Supramodal effects of galvanic vestibular stimulation on the subjective vertical

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Received 9 July 2001; accepted 20 July 2001

This study investigated whether the tilt of the subjective vertical induced by galvanic vestibular stimulation, demonstrated by asking subjects to set a rod to the vertical, was specific to the visual modality or could be found in two tasks relying on proprioceptive and somatosensory cues. In all cases, settings were significantly deviated in the direction of the anode, but errors were smaller in the somatosensory tasks than in the visual task. We propose that the effects observed in the somatosensory modality reflects only a modification of the central representation of gravity, whereas visual effects are also in part the consequence of unregistered ocular torsion. *NeuroReport* 12:1–4 © 2001 Lippincott Williams & Wilkins.

Key words: Gravity; Ocular torsion; Proprioception; Reference frame; Spatial orientation; Vision

INTRODUCTION

Information provided by the vestibular system has been extensively studied for its fundamental role in the neural coding of space [1,2]. One recurrent problem with some methods classically used to stimulate the vestibular system, like head tilt, body tilt or alteration of the gravito-inertial field, resides in the fact that they generate concurrent proprioceptive and somatosensory signals. On the other hand, galvanic vestibular stimulation (GVS) has the particular advantage of selectively activating the vestibular system. This technique consists of applying moderate direct current between the mastoid processess which modulates the spontaneous firing of vestibular nerve fibers: increased frequency on the cathode side and decreased frequency on the anode side [3]. Effects of GVS have been demonstrated on various sensorimotor functions, such as the control of eye movements [4,5], posture [6,7] and walking [8,9].

Recently, several studies have focused on the effects of GVS at the perceptual level. The perception of verticality was assessed by asking subjects to reproduce the subjective tilt of the visual scene experienced during GVS [10,11] or to set a visual line to the vertical [12]. Subjects perceived the visual scene as tilted in the direction opposite to anodal stimulation. As a consequence, when instructed to indicate the visual vertical, subjects committed an error toward the anode. In addition to the perceived tilt of the visual scene, Zink *et al.* [10,11] recorded static torsion of the eyes induced by the same stimulation. Perceptual and oculomotor effects were in the same direction and both were linearly correlated with stimulus intensity, with ocular torsion being of only slightly smaller amplitude than the tilt of the visual vertical. It is tempting to wonder whether the tilt of the visual vertical is the consequence of the unregistered torsion of the eyes or not. This hypothesis is supported by the work of Wade and Curthoys [13], who investigated the relationship between ocular torsion and perceptual tilt of the visual horizontal produced during whole-body tilt. The authors compared two methods of measuring the perceived horizontal, one involving a visual line, the other involving proprioceptive and somatosensory cues, i.e. adjusting a solid rod with the hands in darkness. They observed an effect of tilting the body in the visual modality, but not in the somatosensory modality. Besides, tilt of the visual line and ocular torsion strongly correlated. Wade and Curthoys [13] concluded that the difference between the visual and somatosensory settings was primarily due to the change in ocular torsional position, contradicting previous models which stressed the role of central processing in the genesis of the effects [14].

The aim of the present study was to investigate, in a within-subject design, whether the tilt of the subjective vertical induced by GVS is specific to the visual modality. For this, we compared vertical settings performed by remotely controlling the orientation of a visual rod (visual task) with those performed by holding with one hand a light wooden rod in darkness (somatosensory task). If perceptual effects of GVS were exclusively due to ocular torsion, subjects holding a solid rod to the perceived vertical should not be influenced by the stimulation. On the contrary, somatosensory settings deviated in the direction of anodal stimulation would suggests a change of the central representation of gravity. Whatever the case, any difference observed between the visual and somatosensory tasks could be attributed to visuovestibular effects, with unregistered ocular torsion as a candidate.

