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RESEARCH ARTICLE

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Accuracy level of pointing movements performed during slow passive whole-body rotations

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Abstract Seated observers requested to detect low-velocity passive rotations show a high motion-detection threshold. However, when standing on a slowly rotating platform, their equilibrium is preserved, suggesting that cognitive sensing and sensorimotor reactions do not share the same central processes. The present experiments investigated the ability of observers seated on a slowly rotating chair in total darkness to indicate with their hand the position of briefly flashed targets (Experiment 1) and to indicate the subjective horizon with an outstretched arm (Experiment 2) or with a target driven by a joystick (Experiment 3). The overall hypothesis stated that egocentric coding of the position of a target should not be affected by sensing or not-sensing body rotation (Experiment 1), while geocentric positioning may (Experiments 2 and 3). Our data partially supported the hypothesis. Subjects pointed accurately to the memorized targets (Experiment1), whereas misperception of body orientation was a source of inaccuracy for actions referred to a geocentric frame (Experiments 2 and 3). More interestingly, subjects' perceptions changed as a single, smooth, and monotonic function of tilt, independent of whether the perception of body orientation was present or not.

Keywords Passive body rotation · Subjective horizon · Memorized visual target · Otolith organs · Proprioception

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Introduction

Pointing towards a visual target presented in total darkness is a difficult task by itself, resulting from a complex sensorimotor coordination (Desmurget et al. 1998). It requires a series of processes to transform the visual input about target position expressed in a retinal coordinate system into appropriate motor commands for the execution of the final movement (Jeannerod 1988). It is well known that subjects make consistent errors when asked to indicate the position of memorized targets without vision of the arm (Soechting and Flanders 1989). The errors made are dependent on the experimental condition (e.g., Adamovich et al. 1998; Berkinblit et al. 1995; McIntyre et al. 1997). For instance, it has been shown that movements towards visually defined memorized targets are much less accurate than movements towards kinesthetically defined memorized targets (Soechting and Flanders 1989; Darling and Miller 1993). Whatever the experimental condition, pointing at visual targets in complete darkness, is commonly referred to as an egocentric task in which the target is localized in relation to the position of the body (Soechting and Flanders 1989; Flanders et al. 1992). As a consequence, modifying the position of the body between the presentation of the target and the pointing movement requires subjects to update the target position relative to the new position of the body to maintain an accurate performance. Recently, Medendorp et al. (1999) investigated the subjects' capacity to update target position after a self-induced egomotion (active movement). Subjects performed pointing movements towards memorized targets in a completely darkened room with or without self-made step movements. The authors showed that making an active step induced large pointing errors. They suggested that the subjects tended to underestimate the amplitude of their displacements leading to pointing errors. Blouin et al. (1998) analyzed the accuracy of pointing movements towards memorized targets after a passive whole-body or head rotation. They showed that pointing movements were less accurate in the absence of a passive head rotation. Their results suggested that neck-muscle proprioception can be successfully used for the updating process during trunk rotation and that vestibularly mediated performance is less accurate.

The respective role of vestibular and proprioceptive signals is also of interest when subjects are rotated slowly before the presentation of the target. Gurfinkel et al. (1995) were the first to investigate the effects of very slow platform inclinations on human posture. They showed that, besides operative control assigned to compensate deviations from a reference position, the system of postural control includes at least one additional level, which elaborates this reference using information about mutual position of body links, muscular torques and interaction with the support. More recently, Teasdale et al. (1999) demonstrated that subjects inaccurately coded their body orientation when they were deprived of vestibular information. In a completely darkened room with no visual information, subjects were seated on a platform allowing pitching and rolling movements at very slow velocities (0.01 to $0.05°\cdot s^{-1}$). Tightly constrained in position to also minimize the use of proprioception, they were asked to detect a change in their body orientation while they were pitched or rolled. The results showed that subjects could not detect their body orientation unless the amplitude of rotation exceeded 5°. The question of the accuracy of pointing movements in such restricted conditions becomes central to the present study.

