Exp Brain Res (2004) 155: 385–392
DOI 10.1007/s00221-003-1742-8

RESEARCH ARTICLES

L. Bringoux · K. Tamura · M. Faldon · M. A. Gresty · A. M. Bronstein

Influence of whole-body pitch tilt and kinesthetic cues on the perceived gravity-referenced eye level

Received: 7 February 2003 / Accepted: 24 September 2003 / Published online: 9 December 2003

Abstract We investigated the effects of whole body tilt and lifting the arm against gravity on perceptual estimates of the Gravity-Referenced Eye Level (GREL), which corresponds to the subjective earth-referenced horizon. The results showed that the perceived GREL was influenced by body tilt, that is, lowered with forward tilt and elevated with backward tilt of the body. GREL estimates obtained by arm movements without vision were more biased by whole-body tilt than purely visual estimates. Strikingly, visual GREL estimates became more dependent on whole-body tilt when the indication of level was obtained by arm lifting. These findings indicate that active motor involvement and/or the addition of kinesthetic information increases the body tilt-induced bias when making GREL judgements. The introduction of motor/kinaesthetic cues may induce a switch from a semi-geocentric to a more egocentric frame of reference. This result challenges the assumption that combining non-conflicting multiple sensory inputs and/or using intermodal information provided during action should improve perceptual performance.

Keywords Perception · Horizon · Body orientation · Kinesthetic system · Frame of reference

L. Bringoux · K. Tamura · M. Faldon · M. A. Gresty · A. M. Bronstein (✉)
Department of Neuro-Otology, Division of Neuroscience and Psychological Medicine, Imperial College—Faculty of Medicine, Charing Cross Hospital,
Fulham Palace Road,
London, W6 8RF, UK
e-mail: a.bronstein@ic.ac.uk
Tel.: +44-20-88467523
Fax: +44-20-88467577

L. Bringoux
UMR CNRS 6559 'Mouvement et Perception', Faculté des Sciences du Sport, Université de la Méditerranée,
Marseille, France

Introduction

The perceived eye level is commonly considered as a cardinal reference for distance judgement (Ooi et al. 2001) and for up and down egocentric location (Li et al. 2001; Matin and Li 1995). For instance, when observers in complete darkness state that a luminous visual object appears to be higher or lower than themselves, location is specified to their perception of their own eye level (Raphel and Barraud 1994; Stoper and Cohen 1989). However, in the simplest circumstances, "eye level" can be referred to a plane parallel to the transverse plane of the head (i.e. head-referenced eye level, HREL), or normal to the direction of gravity (i.e. gravity-referenced eye level, GREL; Stoper and Cohen 1989). It should be noted that these planes are coincident when the observer is stationary and erect, but differ when the observer is tilted forward or backward.

Whereas HREL judgements can be assessed in a purely egocentric frame of reference, GREL estimates require to adjust the perceived horizontal direction to eye level, that is to link an external system of coordinates with an egocentric component (Howard 1986). Consequently, the nature of the task, for instance, asking a subject to look "straight ahead" (i.e. HREL judgement) or to look at the "earth horizon" (i.e. GREL judgement) would certainly lead to different results when the body is tilted. Similarly, purely geocentric tasks such as subjective visual vertical or horizontal estimates in the pitch plane (Correia et al. 1968; Ebenholtz 1970) cannot directly be compared to GREL judgements, since they did not specifically rely on eye level (i.e. egocentric component). Nevertheless, any environmental influence on GREL estimates will have important repercussions in the perception of the external space.

This paper aims then at investigating the perception of GREL for different whole-body pitch orientations and under different sensorimotor conditions.

It has been shown that the visually perceived GREL in darkness when the head is upright is lower than the true eye level (i.e. the physical plane passing through the eyes and normal to gravity; Raphel and Barraud 1994), but remains nevertheless highly consistent and accurate (Mc Dougall 1903; Stoper and Cohen 1986). Pitching of the visual environment largely influences GREL estimates with respect to true eye level, from 12 deg downward for 20° forward tilts of the visual field to 11 deg backward for 20° backward tilts of the visual field (Matin and Li 1992). However, this effect is independent of the pitch head orientation over a ±20° range.

Schöne (1964) investigated the influence of different head and body pitch orientations on the GREL perception in darkness under different gravity field strengths. To that purpose, subjects sat in a swing-out centrifuge, able to generate gravitational force levels from 1 to 1.9 g. Head and body pitch position ranged from 30° backward to 20° forward. Judgements were found to be highly modified by body tilt under increased field strength. For instance, GREL estimates varied from about 15 deg upward for −20° backward body tilts to 10 deg downward for 20° forward body tilts under 1.6 g. However, as mentioned by the author himself, the GREL in normogravity was perceived "approximately correctly" within the tested range of body tilt. It should be pointed out, however, that the axis scale of the reported figures in this paper were chosen for representing the large effects of hypergravity on GREL estimates, but could have hidden any weaker potential effects under 1 g. Moreover, GREL values at different tilts under 1 g were not statistically analysed in that study.