A second point of the experiment was to compare two methods of indicating the vertical in the somatosensory modality. Both tasks were quite similar and consisted of adjusting the same wooden rod with one hand to the perceived vertical, but, in one condition, the rod rotated around an axis mounted on an earth-fixed support, whereas, in the other condition, the subjects held the detached rod in front of them. An anchor in space such as the one provided by the earth-fixed device has been showed to influence vestibular-driven illusions. For instance, illusions of torso rotation induced by sinusoidally rotating the head of a stationary subject can be suppressed if the subject is allowed to grasp a spatially fixed handle [15]. Thus, we hypothesized that a space-referenced anchor could prevent a potential tilt of the subjective vertical from occurring in the somatosensory modality.

MATERIALS AND METHODS

Fourteen subjects (three women and 11 men, aged 21–53 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 or near-to-normal vision. Subjects were seated in a chair. Their head was kept in alignment with the trunk by a neck brace. A headrest supported the back of the head and a strap pressed on the forehead to keep the head in a fixed position during the experiment. This method prevented any postural tilt of the trunk or of the head usually associated to GVS.

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 to ensure proper conduction between the skin and the electrodes. The stimuli were computer-controlled and delivered via a battery-powered constant current stimulator. A progressive increase of stimulus intensity was chosen in order to avoid unpleasantness associated to the abrupt onset of a pulse stimulation. In these conditions, GVS was accompanied by mild cutaneous sensation. No pain was reported. Two intensifies of stimulation were used (1.25 mA and 2.5 mA), with the anode either on the right side or on the left side. Those intensities were chosen because they are known to produce a tilt of the visual vertical and ocular torsion without horizontal or torsional nystagmus [4,11]. Control trials were performed without stimulation. The course of one trial is illustrated in Fig. 1. If subjects declared that they were not satisfied with their performance, the trial was run again at the end of the session. The experiment was divided into three sessions, conducted on separate days. One experimental session lasted about 1 h 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 randomized. Rest periods of 30 s were inserted between consecutive trials.

The three experimental sessions differed by their methods of assessing verticality. The order of presentation was counterbalanced. In the visual condition (VSL), 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. During the whole session, the rod and the circular window were the only visible elements in the room. The rod could be rotated back and forth in either direction, by acting on a joystick, that the subject held on his/her lap. The initial orientation of the rod was randomized and its final position was recorded. In the unanchored somatosensory condition (UNS), the subject grasped a lightweight wooden rod (23 cm long, 75 g) at its center, with the thumb in the alignment of the rod. Between trials, the hand holding the rod rested on the subject's lap. When instructed to indicate the vertical, the subject had to raise his/her hand at chest level, straight ahead the body midline, and to keep the rod vertically oriented until the sound signaling the end of the trial occurred. The sensor of a magnetic tracking device (Polhemus Fastrak) was fixed on the top of the rod. Its orientation was monitored and recorded all along the trial to ensure that the response was clearly stabilized before the end of the stimulation. Otherwise, the trial was rejected. In the earth-anchored somatosensory condition (ANS), the wooden rod used in the preceding condition was mounted on a support and thus could only pivot around a fixed central axis, situated in front of the body midline. Prior to the experiment, the subject was trained to reach the rod in darkness without groping around and to grasp it accurately, i.e. in a similar way as in UNS. A small amount of force was necessary to change the orientation of the display. Scanning of the rod, which would have provided additional tactile reformation, was not allowed. The experimenter randomly changed the starting position of the rod between trials.

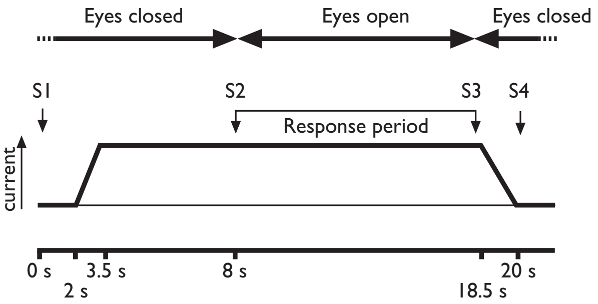

Fig. 1. Time course of one trial. S1, S2, S3 and S4 were computer-generated sounds that punctuated the trial. S1 signaled the beginning of the trial. S2 and S3 respectively defined the beginning and the end of the response period when subjects opened their eyes, whatever the condition (even if it did not involve vision) and set the rod to the vertical. S4 signaled the end of the stimulation and the beginning of the rest period.

