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Dissociation between subjective vertical and subjective body orientation elicited by galvanic vestibular stimulation

Franck Mars[a,*], Jean-Louis Vercher[b], Konstantin Popov[c]

[a] *Institut de Recherche en Communications et Cybernétique de Nantes (IRCCyN), UMR CNRS 6597, École Centrale de Nantes/Université de Nantes/Ecole Nationale Supérieure des Techniques Industrielles et des Mines de Nantes, 1 rue de la Noë, B.P. 92101, 44321 Nantes Cedex 03, France*
[b] *UMR 6152 "Mouvement and Perception", CNRS and Université de la Méditerranée, Faculté des Sciences du Sport, CP 910, 163, avenue de Luminy, F-13288 Marseille Cedex 9, France*
[c] *Institute for Information Transmission Problems, Russian Academy of Sciences, 19 Bolshoi Karetnyi per., 127994 Moscow GSP-4, Russia*

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Abstract

Previous studies demonstrated that sensory stimulation could differentially affect the subjective vertical (SV) and the subjective body orientation (SBO). This suggests that the central nervous system elaborates various references of verticality in function of the task demands and of the available sensory information. In this study, we tested whether the dissociation between SV and SBO appears for a selective stimulation of the vestibular system, by using galvanic vestibular stimulation (GVS). Seated subjects performed vertical settings by controlling the orientation of a visual rod during GVS. Subjects were also instructed to evaluate the orientation of the head and trunk relative to gravity. The results revealed a large variability in the way SV and SBO were affected. In all cases, the effect of GVS on SV was not a mirror image of a distorted SBO. We propose that this dissociation is mainly determined by central processes involved in the estimation of sensory cues reliability. GVS also yielded a tilt of the head when the head was unrestrained. The results suggest that changes in actual head orientation yielded by GVS may be related to the perceived direction of gravity but cannot be explained by a compensation of an illusory orientation of the head.

Keywords: Perception; Vision; Somatosensory information; Multisensory integration; Gravity

1. Introduction

Testing the ability of human subjects to align the orientation of a visual line to the direction of gravity (the subjective vertical test) is a classical protocol used to investigate the multisensory processes involved in the perception of spatial orientation. There are many ways of manipulating visual, vestibular and/or somatosensory signals so that the subjective vertical (SV) substantially differ from the veridical direction of gravity (for a review, see [24]). It was often assumed that any error in estimating the vertical was a consequence of the misperception of one's own body orientation in space (subjective body orientation, SBO). Thus, a clockwise tilt of SV would be the mirror image of a counter-clockwise illusion of body rotation. Although very intuitive, this hypothesis has been proven wrong by several studies that showed that SV and SBO could be differentially affected by a given pattern of stimulation [2,6,9,11,26,27,35,37]. For instance, Ito and Gresty [26,27] demonstrated that a slow pitch tilt of the body was markedly overestimated whereas the orientation of a visual object remained accurate. Conversely, patients with an unilateral vestibular disorder exhibited a significant tilt of SV toward the side of the lesion, but no response bias when their

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[*] Corresponding author. Tel.: +33 2 40 37 69 19; fax: +33 2 40 37 69 30.
E-mail address: franck.mars@irccyn.ec-nantes.fr (F. Mars).

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task was to indicate when they entered or left self-verticality (see [9] for a review). On the basis of such a dissociation between SV and SBO, the idea of a single internal representation of gravity, used by all perceptual and motor systems, can be excluded. More plausible is that the central nervous system (CNS) elaborates various references of verticality in function of the task demands and of the available sensory information.

Van Beuzekom and Van Gisbergen [50] performed an extensive study of SV and SBO during passive tilts of the body in the frontal plane. All subjects showed a large rotation of SV in the direction of body tilt (A effect), whether SV was tested with the classical visual-line test or with an oculomotor paradigm relying on saccadic pointing. When asked to verbally report their sense of subjective body tilt, subjects committed an error in the opposite direction to SV, but of much smaller amplitude. Van Beuzekom et al. [49] also demonstrated that SBO, but not SV, showed a clear improvement when body tilts were actively performed by the subjects, i.e. when additional signals such as efference copies and somatosensory inputs resulting from muscle effort were available. To explain those results, the authors proposed a model in which SV and SBO dissociation depends mainly on signal of non-vestibular origin. Indeed, both percepts would rely on a common representation of head orientation in space, elaborated from vestibular signals, but the nature of somatosensory information used for SV and SBO would be different. For the establishment of SV, tactile and proprioceptive cues would contribute to improve the perception of head orientation relative to gravity by complementing vestibular information. On the other hand, SBO may be more dependent than SV on information from graviceptors in the trunk [38,39], efference copies and pressure cues from the skin.