On the other hand, a recent experiment suggests that GREL perception is influenced by pitch head orientation in complete darkness when the subject's whole-body is slowly rotated (Bourdin et al. 2001). In that situation, the absolute errors in visually adjusting the GREL are directly proportional to the up-to-8° pitch tilt. The shifts in GREL estimates induced by body tilt might have been the consequence of head tilt underestimation due to the extremely slow pattern of rotation ($\omega = 0.05°.s^{-1}$), well below the semicircular canals' threshold (Benson 1990). The first purpose of the present study is thus to investigate whether a comparable GREL perceptual shift can be induced by suprathreshold whole-body rotations to greater angles of pitch tilt.

The second aspect of this work relates to the fact that most experiments involving visual GREL settings were carried out through passive assessments with immobilised subjects, in spite of the fact that numerous studies have shown that action can improve perception (cf. Viviani 1990, for a review). In this respect, Ballinger (1988) investigated the effect of pointing movements on the visually perceived GREL in upright subjects facing a tilted visual field. The magnitude of the mean pointing error due to the tilted visual field was approximately half of the magnitude of the mean error assessed verbally. However, the subjects were not successful at pointing to eye level when they could not see their hand in relation to their surroundings. Fouque et al. (1999) investigated the influence of motor-kinesthetic involvement on the visually perceived HREL (i.e. egocentric judgement) for different whole-body pitch tilts. Comparing passive estimates with pointing errors towards remembered targets located at HREL, the authors concluded that the action of pointing improves the accuracy of judging eye level. However, the presence of a conflicting visual field for HREL passive estimates (e.g. upright visual field with body tilted or vice versa) as well as the difference of task between passive and active conditions (i.e. adjusting a target at a certain height vs. pointing towards a flashed memorized target) might have led to such results.

Nevertheless, recent data suggested that arm lifting movements do provide information about orientation in space by generating additional cues about the direction of gravity (Gooey et al. 2000; Luyat et al. 2001). For instance, the dynamic gravitational torque generated by arm lifting movements may be involved in limb position sense in space (Bock 1994; Gooey et al. 2000; Worringham and Stelmach 1985) and may improve a more general geocentric perception about the direction of gravity (Fitger 1976; Gentaz and Hatwell 1996; Luyat et al. 2001), the latter being involved in GREL judgements (Stoper and Cohen 1989). The second purpose of the present study is then to investigate whether judgements made with active arm lifting movements (i.e. "motor-kinesthetic involvement") can lead to increased accuracy of GREL estimates performed during whole-body tilts.

Herewith we report two experiments, for which we hypothesized that the perceptual GREL estimates would be influenced by whole-body tilt as well as by the method of assessment (i.e. the use of arm movement). More precisely, we expected that large body pitch tilts would lead to a consistent perceptual shift of the GREL in the direction of tilt, which could be attenuated when the moving arm is involved in the judgement.

Material and methods

Subjects

A total of 17 healthy subjects gave informed consent to participate in the present study according to local ethic committee guidance and the Helsinki convention. Ten subjects (five males and five females ranging from 22 to 48 years, mean age = 28±5.7 years) took part in Experiment 1. Three of them also took part in Experiment 2, together with seven new subjects (six males and four females ranging from 22 to 51 years, mean age = 32 years).

Apparatus

The subjects were seated and tightly restrained in a padded chair with a four-points pilot seat belt (Fig. 1A). The chair was supported between bearings within an earth fixed supporting frame and its position could be adjusted so that the subjects' trans-ocular axis coincided with its axis of rotation. The chair was motorized and rotated slowly in pitch. The subjects' head, oriented in the natural upright position when the plane of the seat back was parallel to the gravitational vertical, was firmly restrained by a headrest and a bite bar fixed to the chair frame. Backward and forward tilts were delivered at a constant velocity of $1.5\ deg.s^{-1}$, with initial accelerations and final decelerations ($1.5\ deg.s^{-2}$) above the semicircular canals' threshold (Benson 1990).

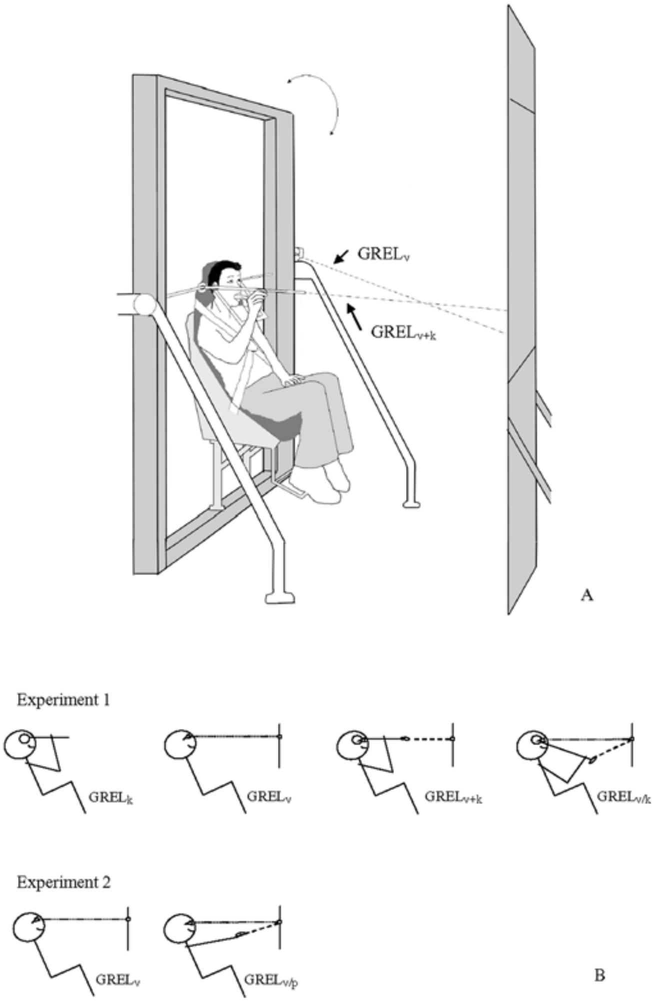


Fig. 1. A Illustration of the experimental setup. The motorized chair rotated around the inter-ocular axis. **B** Schematic representation of the experimental conditions tested in the two experiments