RESULTS

Figure 2 summarizes the averaged data obtained in the experiment. It shows that GVS always resulted in a devia-

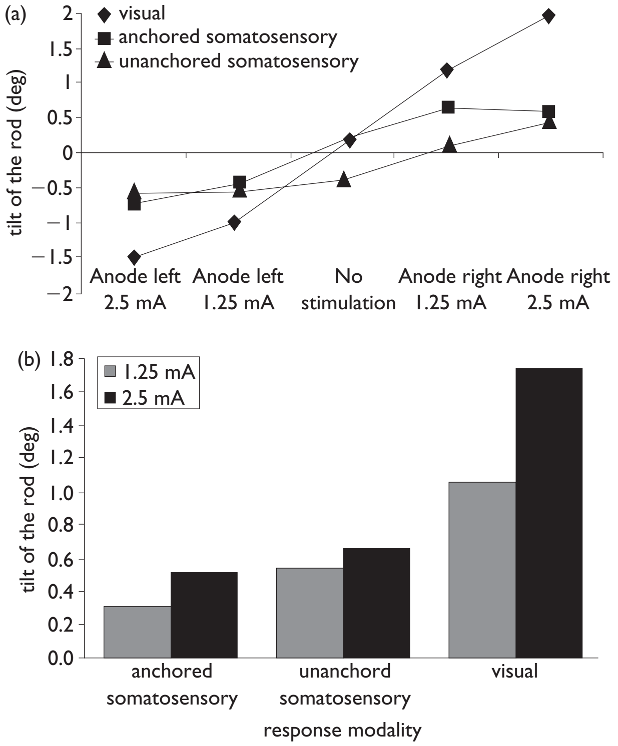

Fig. 2. Effects of GVS on the subjective vertical in function of stimulus intensity, anode position and response modality. (**a**) Positive values of rod tilt correspond to errors on the right (clockwise tilt) relative to the veridical vertical and negative values correspond to errors on the left (counter-clockwise tilt). Whatever the task, vertical setting was deviated by GVS in the direction of the anode, when compared to control conditions (no stimulation). (**b**) Control values were subtracted from settings produced with GVS, so that positive values correspond to a deviation of the settings in the direction of the anode. Results obtained with the anode placed on the right and on the left mastoid were averaged since they did not yield any significant difference.

tion of vertical settings toward the anode, relative to the reference values obtained in the control conditions. For statistical analyses, the error committed in the control condition (no stimulation) was subtracted from the errors committed with GVS (Fig. 2b). Errors in the direction of anodal stimulation and errors in the direction of cathodal stimulation were respectively assigned positive and negative values. A 2 (1.25 mA/2.5 mA) × 2 (anode on the right/ anode on the left) × 3 (VSL/UNS/ANS) repeated-measures ANOVA performed on these data revealed a significant effect of stimulus intensity ($F(1,13) = 6.28$, $p < 0.05$), no effect of the side of the anode ($F(1,13) = 0.04$), and a main effect of response modality ($F(2,26) = 6.22$, $p < 0.01$). There was no significant interaction. Contrast analyses tested whether vertical settings were deviated in the direction of the anode in each modality. The effect was significant in VSL ($F(1,13) = 17.06$, $p < 0.01$), UNS ($F(1,13) = 39.27$, $p < 0.001$) and ANS ($F(1,13) = 7.89$, $p < 0.05$). In addition, Newman–Keul's tests indicated that errors committed in VSL were significantly larger than in UNS ($p < 0.05$) and in ANS ($p < 0.01$). Both somatosensory response modalities did not differ on average. However, correlational analyses revealed some differences between the two somatosensory tasks (Table 1). Indeed, the performance in ANS and UNS did not correlate ($r = 0.20$). Moreover, whereas UNS tended to positively correlate with its visual counterpart, even if both sets of data failed to significantly correlate ($r = 0.47$, $p < 0.10$), ANS did not correlate at all with VSL ($r = 0.06$).