The overall objective of the present experiment was to further study the question of how sensory signals are combined for the perception of spatial orientation. In particular, we investigated the contribution of vestibular signals to the dissociation between SV and SBO by using galvanic vestibular stimulation (GVS). GVS is achieved by applying direct current of moderate intensity between the mastoid processes, which increases (cathode) or decreases (anode) the spontaneous firing of the otholitic and semicurcular canal afferents [21]. GVS is an artificial way of altering the vestibular information and acts on the perceptual and motor systems in a way that has not been completely understood [52]. However, this technique provides controlled and reversible perturbations to vestibular signals, allowing one to probe their influence on perceptual and motor tasks. GVS have been shown to influence various sensorimotor functions, such as the control of eye movements [44,47,54], posture [41,45], walking [4,5,20] and reaching movements [7,33]. Some studies suggested that GVS at low current intensities (below 3 mA) selectively activated otolithic functions, without semicircular canal response [54–56]. However, more recent studies brought contradictory evidence [43,44,51]. Furthermore, in an in-depth and thorough examination of the neurophysiological and behavioral litterature, Fitzpatrick and Day [18] concluded that postural responses to GVS originate from canal afferents and only one part of the uticular macula, the pars medialis.

Studies of the effect of GVS on the perception of spatial orientation are scarce. Some studies demonstrated that subjects perceived the visual scene as tilted in the direction opposite to anodal stimulation when experiencing GVS. As a consequence, when instructed to indicate the visual vertical, subjects committed an error toward the anode [48,55,56]. Mars et al. [34] demonstrated that this effect was not specific to the visual modality: it was also observed in the haptic modality, when subjects had to set a hand-held rod to the vertical in complete darkness. This suggests that GVS influences central processes in charge of spatial orientation. This hypothesis is supported by neurophysiological studies using functional magnetic resonance imaging [3,31]. GVS activated cortical areas related to oculomotor control and vestibular functions, but also multisensory areas, such as the inferior parietal lobule. However, Mars et al. [34] reported that the effect of GVS on SV was larger in the visual task than in the haptic task. This difference may be due to an unregistered torsion of the eyes. Indeed, Zink et al. [55,56] recorded ocular torsion induced by GVS while subjects performed vertical settings. Perceptual and oculomotor effects were in the same direction and both were linearly correlated with stimulus intensity, with ocular torsion being of smaller magnitude than the tilt of the visual vertical. In addition, Watson et al. [54] reported ocular torsion on the order of the difference between visual and haptic settings observed by Mars et al. [34], with both studies using very similar conditions of stimulation. Thus, the effect of GVS on the visual vertical may be the consequence of a tilt of the central representation of gravity in addition to unregistered ocular torsion.

Besides, illusions of self-tilt were reported when GVS was applied. In a standing posture, subjects usually experienced an illusion of body tilt in the direction of the cathode, although Fitzpatrick et al. [17] demonstrated that this illusion only appeared when head and trunk motion was restrained. The illusory tilt is usually a static body tilt. No study ever quantified it. It appears that the magnitude of the illusion is limited by somatosensory information, since Day and Cole [12] showed that a continuous tilting movement (i.e. an illusion of vection) replaced the usually observed static tilt in a patient with severe loss of somatosensory afferents. Fitzpatrick at al. [19] also reported some vection illusions when healthy subjects were stimulated while in a supine position (i.e. without somatosensory input arising from the maintenance of the upright stance).

Previous studies that demonstrated a dissociation between SV and SBO consisted in tilting the body of the subjects relative to gravity. This generates concurrent vestibular and somatosensory stimulation. In the present experiment, using GVS will allow to establish if this dissociation appears for a selective stimulation of the vestibular afferences. If no dissociation occur in these conditions, the conclusion would be that vestibular information contributes to the computation of an unique head-in-space representation, used for the computation of SV and SBO. As a consequence, the previously observed dissociation would rely exclusively on somatosensory information. If, on the contrary, GVS yields a dissociation between SV and SBO, this would suggest that the dissociation depends on vestibular signals or on higher levels of multisensory integration. In order to test this hypothesis, seated subjects performed vertical settings by remotely controlling the orientation of a visual rod in the frontal plane during GVS. Subjects were also instructed to evaluate the orientation of the head and trunk relative to gravity and to report them when the effect of GVS had faded. In previous studies, SV and SBO were often assessed by different methods. While SV was most often measured with the classical luminous rod method, subjects indicated SBO with various methods, such as self-controlled body tilt or verbal reports expressing the magnitude of tilt on a clock scale. Here, the methods used to assess both percepts were identical: the luminous bar used by subjects to indicate SV was also used to estimate SBO. The only difference was that SV was assessed during GVS whereas SBO was necessarily indicated after a delay. The experiment also compared SV and SBO settings when the head of the subjects were either restrained or free to move. This variable was introduced in order to evaluate if head immobility is necessary for body tilt illusions to appear in seated subjects. In addition, the “head free” condition will allow to determine if the postural response of the head to GVS can be related to the effect on SV or SBO.

2. Methods

Nine subjects (three women and six men, aged 22–42 years) were included in the study, which was approved by the local ethics committee. The subjects gave their informed consent after being briefed about the experiment. All were free of known vestibular or neurological problems and had normal vision.