In Experiment 1, GREL estimates were performed by manually adjusting the orientation of a tilting rod, pivoted at eye level, or by setting the height of a small adjustable laser dot projected on a board placed at 1.5 m from the subjects remotely with a dial. The tilting rod (length: 65 cm; diameter: 1 cm) was free to rotate in pitch about one end which was mounted in a bearing fixed to the body tilting device and aligned at the level of the subjects' trans-ocular axis. Subjects were thus able to move the rod up or down with their right hand to adjust its sagittal orientation. The laser pointer was free to rotate about its long axis and was mounted on a small, motorized support, external to the tilting device and coincident with the chair rotation axis. Alternatively the laser pointer could be fixed to the end of the tilting rod at different relative orientations in pitch. The external laser pointer was either controlled by the experimenter or by the subjects themselves, by means of a remote control dial, so that the beam could be positioned vertically in the sagittal plane. The rod and the external laser pointer were connected to a potentiometer, which recorded angular position with an accuracy of 0.05 deg.

In Experiment 2, GREL judgements were either performed by setting the height of the projected laser beam via the dial controlled laser pointer as in Experiment 1, or via arm pointing with the laser fixed with adhesive tape onto the subjects' index finger. For this experiment, measures were directly taken from the dot location on the board, which was recovered with a grid (Fick coordinates; i.e. angular projections on a plane surface). A dim blue light diffused in the experimental room allowed recordings of the dot position with respect to the grid. Subjects wore blue filter goggles, so they could not see the grid.

Procedure

The subjects' task was to judge in darkness their perceived GREL, defined as the plane through the eyes, which is always parallel to the floor. Subjects were also indicated that its projection corresponds to their perceived horizon, defined as "where the sky meets the sea". Drawings illustrating the experimental conditions and the objective GREL plane with tilted subjects (Fig. 1B) were finally presented to avoid any confusion about the nature of the judgement required.

In Experiment 1, the four experimental conditions required the subjects to perform the task 1) under purely kinesthetic control without vision, by setting the orientation of the rod through arm lifting (GREL$_{k}$); 2) under purely visual control without arm movement, by setting the height of the visual target provided by the external laser pointer via the remote control (GREL$_{v}$.); 3) under visual and kinesthetic control, by setting the height of the visual target provided by the rod-fixed laser through arm lifting. In this condition, both the rod and the laser were co-planar (i.e. coplanar visual and kinesthetic information: GREL$_{v+k}$); and 4) under visual control with no "goal-directed" kinesthetic information, by replicating the same condition as in 3, except that the sagittal orientations of the rod and the laser were divergent about 20° (i.e. non-coplanar visual and kinesthetic information: GREL$_{v/k}$). In Experiment 2, two conditions were presented. The first one replicated the GREL$_{v}$ protocol. For the second condition, subjects used natural arm pointing movements to project the visual dot towards their perceived GREL (GREL$_{v/p}$). Subjects were asked to concentrate on the visual dot location rather than on arm position.

The experimental conditions were randomly presented in separate sessions lasting 30–45 min. Six whole-body pitch orientations were deployed (upright; backward tilts: 10°, 20°, 30°; forward tilts: −10°, −20°). Larger angles of tilt would have interfered with the visual perception of the target onto the board. A session began and ended in "upright" position, between which subjects were tilted randomly into successive pitch orientations. Ten GREL estimates were executed for each orientation within a time interval of 2 min. Once tilted, the subjects waited still during approximately 20 s (allowing the semi-circular canals' response to be close to zero) before being asked to perform their first setting. They were told to keep their eyes closed during the entire experiment (GREL$_{k}$) or before and after each visual setting (GREL$_{v}$; GREL$_{v+k}$; GREL$_{v/k}$; GREL$_{v/p}$). This allowed the experimenter to position the visual target at a random location, above or below the physical projection of GREL (GREL$_{v}$), or the subjects to bring back the rod or their arm in the same initial resting position (GREL$_{k}$; GREL$_{v+k}$; GREL$_{v/k}$; GREL$_{v/p}$). Once the ten settings were performed, the chair was brought back to the upright for 20 s before a new re-orientation was presented.

Results

Experiment 1

When seated upright, subjects tended to estimate their perceived GREL lower than the physical reference (i.e. true eye level) for all the conditions (mean position: −2.4 deg). No significant difference was found between conditions in this upright orientation.

