceptual judgements? The OCHART test described here demonstrates that it is not.

This study has shown that two different perceptual directions of up can be identified. These are conceptually different directions and it is only a coincidence that they are both called 'up'. We distinguish these directions as the SVV and we have introduced the term PU to describe the second direction. The SVV indicates the perceived direction of gravity whereas the PU indicates the orientation in which objects are most easily recognized. These directions can be dissociated because although the orientation of gravity, body and the visual background affects both measures, there is a larger effect of the visual background orientation on the PU and a larger effect of

Table 1 The variances in deg² obtained in the four conditions listed in the first column. The variances were obtained as the square of the standard deviation provided by the sigmoidal fits through the data sets for each individual observer of the type shown in Fig. 1. Means and standard errors across subjects are given

Conditions	OCHART variance (deg ²)	SVV variance (deg ²)
(i) upright with visual background Cues involved: vision, body and gravity	39.2 ± 11	0.13 ± 0.09
(ii) supine with visual background; Cues involved: vision and body	49.1 ± 15	-
(iii) upright with grey background; Cues involved: body and gravity	49.3 ± 16	2.9 ± 1.1
(iv) supine with grey background; Cues involved: body only	72.0 ± 23	_

gravity on the SVV. Thus when the gravity and body cues are dissociated by lying recumbent, the SVV remains closer to the direction of gravity while the PU remains closer to the body. This is summarized in Fig. 4 in which the width of the shaded segments indicates the total range that the perceived direction of each up can be shifted by tilts of the visual background: the PU and the SVV can diverge and observers hold at least two different 'ups'.

Modelling the influence of the orientations of background, body and gravity on the subjective visual vertical and the perceptual upright

Inspired by the work of Mittelstaedt (1983, 1986), we modelled the effect of visual cues, the body and gravity on the PU and SVV by representing the orientations of these cues as vectors (in their veridical orientations) with lengths proportional to their relative weights as shown in Fig. 5. Although Mittelstaedt suggested this method of analysis, he did not himself collect data with a full range of visual background orientations. Our weighted vector model assumes that the directions of the contributing inputs are coded accurately in each sensory system (but see below for a discussion of the possible role of torsion) and thus has only two variables: the weights of the visual and body vectors relative to the gravity vector. This is considerably simpler than Mittelstaedt's detailed and sophisticated modelling (Mittelstaedt 1983, 1986) which attempts to capture the nuances of the variation of the SVV with changes in the orientation of the visual background (Bischof 1974). Mittelstaedt's model predicts the SVV well at tilts less than 90° although it is prone to failure at larger tilts (Kaptein and Van Gisbergen 2004). Our simple model was fitted to the PU and SVV data sets shown in Fig. 3, and the optimal lengths of the vectors found using an established optimization algorithm (the Marquardt-Levenberg technique, see Press 1988). The best fit to the OCHART data was with weightings of the vision and body vectors of 1.2 (SE±0.1) and 2.6 (SE±0.18), respectively relative to gravity which was arbitrarily assigned the value 1.0. The best fit to the luminous line data was with weightings of the vision and body vectors of 0.1 (SE±0.02) and 0.2 (SE±0.02), respectively relative to gravity (weight = 1.0). The output of the model for all the tested conditions (upright, right side down and supine) is plotted through the data (shown relative to the body) in Fig. 6. The output for the supine condition was obtained by using only two vectors (body and vision) with the



Fig. 5 A weighted vector sum model of how gravity, body orientation and visual cues are summed to generate an estimate of vertical. The prediction is shown by the direction of the *dotted* white line representing the vector sum

Fig. 4 A polar summary in earth coordinates of the extent of the effect of the visual background for the SVV (*solid* grey area) and PU (*hatched* area) for a upright and b rightside-down body postures. The shaded segments indicate the full extent of effect that the orientation of the visual background had on the respective measures



Fig. 6 The results of the weighted vector sum model compared to the experimental data from Fig. 3. Conventions and data as for Fig. 3. The weights assigned to each of the three vectors are given in the inserted table. Note the greater significance of the body in determining the PU, measured by the OCHART, and the strong dominance of gravity in determining the SVV measured by the luminous line test



relative lengths provided above. The model predicts that with no polarized background the SVV should shift by 12.3° from gravitational vertical (actual shift 8.4°) and that the PU should shift by 21° from the body axis (actual shift 12°).