The subjects were seated in an adapted sport car seat. Straps restrained trunk movements. This setup prevented any postural tilt of the trunk usually associated to GVS. In a first experimental session, the head was kept in alignment with the trunk by two presses placed on the temples. In a second session, the head was free to move. Both sessions were conducted with one or two days of interval and their order of presentation was counterbalanced.

A computer-generated white rod subtending 12° of visual angle was displayed on a monitor screen, in front of the subject. A mask was attached over the front of the monitor to remove visual references provided by the borders of the screen. The rod appeared through a circular aperture, cut at the center of the mask and covered by a translucent film. The film was added to prevent the subject from using the vertical alignment of pixels to orient the rod. When the subject had his/her eyes opened, the rod and the circular window were the only visible elements in the room. The visual rod could be rotated clockwise and counterclockwise in either direction, by acting on a joystick, that the subject held on his/her lap. The initial orientation of the rod was randomised and its final position was recorded when the subject pressed the joystick trigger.

A Fastrak magnetic receiver was attached to an adjustable light helmet. When a SV or SBO setting was validated, the orientation of the head relative to the trunk was recorded. Preliminary tests checked that the metallic parts of the experimental setup did not interfere with the measurements. In the “head free” condition, the subjects were warned that GVS might influence them into tilting the head in one direction or another. They were instructed neither to resist this movement, nor to accentuate it.

Two homemade stimulating electrodes consisting of plastic cups (diameter: 3 cm), filled with pieces of cloth, were kept in place binaurally over the mastoid bones by an extensible rubber headband. The pieces of cloth were saturated with salted water in order to insure proper conduction between the skin and the electrodes. The stimuli were delivered via a isolated battery-powered constant current stimulator. A progressive increase of stimulus intensity was chosen in order to avoid unpleasantness associated with the abrupt onset of a pulse stimulation. In these conditions, GVS was accompanied by mild cutaneous sensation. No pain was reported. Two intensities of stimulation were used (1.5 mA and 3 mA), with the anode either on the right side or on the left side. Control trials were performed without stimulation. One experimental session lasted about one hour and consisted of 25 trials, which corresponded to five different stimuli (two anodal stimulations on the left, one control without stimulation, two anodal stimulations on the right), repeated five times. The order of presentation of the stimuli was randomised. Rest periods of 30 s were inserted between consecutive trials.

The time course of one trial is represented by Fig. 1. Each trial began with a progressive increase of stimulation from 0 mA to the desired intensity in 2 s. Five seconds later, the experimenter asked the subject to open the eyes and to set the rod to the vertical. The vertical was defined to the subject as the direction of gravity, parallel to the surrounding walls, to a tree trunk or to a plumb line. Ten seconds were allowed to do the task, after which the subject was instructed to close

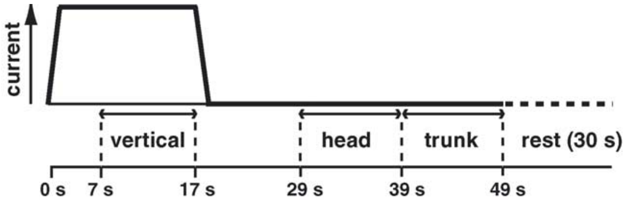

Fig. 1. Time course of one trial. Vertical settings were performed 5 s after GVS reached the desired intensity. Head and trunk orientation were estimated 10 s after the end of GVS.

the eyes. At that time, the intensity of stimulation was progressively reduced to zero. If the subject declared that he/she was not satisfied with his/her performance, the trial was ran again at the end of the session.

Ten seconds after the end of GVS, the subject indicated with the luminous rod the orientation of his/her trunk and his/her head, as they were perceived when the stimulation was applied. Preliminary tests showed that indicating the absolute orientation of the head in space seemed more natural and easier than indicating the head-on-trunk orientation.

At the end of each trial, qualitative data was collected. Subjects were asked to describe how they perceived the effect of stimulation. For instance, they were asked about the evolution of head and body tilt illusions in time. They were also asked to report the presence of vection (illusion of continuous rotation of the body).

3. Results

3.1. Group analyses

Fig. 2 represents the effect of GVS on the subjective vertical (SV), the perceived orientation of the trunk relative to gravity (subjective trunk orientation: STO) and the perceived head-on-trunk orientation (subjective trunk orientation: SHO). SHO was computed by subtracting STO to the subjective head-in-space orientation that was indicated by the subject. Results were very similar on average in the “head free” and “head fixed” conditions. SV was deviated in the direction of the anode when compared to the control condition (without stimulation). The trunk was perceived as tilted in the opposite direction (toward the cathode). The effect was markedly larger than the effect on SV: 3.2 times higher on average. The head was also perceived as tilted on the trunk toward the cathode. The magnitude of the effects observed on SHO and STO were similar.