In order to test whether there is a linear relationship between perceived GREL and whole-body tilt, a linear regression analysis was applied to the mean individual data recorded in the six body orientations for each of the four experimental conditions. The results, summarized in

Table 1, showed a significant linear influence of the angle of tilt on GREL$_k$ ($F_{(1,58)}=27.82$; $p<.001$), GREL$_v$ ($F_{(1,58)}=5.93$; $p<.01$), GREL$_{v+k}$ ($F_{(1,58)}=13.57$; $p<.001$), and GREL$_{v/k}$($F_{(1,58)}=26.35$; $p<.001$). All GREL estimates seemed to be lowered with forward tilts and elevated with backward tilts (Fig. 2).

In order to study the magnitude of this "body tilt effect" (that is, the displacement of GREL in the direction of the tilted body) in each of the experimental conditions, an analysis of variance (ANOVA) was applied to the slope coefficients calculated for each individual regression line in the four experimental conditions. Results showed a main effect of condition, i.e. a difference in the magnitude of the body tilt influence upon GREL settings according to condition ($F_{(3,27)}=12.15$; $p<.001$). Post hoc analyses (Newman-Keuls test) showed that the tilt effect was not significantly different between GREL$_v$ and GREL$_{v+k}$. However, it became significantly higher for GREL$_{v/k}$vs. GREL$_v$($p<.05$) and for GREL$_k$vs. GREL$_{v/k}$ ($p<.01$; Fig. 3).

In order to determine whether response variability was affected by the experimental condition, an ANOVA was performed on the mean intra-subjects standard deviations. A main effect of the experimental condition was found ($F_{(3,27)}=24.13$; $p<.001$). Post-hoc analyses (Newman-Keuls test) showed that the GREL$_{v+k}$ and GREL$_{v/k}$ conditions yielded a lower intra-subjects' variability than the GREL$_v$ condition ($p<.05$), whereas the GREL$_k$ condition yielded a higher intra-subjects' variability than all other conditions ($p<.001$; Fig. 4).

Experiment 2

GREL settings performed in upright body orientation appeared also lower than the physical reference for both conditions (mean position: −2.2 deg). No significant difference was found between the conditions in this vertical body orientation.

The linear regression analysis, applied to the mean individual GREL estimates recorded in the six body orientations for each experimental condition, showed a significant linear influence of the angle of tilt on GREL$_v$ ($F_{(1,58)}=5.62$; $p<.05$), and GREL$_{v/p}$($F_{(1,58)}=70.63$; $p<.001$; Table 2). GREL estimates were again lowered with forward tilts and elevated with backward tilts (Fig. 5).

A *t*-test, between the slope coefficients calculated for each individual regression trend line in the two experimental conditions, showed that these were statistically different, reflecting a difference in the magnitude of the body tilt influence ($t(9)=-3.90$; $p<.01$; Fig. 6). This indicates that using the outstretched arm to assess visual estimates of GREL (GREL$_{v/p}$) increased the "body tilt effect".

Table 1 Results of the linear regression analysis between the mean individual GREL estimates and the different body orientations in pitch (Experiment 1)

Experimental conditions	β	R^2	*p*<	*Slope coefficient*
GREL$_k$	.57	.32	.001	.34
GREL$_v$	.31	.09	.01	.07
GREL$_{v+k}$	.44	.19	.001	.11
GREL$_{v/k}$	.56	.31	.001	.18

Table 2 Results of the linear regression analysis between the mean individual GREL estimates and the different body orientations in pitch (Experiment 2)

Experimental conditions	β	R^2	*p*<	*Slope coefficient*
GREL$_v$	.30	.09	.05	.07
GREL$_{v/p}$	.74	.55	.001	.19

A *t*-test was conducted on the mean intra-subjects standard deviations of the GREL estimates for the two experimental conditions to analyse the variability of subject's performance. It revealed that intra-subject variability was lower when visual GREL was assessed through arm pointing movements ($t(9)=5.20$; $p<.001$; Fig. 7).

Discussion

In the present experiments, all GREL estimates recorded in upright body orientation were consistently lower than the physical reference (i.e. below the earth-referenced horizon or "true" horizontal eye level), in agreement with the data reported in the literature (Raphel and Barraud 1994; Stoper and Cohen 1986). In addition, our study shows the existence of a main effect of body orientation on the perceived GREL, namely a linear attraction of the GREL estimates towards the tilted body, at our stimulus parameters. More strikingly, this influence extended to perceptual judgements involving different sensory modalities and/or different levels of motor activity. The second main finding of this study is the absence of perceptual improvement in GREL judgements (i.e. in terms of a lower dependency on body orientation) when arm movements were used (motor-kinesthetic involvement). Even adding a kinesthetic component to a visual assessment (GREL$_{v/k}$) led to an increasing influence of body tilt, compared with a passive visual task (GREL$_v$).