The purpose of the present experiments was to investigate how subjects are able to perform accurate goal-directed movements when body orientation is passively modified at a very low velocity. Experiment 1 evaluated the extent to which subjects can point precisely to memorized targets, that is, in absence of any visual information during the movement. In that condition, knowledge of body orientation may not be necessary to execute the task: only the localization of the target and the position of the arm were necessary to perform accurate pointings (egocentric task). Experiment 2 investigated how subjects are able to indicate their subjective horizon, in absence of visual information. This geocentric task requires the subjects to take into account not only the direction of the movement relative to gravity (as in Experiment 1), but also their own body orientation (Paillard 1990). Experiment 3 investigated how subjects are able to indicate their subjective horizon, in absence of arm movement. In that second geocentric task, subjects could use visual information about target position with respect to eye-fixed coordinates, but were not allowed to use proprioceptive information issued from the movement of the arm. It was hypothesized that subjects make no errors, when taking into account that their body orientation was not necessary for executing the task (Experiment 1). Conversely, when knowledge of body orientation was determinant for realizing the adjustments, significant errors were expected (Experiments 2 and 3).

Experiment 1

In Experiment 1, subjects had to point towards visually memorized targets at different angles of body orientation. In this condition, to point accurately, subjects only needed to precisely estimate target position and arm position, independent of body orientation. Thus, a rather good accuracy of the pointing movements was expected.

Materials and methods

Subjects

Seven healthy human volunteers (five females and two males, mean age =23 years) participated to the experiment. They were naive as to the purpose of this experiment and gave informed consent prior to the beginning of the session. This experiment and the following were carried out with subjects' signed informed consent in compliance with the Huriet Law (i.e., Helsinki Convention), which governs and regulates human experimentation in France.

Apparatus

The tilt apparatus (Fig. 1), installed in a completely darked room to suppress all visual references, was composed of an aircraft seat strongly fixed onto a vertical structure (1.5 m wide × 2 m high) attached to a computer-motorized axis allowing pitching movements. The axis of rotation was in the middle of the rotating structure, 1.5 m above the floor. The velocity of rotation of the structure was $0.05°\cdot s^{-1}$, following an initial acceleration phase of $0.005°\cdot s^{-2}$. Emergency buttons at different locations of the experimental room allowed the rotation of the structure to be immediately stopped if necessary. A vertical electronic plotting board painted in black faced the subjects. It was totally independent of the tilt apparatus and immobile. It was disposed so that the vertical axis of the board was aligned with the subjects' medio-sagittal plane. According to the morphology of the subjects, the distance of this vertical board was precisely regulated so that the gap between the subjects' index finger with the arm stretched and the board was equal to 5 cm. A red light-emitting diode (LED) was fixed to the pencil holder of the electronic plotting board and served as a target. The position of this LED was strictly controlled via a computer, allowing the experimenter to present this target at any vertical randomized position in the subjects' medio-sagittal plane. Its displacement accuracy was ±0.05 mm.

A Hamamatsu infrared camera, strictly independent of the structure and immobile, was positioned laterally, 2 m to the right of the apparatus. This camera served to record the terminal position of the right index fingertip at the end of the pointing movements. An infrared emitting diode (IRED) attached to the right index fingertip of the subjects (extremity of the third phalanx) allowed the final position to be sampled at 200 Hz (12-bit A/D converter).

Procedure

The subjects were seated and held tightly in position with hip and shoulder straps. The head was also fixed to the seat using a forehead strap to prevent any movement and, thus, to limit the use of neck proprioception. Earphones, providing white noise, masked the noise induced by the motor of the platform.

The subjects' task was to point as accurately as possible with the extended arm towards a memorized target during slow passive rotations of the entire body. The target was randomly presented for 200 ms in one of three different locations: +50, 0, and –50 mm with respect to the physical subjects' eyes level. The order of presentation of the three targets was counterbalanced across all trials. The session began with ten training trials followed by 18 experi-