A 5 (−3 mA/−1.5 mA/0 mA/1.5 mA/3 mA) × 2 (head free/head fixed) repeated-measures analysis of variance (ANOVA) was performed on the three dependent variables (SV/SHO/STO). The three ANOVAs lead to the same results. They revealed a significant effect of the intensity of stimulation [SV: $F(4, 32) = 4.64$, $p < 0.01$; SHO: $F(4, 32) = 5.47$, $p < .01$; STO: $F(4, 32) = 5.76$, $p < .01$], no effect of head mobility condition [SV: $F(1, 8) = 0.16$; SHO: $F(1, 8) = 0.01$; STO: $F(1, 8) = 1.64$] and a non-significant interaction between both variables [SV: $F(4, 32) = 1.10$; SHO: $F(4, 32) = 0.05$; STO: $F(4, 32) = 0.75$]. Contrasts analyses were used to test the linearity of the effect of stimulation intensity on each variable. The effect was significantly linear for SHO [$F(1, 8) = 6.01$, $p < 0.05$] and STO [$F(1, 8) = 5.87$, $p < 0.05$]. The test barely failed to reach statistical significance for SV [$F(1, 8) = 4.73$, $p = 0.06$].

In the “head free” condition, the real orientation of the head was deviated towards the anode compared to the reference condition. An univariate ANOVA revealed that the effect of stimulus intensity did not reach statistical significance [$F(4, 32) = 2.37$; $p = 0.07$]. Fig. 3 illustrates the actual response of the head to GVS, together with SHO and SV in the “head free” condition.

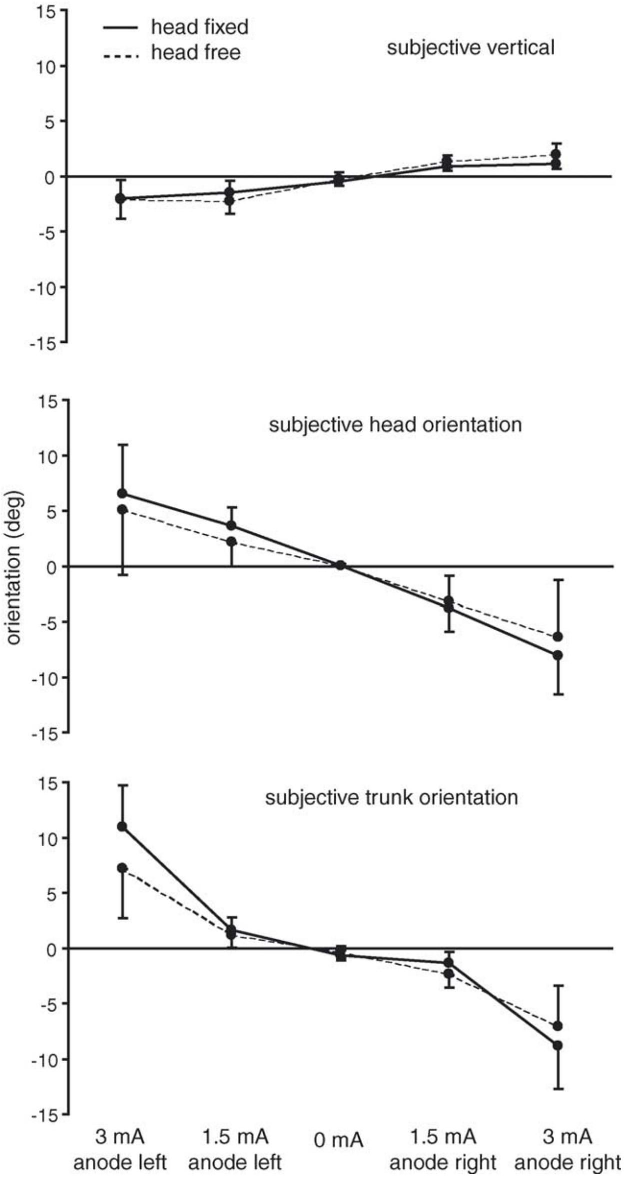

Fig. 2. Effects of GVS on the subjective vertical, the subjective head-on-trunk orientation and the subjective trunk-in-space orientation in function of stimulus intensity and polarity. Positive values correspond to errors on the right (clockwise tilt) relative to the veridical vertical and negative values correspond to errors on the left (counterclockwise tilt). Errors bars represent S.E.M.

3.2. Individual analyses

Tables 1 and 2 summarize the individual data for the “head fixed” and “head free” conditions, respectively. For simplicity, synthetic values are presented. They were computed by subtracting the value obtained in the control condition (without stimulation) to the data obtained with stimulation, by

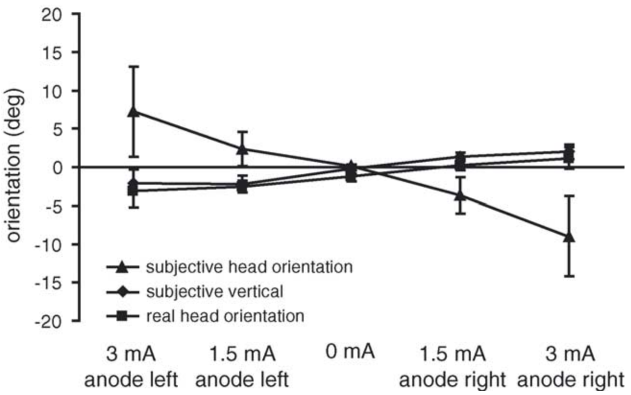

Fig. 3. Compared effects of GVS on the subjective vertical, the subjective head orientation and the real head orientation (“head free” condition). Vertical settings were deviated in the same direction and by a similar amplitude than the head. At the same time, the head was perceived as being markedly tilted in the opposite direction. Errors bars represent S.E.M.