DISCUSSION

As reported in previous studies [10–12], GVS yielded a tilt of the visual vertical toward the anode. It was also demonstrated for the first time that this effect was not specific to the visual modality: it could also be observed when subjects had to set to the vertical a solid rod held with one hand in darkness, a task relying on proprioceptive and somatosensory information. The effect was smaller when vision was excluded, but remained very consistent, especially when the display did not provide an earth-fixed reference. Both somatosensory tasks did not differ on average when they were used to assess the subjective vertical. However, when the device was not anchored to a earth-fixed support, the effect of GVS was more consistent. This could be predicted, as a stable anchor in space has been demonstrated to suppress vestibular-driven illusions [15] and to increase postural stability [16].

GVS produced large interindividual variability in the magnitude of the effects on the subjective vertical, as already reported in previous studies, and some subjects were differently affected by the stimulation in function of the task. In spite of this variability and of the reduced pool of tested subjects, the fact that visual and unanchored somatosensory settings tended to correlate suggests that both effects share, at least partially, some common processes. We propose that the effects observed in the somatosensory modality reflect a modification of the central representation of gravity. This hypothesis is supported by neurophysiological studies using functional magnetic resonance imaging [17,18]. GVS activated cortical areas related to oculomotor control and vestibular functions, but also

Table 1. Mean effects of GVS, independently of stimulus intensity and anode position, in function of response modality.

Subject	Visual	Unanchored somatosensory	Anchored somatosensory
1	4.52	0.95	0.83
2	3.43	0.96	**0.11**
3	2.54	0.86	**−0.24**
4	1.67	0.66	0.81
5	1.51	0.25	0.83
6	1.25	**0.18**	0.93
7	1.08	0.42	**−0.25**
8	0.98	1.29	**−0.04**
9	0.66	**0.16**	0.46
10	0.66	0.97	**0.02**
11	0.63	0.66	0.53
12	0.59	0.64	0.96
13	0.43	0.45	1.40
14	**−0.18**	**0.11**	**−0.44**
Mean	1.41	0.61	0.42

Data are ordered in function of the magnitude of the effects obtained in the visual condition. Bold values signal conditions in which no effect of GVS could be described.

multisensory areas, such as the inferior parietal lobule, which is involved in the building of internal reference frames.

In Zink *et al*. [11], a GVS of 2.5 mA induced a tilt of the subjective vertical which was on average 0.7° larger than the amount of occular torsion. Interestingly, the effect observed in the present study on somatosensory settings is about the same magnitude. This could suggest that the effects observed in the visual modality would be the consequence of a tilt of the central representation of gravity in addition to ocular torsion. This hypothesis would imply that galvanically-induced ocular torsion is not taken into account by the perceptual system (either via efference copy or proprioception of the eye muscles) in making visual judgments of orientation, as has already been proposed [19,20]. However, some conflicting results exist. Indeed, Nakayama and Balliet [21] and more recently Haustein and Mittelstaedt [22] studied the relation between the visual vertical and eye torsion induced by oblique position of gaze, according to Listing's law. They concluded that, although the vertical judgments were not peridical, they did not conform to a retinotopic prediction. Thus, an extra-retinal signal, probably derived from the efference copy of gaze direction command, would allow compensating in part for ocular torsion. Whether or not the difference between visual and somatosensory settings reported here corresponds to the amount of ocular torsion remains to be determined. Watson et al. [4], who recorded ocular torsion during maintained GVS as in the present study, gave credence to this hypothesis. They observed that a GVS of 3 mA produced some tonic torsion of about 0.8°, that is in the order of the difference between visual and somatosensory settings at 2.5 mA. A replication of the present study with recorded ocular torsion would certainly clarify this point.

CONCLUSION

This study demonstrated for the first time that the influence of GVS on the subjective vertical could also be found when vision is excluded. In that case, the biased perception of the vertical direction was most probably the consequence of a tilt of the gravitational reference frame, produced by asymmetric vestibular stimulation in the absence of head tilt. When estimating the subjective vertical in the visual modality, additional effects linked to lower-level visuo-vestibular interactions came into play.

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Acknowledgments: This word was supported by grants from CNRS FRE 2099 and Dassault Aviation. K.P. was supported as an invited researcher by the Centre National de la Recherche Scientifique (CNRS).

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