Regarding the first aim of the present study, our results confirm that GREL perception is not invariant in total darkness, but appears to be dependent on body orientation. Bourdin et al. (2001) showed a similar linear shift of GREL estimates towards the tilted body for rotations well below semicircular canals threshold rotations and small pitch angles. Our results indicate that it is possible to generalize this influence to larger body tilts induced by suprathreshold rotations. Taken together, the findings have important consequences for the manner observers judge the height of an object with respect to external space. For instance, the concomitant elevation of GREL with backward tilts found in this study would imply a relative lowering of the perceived location of an immobile target in a dark environment. Schöne (1964) has already suggested

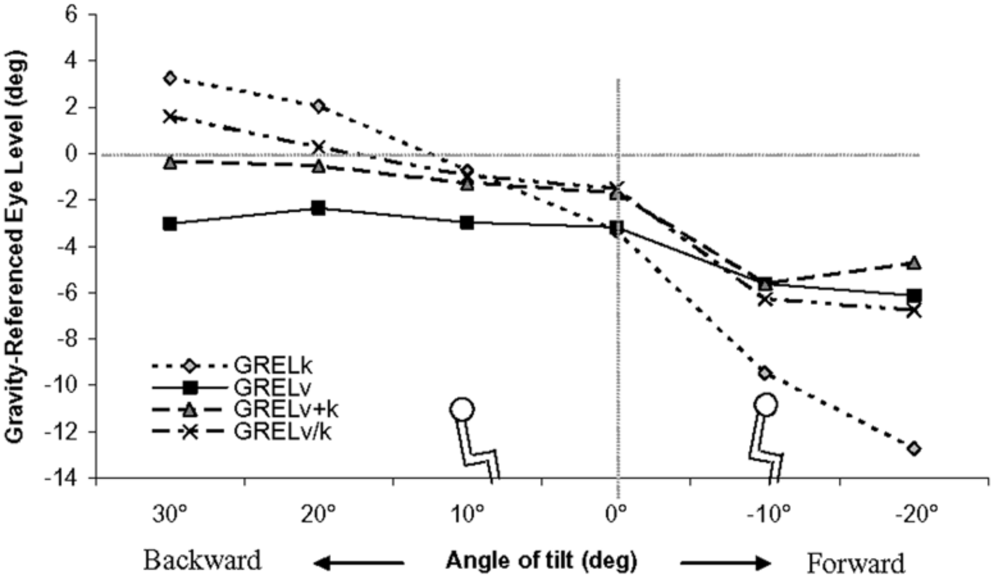


Fig. 2 Mean perceived GREL with respect to whole-body tilt for the four experimental conditions (Experiment 1)

that “under the influence of increased field strength, the space appears to shift in the same direction as the movement of the head”. Our findings enable us to extend the influence of head and body orientation, in a smaller scale but consistently, to a normogravity environment.

Such results can be interpreted in terms of body tilt underestimation. Subjects would adjust the spatial reference as if they were less tilted than they actually were, suggestive of a failure of the graviceptive sensory systems needed to correctly perform the necessary transformation of coordinates required by the task (Schöne 1964). This hypothesis is comparable to explanations of the Aubert-effect for subjective visual vertical estimates (Lechner-Steinleitner 1978). However, several studies showed that there is no direct link between the estimated body orientation and the perception of geographical directions such as vertical or horizontal (van Beuzekom and van Gisbergen 2000; Bronstein 1999; Ebenholtz 1970; Mast and Jarchow 1996; Mittelstaedt 1995).

An alternative to the tilt underestimation hypothesis could emerge from the analysis of the task constraints of the present experiments. Since estimating the GREL consists of selecting, amongst all the horizontal planes (geocentric component), the one which passes through the eyes (egocentric component), the task involves a semi-geocentric frame of reference. The effect of tilting the body on GREL estimates could then be interpreted as a bias induced by the egocentric component of the task. This interpretation is in line with the idiotropic vector hypothesis formulated for subjective visual vertical estimates (Mittelstaedt 1983; 1999), that is, a central tendency to shift judgements towards the subjects’ own longitudinal axis. A comparable “egocentric attraction” was also reported in previous reports involving geocentric judgements, showing that head or body tilt can affect the hand orientation with respect to earth-fixed horizontal (Chelette et al. 1995) or the forearm orientation relative to earth fixed vertical (Darling and Hondzinski 1999).