Table 1
Individual effects of GVS on the subjective vertical, the subjective head-on-trunk orientation and the subjective trunk-in-space orientation, in the “head fixed” condition

“Head fixed” condition			
Subject	SV	SHO	STO
1	−0.38 ns	−2.57***	−5.61***
2	0.38 ns	−16.79***	−5.62***
3	0.49 ns	−8.79***	−1.64 ns
4	0.99***	0.05 ns	3.91 ns
5	1.07***	−0.91 ns	0.12 ns
6	0.81*	−7.28***	−14.53***
7	1.81***	−2.39***	−15.55***
8	1.98***	−11.65***	−7.71**
9	5.39***	−4.09***	−4.74***
Mean	1.39	−6.05	−5.71

A positive value represents a deviation towards the anode for a theoretical intensity of stimulation of 2.25 mA (see text). A negative value represents a tilt towards the cathode.
ns, non-significant; $^{*}p < .05$; $^{**}p < .01$;$^{***}p < .001$.

Table 2
Individual effects of GVS on the subjective vertical, the subjective head-on-trunk orientation, the subjective trunk-in-space orientation and the real orientation of the head, in the “head free” condition

“Head free” condition				
Subject	SV	SHO	STO	RHO
1	1.03 ns	−12.87***	1.92 ns	−3.27***
2	−0.66 ns	13.20***	−1.86 ns	7.93*
3	0.61 ns	4.47***	0.10 ns	2.20***
4	1.10**	0.60 ns	0.04 ns	1.34***
5	1.29**	−7.45***	−8.86***	1.07*
6	1.43*	−12.69**	−11.33**	1.05**
7	2.11***	−2.13***	−17.29***	1.68**
8	1.39***	−20.59***	−2.25**	0.97**
9	8.82***	−12.83***	−1.09 ns	2.90***
Mean	1.90	−5.59	−4.44	1.76

A positive value represents a deviation towards the anode for a theoretical intensity of stimulation of 2.25 mA (see text). A negative value represents a tilt towards the cathode.
ns, non-significant; $^{*}p < .05$; $^{**}p < .01$;$^{***}p < .001$.

reversing the signs of the data obtained when the anode was placed on the left ear, then by averaging the resulting four values. Thus, a positive value represents a deviation towards the anode for a theoretical intensity of stimulation of approximately 2.25 mA, since the effect of stimulus intensity was always linear or quasi-linear. For each value, the tables indicate the statistical significance of the effect, as revealed by univariate ANOVAs, which tested the effect of the intensity of stimulation (−3 mA/−1.5 mA/0 mA/1.5 mA/3 mA) for each subject and each dependent variable, with five observations in all cases.

In Table 1, the values are ordered to highlight three groups of subjects with different behaviours. Subjects 1–3 did not show an effect of GVS on SV, but reported significant illusions of head and/or trunk rotations. Subjects 4 and 5 showed an opposite profile, i.e. a significant bias of SV toward the anode without illusion of body rotations. Subjects 6–9 demonstrated an effect of GVS on SV, SHO and STO simultaneously.

In the “head free” condition (Table 2), the real orientation of the head was influenced by GVS for all subjects. The effect was directed toward the anode, except for subject 1. The effects of GVS on SV were very close to those observed in the “head fixed” condition ($r^2 = 0.87$, $p < .001$). On the contrary, the magnitude of effect on STO and SHO varied in some subjects from one condition to the other (see Table 2 for details).

A last noticeable observation is illustrated by Fig. 4: there was a striking parallelism between the direction of SV and the head orientation in five out of the six subjects who showed a significant effect of GVS on SV. The exception was subject 9 who showed a larger effect on SV than on the head posture.

3.3. *Subjective reports*

When GVS was applied, subjects who experienced body tilt illusions reported that about 5 s (including the 2 s when the intensity of stimulation was progressively increased) were needed for the effect to reach a maximum and stabilize. Subjects 6 and 8 reported pure static body tilts. The remaining subjects described an additional illusion of continuous motion (vection). This gave rise to a mixed illusion with a static component and a dynamic component. For subject 7, this translated as if the body was oscillating around a fixed tilted orientation. For the others, vection “blurred” the static body tilt, which made the SBO tasks slightly more difficult to perform than the SV task. In all case, subjects were instructed the reproduce the average orientation of the head and of the body, i.e. the static component of the illusion.