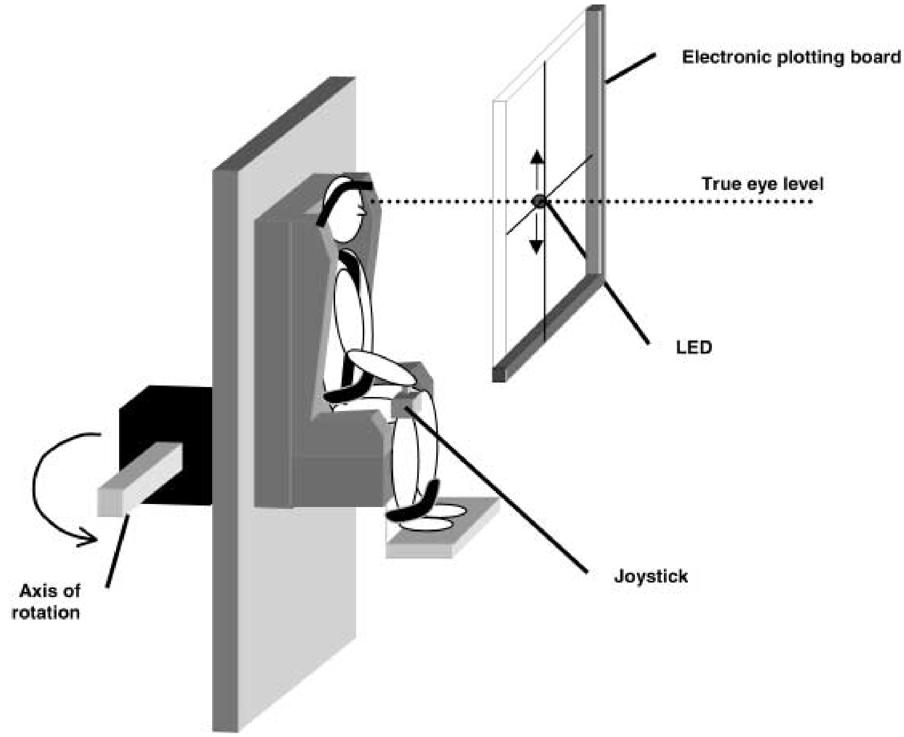


Fig. 1 Schematic representation of the experimental setup used for the three experiments. Subjects were firmly attached with head, shoulder, hip, and foot belts to prevent any movement. In Experiment 3, the adjustment of the LED placed in front of the subjects (visually perceived eye level) was realized through the use of a joystick

mental trials (six forward rotations, six backward rotations, and six blank trials), executed randomly. During the training trials, no feedback was given to the subjects concerning their accuracy level. However, only information regarding the respect of the instructions were given during these trials. During the training and experimental sessions, subjects performed three pointing movements per trial, one toward each target location, immediately after target offset. When in the final position (at the end of each pointing movement), subjects were instructed to validate verbally their final position to the experimenter and then to come back to their starting position. The targets were presented when the pitch angle, ν, reached 2, 4, and 8°. During blank trials, the targets were presented at times equivalent to those pertinent for trials in which a rotation occurred. In addition to the pointing movements, subjects had to indicate verbally when they detected a rotation of the platform, in which direction, and how confident they were of their response in order to prevent them from guessing. A complete session lasted approximately 2 h. Rest periods were systematically provided between trials, during the return of the rotating structure in the vertical position. For the blank trials, rest periods of approximately the same time were also provided.

Data collection and analysis

To assess the possible influence of body rotation on the accuracy of pointing movements, a reference position was first calculated for the three targets. For each target, the averaged final index position recorded during the blank trials (the rotating structure was motionless and vertical) served as reference values. Signed errors, Δ, were computed by subtracting the final position of the pointing movements during a rotation of the structure to the reference computed for the blank trials. Positive errors indicated an overestimation of target position (pointing above target position) and negative errors indicated an underestimation of target position (pointing below target position). A 2 (Direction: forward and backward) × 3 (Angle: 2, 4, and 8°) ANOVA with repeated measures on both factors was applied to the pointing errors of the memorized targets.