The modelling quantifies the extent to which the PU and SVV are influenced by all three factors and shows that the effects are more evenly weighted in their contributions to the PU. For the PU, the body axis (idiotropic vector) dominates although gravity and visual cues have significant and approximately equal influences. For the SVV gravity was ten times more influential than the visual background and five times more influential than the body axis. Adding non-linear interactions between the terms of the model, as employed by Mittelstaedt (1983, 1986, 1988, 1999) was not necessary to explain most of the data. The ratio of body to vision is approximately 2:1 in both the SVV and the PU: it is their significance relative to gravity that varies. A useful corollary of the fact that the PU is significantly affected by all three factors is that the PU can potentially be used as a sensitive indicator of the functioning of all three systems in a variety of environments and clinical conditions where one or more of the systems may be compromised.

Assigning the weights of the contributing factors

The weighted vector sum model describes the SVV and PU, but how might the relative weights, which differ enormously for the SVV and PU, be assigned by the brain? For the PU, the Bayesian combination can be used to derive the relative weighting of each cue setting them inversely proportional to that cue's variance: more reliable cues are weighted higher (Ernst and Banks 2002;

Hillis et al. 2002). In order to test how well the reliability of the various cues predicted the weightings that gave the best fits in the vector sum model (Figs. 5, 6), we assessed the variance associated with each cue. This method cannot be used for assessing the weights of the SVV because in that case subjects are comparing an internal model of gravity with the orientation of a line. Although we might be able to predict the weightings of the internal representation of gravity, we have no independent measures of how well subjects can set the orientation of a line and the interactions between such settings and the comparison (gravity in this case). Therefore, we restrict our discussion here to assessing the weights of the PU. The variances were obtained from the standard deviations of the psychometric functions of the type shown in Fig. 1e. We were not able to measure the variances associated with each of the three contributing factors separately because, although the contributions of vision and gravity could be temporarily removed by using a blank background or changing body orientation so that gravity was orthogonal to the screen, the body was always present. The variances obtained with the combinations of cues listed in Table 1 were used. Further estimates of the variances for each factor alone and other combinations of factors could then be obtained under the assumption that the reciprocals of variances are additive, e.g. $1/var_{(body,vision,gravity)} =$ $1/var_{(body)} + 1/var_{(gravity)} + 1/var_{(vision)}$.

Least-squares analysis of the variances obtained under the four conditions listed in Table 1 provided best estimates of the variances due to each factor. These are listed in Table 2. The reciprocals of these variances, normalized to gravity = 1, resulted in relative weightings of body:vision:gravity of 2.5:1.0:1.

Table 2 compares these values with the weighting obtained from the vector fit modelling described above.

Table 2 Weightings predicted from the inverse of the variances, compared to the weightings of the vector sum model for the perceptual upright (PU). The rows shaded in pale grey are the ratios derived from the variance analysis which are to be compared to the rows shaded in darker grey which are deduced from the vector analysis (see Fig. 6)

PERCEPTUAL UPRIGHT				
	Weighting	Weighting of	Weighting of	
	of the body	gravity	vision	
Estimates of variance	70.4	173.3	170.9	
Reciprocals	0.014	0.0057	0.0059	
Normalized to g	2.5	1	1.0	
Weightings from fig. 6	2.6	1	1.2	

There is a remarkable agreement between the two methods of arriving at the weights. Fitting three vectors produces a ratio of 2.6:1.2:1 between body, vision and gravity (see Fig. 6) whereas the weightings derived from the variances produce a ratio of 2.5:1.01:1 (see Table 2). This is the first time that the weightings between different reference frames have been confirmed as corresponding to a Bayesian model.

Inter-subject variation

The presentation of the results and the subsequent modelling pooled the data across subjects. Since the early investigations in this field, using the rod-and-frame test, it has been known that there is considerable variation between subjects in how susceptible their SVVs are to visual influence (Asch and Witkin 1948). People who's SVV is shifted most are described as 'field dependent' and there are correlations between field dependence and gender and age (Nyborg 1980; see Howard 1982). Our subjects also showed considerable variability in how much their judgements of both SVV and PU were influenced by gravity, visual background and the body axis. For all subjects, however, the distribution of the weightings of these cues was comparatively even when they were combined to determine the PU, whereas gravity overwhelmingly dominated vision and the body in determining the SVV. This evenness of influence of the three cues on the PU makes the OCHART technique, which assesses the PU, more sensitive to individual differences between any of the cues. Inter-subject variations and the correlation of the SVV and PU with each other and with other factors such as gender and age are the subject of ongoing research.