4. Discussion

As reported in previous studies, GVS yielded a tilt of SV toward the anode [34,48,55,56]. The stimulation produced at

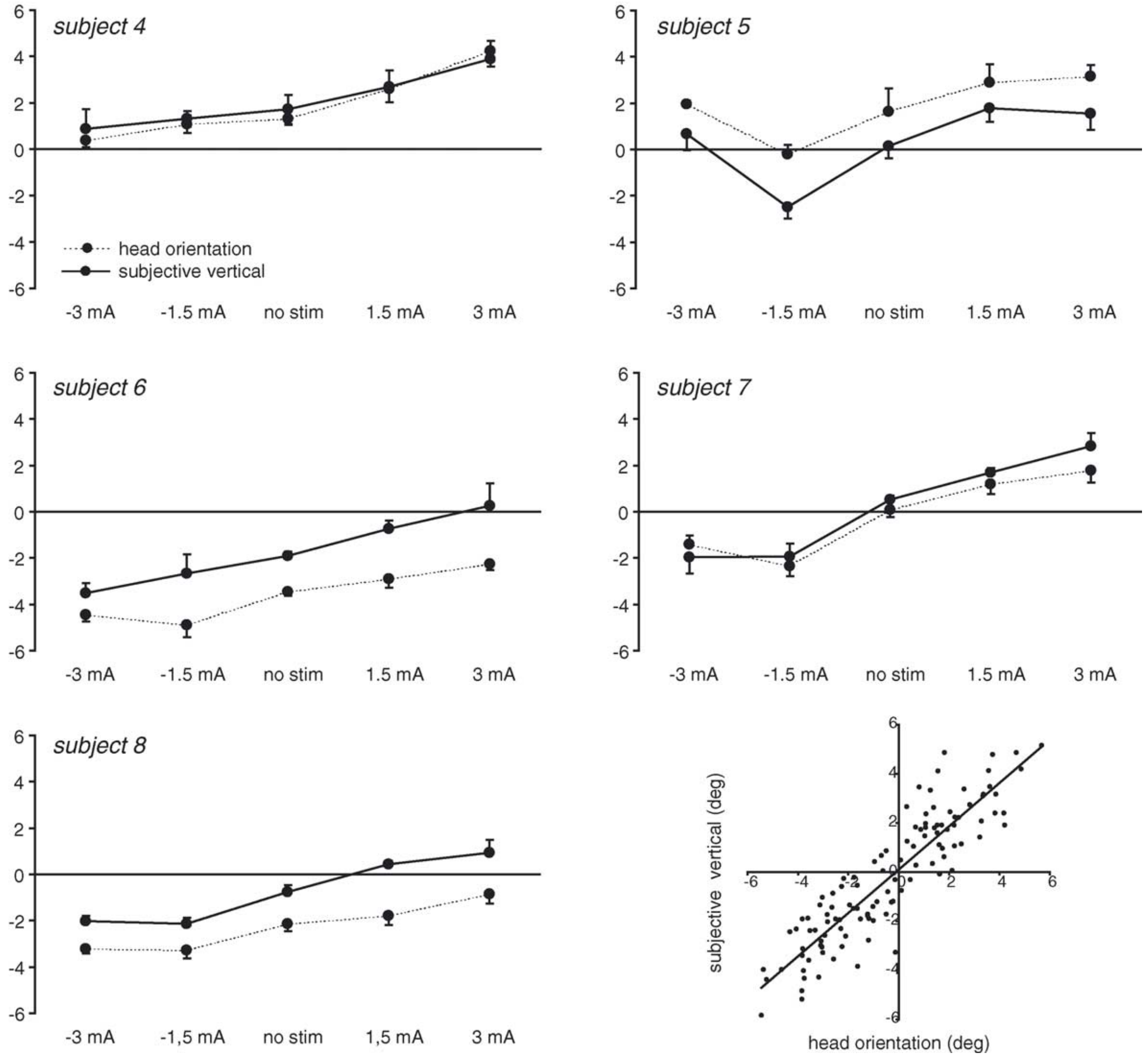

Fig. 4. Effects of GVS on the subjective vertical and the real orientation of the head in five subjects (“head free” condition). The strong correlation between the perceptual and postural responses ($r^2 = 0.82$) is illustrated by the below-right graph, in which all trials were pulled together. Errors bars represent S.E.M.

the same time some illusion of self-tilt in the opposite direction. The latter effect was, on average, markedly larger than the former. Individual analyses revealed a large inter-subject variability in the way SV and SBO were affected, but in all cases, the effect of GVS on SV was not a mirror image of a false perception of body orientation. Thus, altering vestibular signals induced a strong dissociation between SV and SBO. On average, the results were similar when head movements were either restrained or allowed. However, individual analyses revealed that, in some cases, head mobility could significantly modify the effect of GVS on SBO, but not on SV. GVS also yielded a tilt of the head when the head was unrestrained. In some subject, this postural response was similar in amplitude and direction to the effect observed on SV. In the following discussion, we will examine in more details the nature of the dissociation between SV and SBO and how postural and perceptual responses might be related.