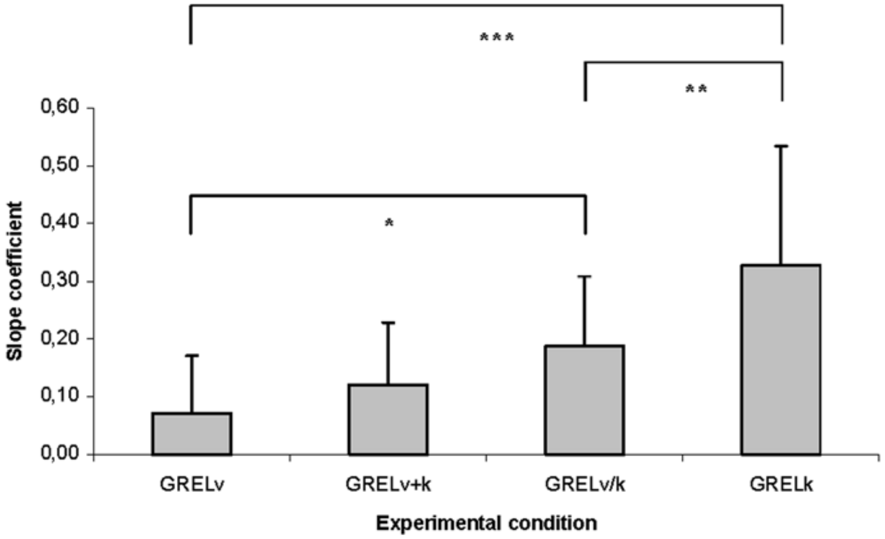
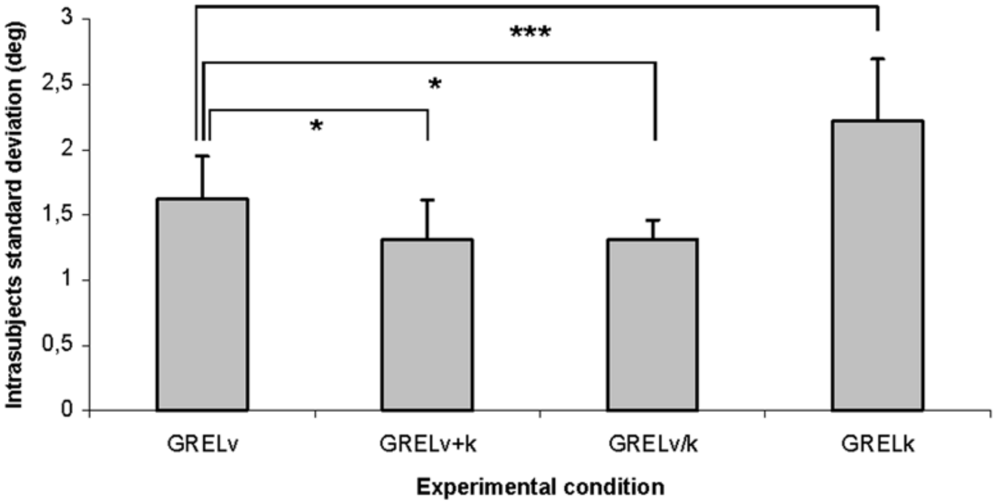


Fig. 3 Mean slope coefficient of the linear regression trend lines between the mean individual GREL estimates and the different body orientations, and inter-subjects standard deviation for the four experimental conditions (Experiment 1). The slope coefficient represents the weight of the “body tilt effect”, i.e the shift of GREL estimates towards the body tilt

Fig. 4 Mean intra-subject variability and inter-subjects standard deviation for the four experimental conditions (Experiment 1)



The second major finding of this study is the influence of experimental condition upon the general tilt effect discussed above. GREL estimates performed through arm movement only (GREL$_k$) or visually performed with non goal-directed arm movement (GREL$_{v/k}$ or GREL$_{v/p}$) were more dependent on body orientation than purely visual settings (GREL$_v$). Therefore, the results do not support the hypothesis that arm movements against gravity should reduce the tilt-based shift in GREL settings.

Bock (1994) and Gooey et al. (2000) showed that arm position sense was significantly improved or became less variable when gravity cues were not disturbed compared with weightless environments or when adjustable loads were added to the arm. These observations suggested that lifting the arm in normal circumstances on earth might provide additional positional information about arm orientation in space. Although still under discussion, several studies have shown that the gravitationally generated torque around the shoulder of an extended arm could be involved in arm position sense (Darling and Miller 1995; Worringham and Stelmach 1985) and also in a more general perception about the direction of gravity (Fitger 1976; Gentaz and Hatwell 1996; Luyat et al. 2001). Considering these findings, we expected that any additional gravitational cues would help the subjects in perceiving their own body orientation better, and would thus lead to reduce the tilt effect on GREL estimates. However, our data suggested that there is no direct link between the perception of body orientation and the judgement of a semi-geocentric reference such as GREL. If arm movements provide any additional input for perceiving body position in space, they nevertheless seem to enhance the GREL shift towards the subjects' longitudinal axis. These findings indicate that active motor involvement and/or the addition of kinesthetic input to the GREL estimates acts as a perturbing factor, inducing a switch towards a more egocentric frame of reference. This calls into question the assumption that summing non-conflicting multiple sensory inputs (Howard 1997) or using intermodal information arising from action (Fouque et al. 1999) should systematically improve perceptual performance. For tasks defined in a purely geocentric

Fig. 5 Mean perceived GREL with respect to whole-body tilt for the two experimental conditions (Experiment 2)