Role of ocular torsion

Our modelling assumes that the directions of the three contributing factors (body, vision and gravity) are

known and do not show systematic biases. However, lying on one side causes the eyes to roll in the opposite direction to the head tilt (Miller and Gravbiel 1971; Bockisch and Haslwanter 2001) which might complicate the interpretation of the orientation of the visual background. Such ocular counter-roll is stable over many hours for a given head tilt (Miller and Graybiel 1972). Ocular counter-roll has been reported to have a significant effect on measurement of the SVV (Wade and Curthoys 1997) implying that torsion is not taken into account and that therefore SVV judgements are made relative to a retinal axis. However, other experiments indicate that there can be compensation for the torsional position of the eye (Mast 2000). When subjects were tilted right side down, the fit of the model's output to the data could be improved if the orientation of the visual vector was rotated slightly in the clockwise direction (i.e. the model's output curve slid to the left along the axis of Fig. 6). This small systematic displacement of the data from the model's prediction is in the correct direction to be at least partially explained by an uncompensated torsional eye displacement. However, the magnitude of our shifts is much larger than would be expected from counter-roll due to tilt relative to gravity alone (Miller and Graybiel 1971; Bockisch and Haslwanter 2001) and much larger than the torsion expected due to rotation of the background (Goodenough et al. 1979; Howard and Templeton 1964). Although torsional eye position influences the SVV and PU, the shifting of the SVV and PU with vision and body tilt can largely be explained by the vector sum model without reference to torsional eye position.

Application of the OCHART

It is of practical importance to be able to predict the perception of verticality in unusual circumstances such as in a moving vehicle or while in microgravity (Mars et al. 2004; Jenkin et al. 2005). Furthermore, knowing the normal effect of the sensory contributions to the SVV and PU allows these measured directions to be used as an objective clinical test of sensory function. The usefulness of the SVV in both these regards has, however, been limited by the complex interactions of the various systems involved. Despite the extensive use of the SVV, surprisingly few studies have actually investigated these interactions, research mostly having concentrated on the effect of body orientation relative to gravity (see for typical examples, Guerraz et al. 1998; Van Beuzekom and Van Gisbergen 2000; Guerraz et al. 1998) and even here the SVV cannot be linked to the perception of body posture (Kaptein and Van Gisbergen 2004). Here we show that for the PU, the influence of the orientation of the visual background is large and systematic and can be predicted from a simple model whose weightings are assigned according to the reliability of the contributing cues in agreement with what appears to be the emerging principles of multisensory integration.

The co-existence of the PU and SVV confirms that we have at least two perceptual up directions each involved in different aspects of perception and each influenced differently by the orientation of the body, visual scene and gravity. We postulate that as in the dissociation between visual and somatosensory measures of verticality (Bronstein et al. 2003; Wade and Curthoys 1997) SVV and PU may serve different needs. We speculate that the SVV and PU may correspond to the orientation reference directions most relevant to spatial vision and pattern perception, respectively. The SVV is closely tied to physical gravity (see Fig. 4) and may be most involved in controlling action. The SVV becomes meaningless when the direction of gravity is unspecified as is the case in microgravity environments. The PU is most likely tied to the optimal orientation to view objects for perceptual or recognition tasks (see Rock and Heimer 1957; Corballis et al. 1978; Rock and Heimer 1957; Jolicoeur 1985). Here we have measured the PU through the interpretation of an ambiguous symbol; other tests with which it correlates well include the orientation at which a flat shaded disc appears most convex (e.g. Jenkin et al. 2004). Further research is required to clarify the nature of the difference between SVV and PU.

The relative weightings of the three factors that generate the PU quantify for the first time the relative influence of body, background visual cues and gravity on object recognition and is commensurate with the emerging realization of the relative significance of both exocentric and egocentric factors in visual perception (Milner and Goodale 1995; Wexler et al. 2001a, b). By using the simple model presented here we can predict the circumstances when the SVV and PU will differ, and identify the ideal orientation for an object to be recognized when posture, gravity and the visual background are either misaligned or ambiguous.

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