4.1. Dissociation between the subjective vertical and the subjective body orientation

Our results showed that the effect of GVS on SBO was on average markedly higher than the effect on SV. However, the dissociation between SV and SBO did not take the same form in all subjects. Some of them showed a perceptual bias while estimating the vertical without any effect on SBO. In others, GVS induced large illusions of body tilt but did not affect SV. When both percepts were affected, the amplitude of the illusions were always different. Thus, the effect on SV cannot be interpreted as the mirror image of a erroneous perception of body orientation. This clearly contradicts the idea that SV and SBO are computed relative to a common spatial reference, as claimed by Jaggi-Schwarz et al. [30]. On the contrary, it supports the idea that the processing of sensory information differs in both percepts.

Several studies stressed the role of somatosensory signals in the occurrence of the dissociation between SV and SBO. For instance, patients with acute unilateral vestibular disorder showed a systematic bias of SV, but remained capable of indicating when they entered and left self-verticality while they were tilted randomly in roll and pitch [2,6]. These results imply that somatosensory signals can provide an accurate mean estimate of body uprightness (although the variability of the response is much higher when vestibular information is absent), but cannot help for estimating the orientation of a visual object. Van Beuzekom and colleagues also emphasized the role of somatosensory information in the dissociation between SV and SBO. In a first experiment, subjects were seated in a motor-driven chair and were passively tilted in the frontal plane. In these conditions, subjects committed an error both on SV and on SBO, although the former was significantly larger than the latter [50]. In a second experiment, the same tasks were required, but this time the body tilts were actively performed by the subjects. The performance regarding SV was the same as in the previous experiment. By contrast, the error on SBO nearly disappeared [49]. Thus, enhancing somatosensory and motor cues by allowing subjects to perform active body tilts improved the perception of self-orientation, but did not influence SV.

Our results do not support the idea that the weight of somatosensory information is greater for SBO than for SV, in an absolute way. By using GVS in upright seated subjects, we induced a strong vestibular asymmetry while somatosensory input was unchanged and unambiguous. For most of the subjects, this yielded large illusions of body rotation and a small, but consistent, illusion of tilt of SV. So, it appears that SBO was much more determined by vestibular input than SV in our experimental conditions, by contrast to experiments using tilts of the body. This suggests that the relative contribution of somatosensory information relative to vestibular information for SV and SBO is task-dependent, context-dependent, and also subject-dependent as attested by the large intersubject variability we observed.

We propose that the dissociation between SV and SBO is mainly determined by central processes involved in the estimation of sensory cues reliability. According to the maximum likelihood estimation model, high weights are allocated to reliable cues and low weights to unreliable ones in order to optimize sensory integration and to resolve sensory conflicts (for a review, see [16]). Jacobs [29] defined two rules for the estimation of cue reliability. First, it is related to the ambiguity of the cue: a cue is reliable if the distribution of inferences based on that cue has a relatively small variance, otherwise the cue is regarded as unreliable. This process can be modelled as an extended Kalman filter and predicts that adding noise to a sensory cue would lower its weight in the integration process, thus diminishing its contribution to the final percept [14]. Second, cue reliability can be based on cue correlations: a cue is regarded as reliable if the inferences based on that cue are consistent with the inferences based on other concomitant cues. This would allow the CNS to discard one source of discrepant information when two other cues vary in time in the same manner, for instance. However, when the informational conflict is too strong (i.e. when spatial or temporal correlations among available cues are weak), the perceptual system may determine cue reliability on some other basis, depending of the task. In our experimental conditions where a strong tonic vestibular asymmetry coexisted with stable symmetric (i.e. with the body in the upright position) somatosensory signals, it appears that, in most subjects, vestibular cues were estimated as more reliable than somatosensory cues for judging self-orientation, but not for assessing the orientation of a visual object relative to gravity. Passive and active body tilts, on the contrary, produce somatosensory asymmetries that seems to improve the reliability of the corresponding cues, especially for SBO [9,35,37,49,50].

In addition to the bottom-up processes described above, top-down influences can be added to the model. For instance, the brain may learn to take into account some bias in the processing of sensory information [1,15]. As a consequence, individual sensory experiences could influence multisensory integration and contribute to the existence of perceptive style. Such idiosyncrasies would explain the intersubject variability we observed in the present experiment. This part of sensory integration can be modeled as independent Gaussian distributions, called priors, that modify the linear sum of the maximum likelihood estimation. These mechanisms are compatible with the model of spatial perception proposed by Van Beuzekom and Van Girsbergen [50]. Indeed, that model proposed that the brain relies partly on an assumption about the a priori probability that a particular tilt of the earth-vertical relative to the body may occur. This computational strategy is dependent of the orientation of the body and may differ for SV and SBO since it operates on different signals and subserves different task requirements.