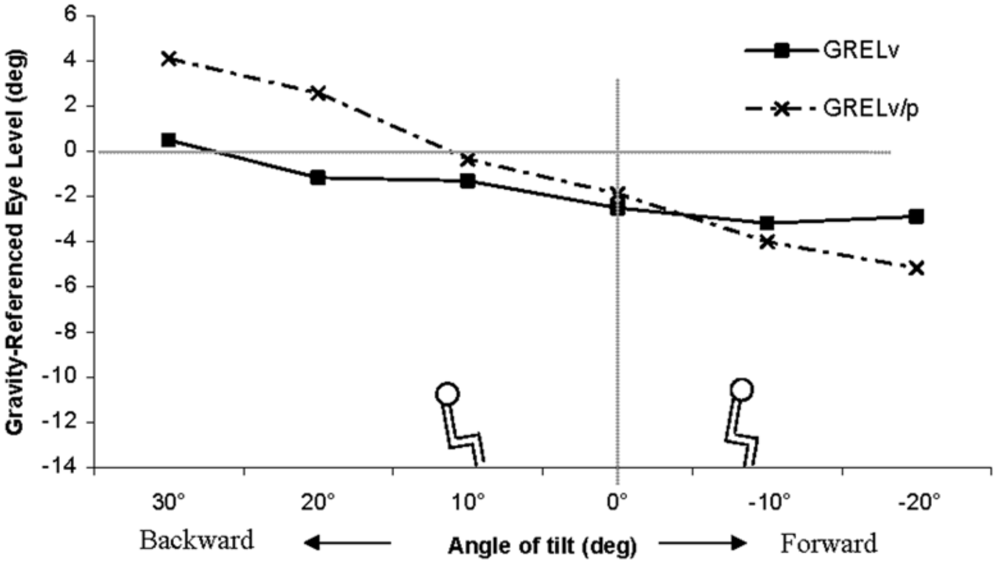


Fig. 6 Mean slope coefficient of the linear regression trend lines between the mean individual GREL estimates and the different body orientations, and inter-subjects standard deviation for the two experimental conditions (Experiment 2)

frame of reference such as the subjective vertical (Luyat et al. 2001) or the subjective zenith (Mittelstaedt 1983) assessed haptically, additional arm gravitational cues offered by arm lifting can be helpful. However, in the present semi-geocentric tasks, the movement of the arm can reinforce the egocentric component of the frame of reference used.

One might argue nevertheless that lifting a rod against gravity with a bent arm (Experiment 1) could require a more complicated transformation of coordinates, providing less precise or relevant kinesthetic information than would be obtained from reaching an outstretched arm through a more natural pointing movement (Experiment 2). As proposed by Gooey et al. (2000), the brain could assign a particular significance to kinesthetic cues when movements are performed through natural patterns often experienced. However, both experiments led to the same increase of the tilt effect on visual GREL estimates when using an additional arm movement ($GREL_{v/k}$ or $GREL_{v/p}$). Therefore, whether the movement was natural or not, adding a motor-kinesthetic component to the task interfered with the subjects' perception. On the other hand, analysis of the intra-subject standard deviations showed that combining visual and kinesthetic information ($GREL_{v+k}$; $GREL_{v/k}$; $GREL_{v/p}$) reduced the perceptual variability with respect to that measured for estimates involving a single sensory channel ($GREL_v$ $GREL_k$), as predicted by Bayes' law (Ernst and Banks 2002). This finding also has a correlate in the visual vertical. Whereas the tilt-induced bias known as "A-effect" disappears when a hemi-anesthetic patient lies on the anesthetic side, variability and inconsistency of visual vertical estimates rise significantly (Anastasopoulos and Bronstein 1999).

In conclusion, the present study demonstrates that the perception of the Gravity-Referenced Eye Level can be modified by body tilt and motor-kinesthetic involvement. These two factors might depend on the same cognitive process consisting in a more or less pronounced shift from a semi-geocentric frame of reference to a more egocentric frame of reference. This interpretation is supported by recent work, suggesting that egocentric and geocentric frames of reference are pre-existing neurophysiological structures between which subjects could switch easily, depending on the task demand (Ghafouri et al. 2002). These findings could be of value in man-machine interfaces where subjects have to accurately locate their perceptual horizon and related objects in a visually impoverished environment.

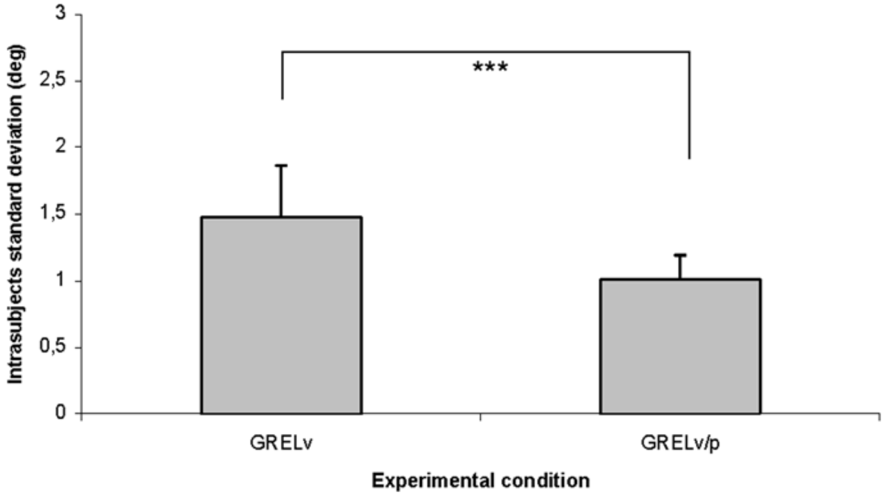


Fig. 7 Mean intra-subject variability and inter-subjects standard deviation for the two experimental conditions (Experiment 2)

Acknowledgements This work was supported by the Medical Research Council of the UK, by a post-doctoral study grant from the Fyssen Foundation and by the European Commission Improving Human Potential Programme, contract number HPRI-CT-1999-00025.

References

Anastasopoulos D, Bronstein AM (1999) A case of thalamic syndrome: somatosensory influence on visual orientation. J Neurol Neurosurg Psychiatry 67:390–394

Ballinger CJ (1988) The effect of a pitch field orientation on hand-eye coordination. Master Thesis. Naval Postgraduate School, Monterey, CA

Benson AJ (1990) Sensory functions and limitations of the vestibular system. In: Warren R, Wertheim AH (eds) Perception and control of self-motion. Erlbaum, Hillsdale New-Jersey, pp 145–170

Beuzekom AD van, Gisbergen JAM van (2001) The subjective vertical and the sense of self orientation during active body tilt. Vision Res 41:3229–3242

Bock 0 (1994) Joint position sense in simulated changed-gravity environments. Aviat Space Environ Med 65:621–626

Bourdin C, Nougier V, Bringoux L, Gauthier GM, Barraud PA, Raphel C (2001) Accuracy level of pointing movements performed during slow passive whole-body rotations. Exp Brain Res 138:62–70

Bronstein AM (1999) The interaction of otolith and proprioceptive information in the perception of verticality: the effects of labyrinthine and CNS disease. Ann N Y Acad Sci 871:324–333

Chelette TL, Martin EJ, Albery WB (1995) The effect of head tilt on perception of self-orientation while in a greater than one G environment. J Vestib Res 5:1–17

Correia MJ, Hixson WC, Niven JI (1968) On predictive equations for subjective judgments of vertical and horizon in a force field. Acta Otolaryngol Suppl 230:1–20

Darling WG, Hondzinski JM (1999) Kinesthetic perceptions of earth- and body-fixed axes. Exp Brain Res 126:417–430

Darling WG, Miller GF (1995) Perception of arm orientation in three-dimensional space. Exp Brain Res 102:495–502

Ebenholtz SM (1970) Perception of the vertical with body tilt in the median plane. J Exp Psychol Hum Percept Perform 83:1–6

Ernst MO, Banks MS (2002) Humans integrate visual and haptic information in a statistically optimal fashion. Nature 415:429–433

Fitger C (1976) Tactile-kinesthetic space estimation: the influence of gravity. Psychol Rev 39:113–135

Fouque F, Bardy BG, Stoffregen TA, Bootsma RJ (1999) Action and intermodal information influence the perception of orientation. Ecol Psychol 11:1–43

Gentaz E, Hatwell, Y (1996) Role of gravitational cues in the haptic perception of orientation. Percept Psychophys 58:1278–1292

Ghafouri M, Archambault PM, Adamovich SV, Feldman AG (2002) Pointing movements may be produced in different frames of reference depending on the task demand. Brain Res 929:117–128

Gooey K, Bradfield O, Talbot J, Morgan DL, Proske U (2000) Effects of body orientation, load vibration on sensing position and movement at the human elbow joint. Exp Brain Res 133:340–348

Howard IP (1986) The perception of posture, self motion, and the visual vertical. In: Boff K, Kaufman L, Thomas J (eds) Handbook of perception and human performance. Willey, New York, pp 1–62

Howard IP (1997) Interactions within and between the spatial senses. J Vestib Res 7:311–345

Lechner-Steinleitner S (1978) Interaction of labyrinthine and somatoreceptor inputs as determinants of the subjective vertical. Psychol Res 40:65–76

Li W, Dallal N, Matin L (2001) Influences of visual pitch and visual yaw on visually perceived eye level (VPEL) and straight ahead (VPSA) for erect and rolled-to-horizontal observers. Vision Res 41:2873–2894

Luyat M, Gentaz E, Regia Corte T, Guerraz M (2001) Reference frames and haptic perception of orientation: body and head tilt effects on the oblique effect. Percept Psychophys 63:541–554

Mast F, Jarchow T (1996) Perceived body position and the visual horizontal. Brain Res Bull 40:393–397

Matin L, Li W (1992) Visually perceived eye level: changes induced by a pitched-from-vertical 2-line visual field. J Exp Psychol Hum Percept Perform 18:257–289

Matin L, Li W (1995) Multimodal basis for egocentric spatial localization and orientation. J Vestib Res 5:499–518

Mc Dougall R (1903) The subjective horizon. Psychol Rev Monograph Suppl 4:145, 166

Mittelstaedt H (1983) A new solution to the problem of the subjective vertical. Naturwissenschaften 70:272–281

Mittelstaedt H (1995) The formation of the visual and the postural vertical. In: Mergner T, Hlavacka F (eds) Multisensory control of posture. Plenium Press, New York, pp 147–155

Mittelstaedt H (1999) The role of otoliths in perception of the vertical and in path integration. Ann N Y Acad Sci 871:334–343

Ooi TL, Wu B, He ZJ (2001) Distance determined by the angular declination below the horizon. Nature 414:197–200

Raphel C, Barraud PA (1994) Perceptual thresholds of radial accelerations as indicated by visually perceived eye level. Aviat Space Environ Med 65:204–208

Schöne H (1964) On the role of gravity in human spatial orientation. Aerospace Med 35:764–772

Stoper AE, Cohen MM (1986) Judgments of eye level in light and darkness. Percept Psychophys 40:311–316

Stoper AE, Cohen MM (1989) Effect of structured visual environments on apparent eye level. Percept Psychophys 46:469–475

Viviani P (1990) Motor-perceptual interactions: the evolution of an idea. In: Piattelli Palmarini M (ed) Cognitive science in Europe: issues and trends. Golem, pp 11–39

Worringham CJ, Stelmach GE (1985) The contribution of gravitational torques to limb position sense. Exp Brain Res 61:38–42