4.2. *Perceptual illusions and postural responses induced by GVS*

Many studies used GVS to investigate the role of the vestibular system in the control of stance [8,10,40,42,45]. Typically, GVS elicited short (60 ms)- and medium (100 ms)-latency EMG responses in leg muscles, presumably mediated by vestibulospinal and reticulospinal pathways, respectively. Those changes in muscles activity gave rise to small transient postural sways. The transient responses were followed by a larger prolonged sway which was not attributable to the activity in leg muscles but rather to an involuntary response due to a central interpretation of vestibular signals, as demonstrated by Fitzpatrick et al. [17]. The CNS appears to extract some meaning from the altered vestibular input since the motor response is well organized and highly adaptable. For instance, the direction and amplitude of the prolonged sway is known to be determined by the orientation of the head or the gaze with respect to the feet [28,32], the availability of other sensory inputs [23], the relative timing between the stimulus and a voluntary movement of the trunk [46] or whether the stimulus is triggered voluntarily or not [22]. Hence, the motor response to GVS is highly context-dependent with characteristics which suggest it is organized to serve some function. Then, the question is what is the CNS “attempting” to control with these postural responses? Although the present study was not designed to answer this question, we will now consider some observations that may be relevant to it.

The effect of GVS on SBO breaks up into two parts: an illusion of trunk tilt relative to gravity and an illusion of head tilt relative to the trunk, both in the direction of cathode. These illusions are symmetrical in direction to the postural body tilts reported in other experiments, in which the orientation of the pelvis, the chest and the head was measured during GVS [13,41]. Indeed, the body seemed to bend in an arc towards the anode. This behaviour was observed in standing subjects, and also in seated subjects although the response was very small in that case [13]. The similarity in shape between illusions of body tilt and actual postural responses does not necessarily mean that the latter is the consequence of the former. Indeed, Fitzpatrick et al. [17] demonstrated that perceptual illusions only appeared in standing subjects when trunk motion was prevented. When stance was unsupported, most subjects reported a direction of tilt that corresponded with their actual GVS-induced body sway. Here, we studied the perception of self-orientation in seated subjects, with or without restriction of head motion. In both cases, large illusions of head and/or trunk tilt were experienced by the subjects. When the head was unrestrained, GVS yielded a tilt of the head in the opposite direction, but the magnitude of this motor response was unrelated to the magnitude of the illusions. This shows that if trunk immobilization is critical for the body tilt illusions to appear, head immobilization is not. More importantly, it confirms that postural responses to GVS cannot be explained by a compensation of a conscious misperception of body orientation.

Two other hypothesis have been proposed to explain the postural adjustments yielded by GVS. On the one hand, Day et al. [13] proposed that GVS evokes a signal akin to that produced by a tilt of the head in a gravitational field and that this would be interpreted by the CNS as a tilt of the support surface. The function of the postural response would be to help keep the body in balance in face of the tilting. According to this assumption, the postural adjustment may be thought as a protective manoeuvre that is organized to avoid any threat to balance by keeping the vertical projection of the centre of mass of the body within safe limits. On the other hand, some authors observed that the effect of GVS was larger on the movement of the trunk segment in space than on the body’s centre of mass, suggesting that the vestibular system acts to control trunk orientation rather than whole body posture [23,25]. They proposed that GVS induces a pattern of vestibular nerve activity resulting in a shift of the perceived direction of the gravitoinertial vector. The body realignment that occurs in response to GVS would be aimed at bringing the head and trunk into alignment with this perceived direction of gravity. This hypothesis is compatible with the model of Mergner and Rosemeier [36], which suggests that the vestibular system primarily controls the orientation of the head and trunk in space rather than whole body centre of mass. Interestingly, we observed in some subject a striking parallelism between the effect of GVS on SV and the head posture. This gives some credence to the second hypothesis. However, one can note that GVS evoked a tilt of the head in all subjects, including those who did not show a significant deviation of SV. This suggests that GVS induces very automated responses to stabilize the head in space. GVS-induced tilt of SV may be determined similarly in some subjects but may be influenced by additional factors for others. Besides, Wardman et al. [53] compared GVS-evoked body tilt and SV in standing subjects under various conditions of stability. They showed that body tilts increased with the level of unstability whereas SV remained identical. Thus, when the whole balance system is solicited (i.e. when the influence of extra-vestibular information is increased), postural responses do not seem to consist in an alignment on the perceived direction of gravity.

5. Conclusion

By using GVS, this study investigated the role of vestibular signals in the perception of verticality and in the perception of self-orientation. The results confirmed that the two percepts relied on different processes and thus that the CNS elaborates various references for the perception of spatial orientation. In particular, we demonstrated that vestibular signals were given a greater weight for SBO than for SV, in contrast with conclusions from previous studies which used whole body tilts and stressed the role of somatosensory information for SBO. A majority of subjects showed a larger effect of GVS on SBO than on SV, but a large intersubject variability was observed. This suggests that processes of multisensory integration, supposedly relying on the estimation of sensory cues reliability, are central in the dissociation between SV and SBO. Individual sensory experience may influence those processes and contribute this way to the existence of idiosyncrasies.

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