Table 1 Mean deviation of the estimated angle from accuracy (signed error Δ) and standard deviation in pointing to memorized targets for the three angles and the two directions of tilt (ν)

Subjects		Forward			Backward		
		–2°	–4°	–8°	2°	4°	8°
1	Mean	–3.11	–1.35	–1.48	–0.53	–0.26	–0.21
	SD	2.42	2.42	1.51	2.79	2.10	2.10
2	Mean	–1.22	0.75	–1.93	–0.37	–0.50	2.05
	SD	1.81	2.05	–	1.66	1.55	–
3	Mean	–0.12	–1.22	–1.57	–0.32	–0.10	1.14
	SD	3.09	2.11	–	0.89	1.57	2.89
4	Mean	0.11	1.31	1.09	0.47	2.32	0.36
	SD	2.91	2.76	1.86	3.47	1.72	4.90
5	Mean	–1.63	–1.83	–1.65	1.11	1.32	1.11
	SD	2.54	1.98	1.82	1.12	1.97	1.78
6	Mean	–0.46	–1.17	–0.50	0.69	2.16	–2.86
	SD	2.38	1.45	1.87	1.88	3.01	5.62
7	Mean	–0.88	0.73	–0.88	–0.69	–1.12	–3.28
	SD	1.14	2.72	–	1.57	1.63	2.47
All	Mean	–1.04	–0.39	–0.98	0.05	0.54	–0.24
subjects	SD	1.09	1.27	1.03	0.69	1.37	2.05

Results

Errors in pointing to memorized targets

Subjects were required to point towards memorized targets with the extended arm. Table 1 summarizes the mean signed error, Δ, and SD for the seven subjects. The ANOVA yielded no main effects of Direction and Angle and no significant interaction (P>0.05). As illustrated in Fig. 2, the accuracy of the pointing movements was not significantly altered by slow, passive, and unconscious rotations of the entire body. Interestingly, the threshold for tilt perception was at 5.2° on average, as indicated in Fig. 2.

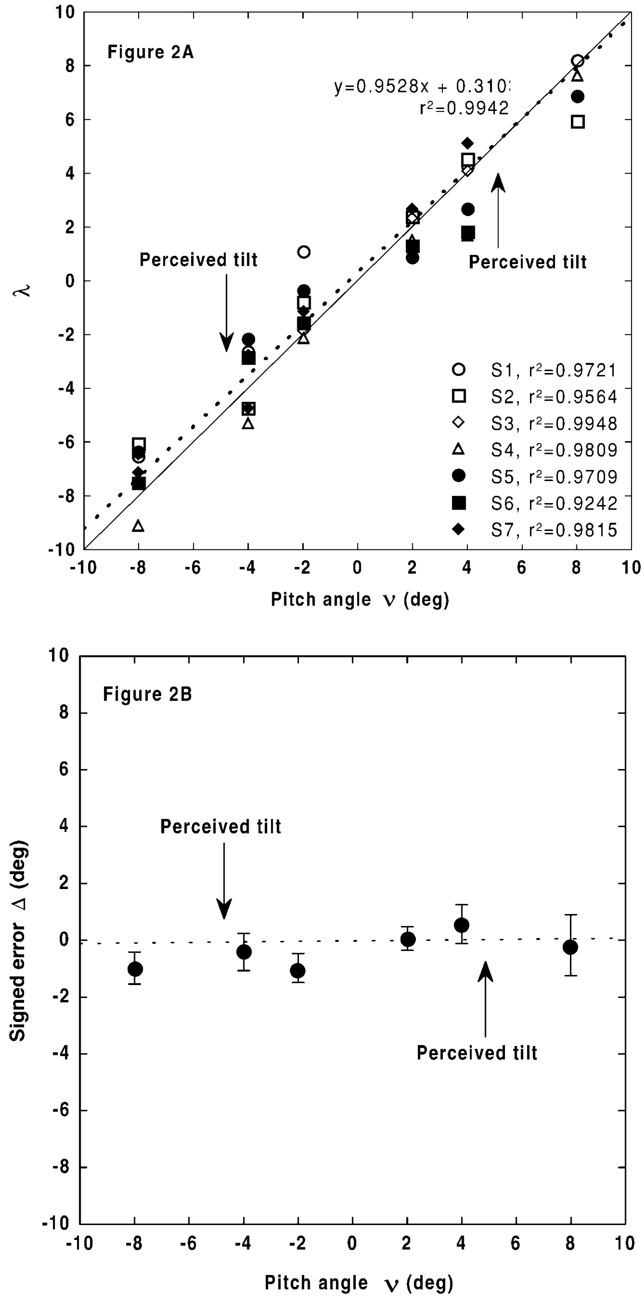


Fig. 2 **A** For each subject, the deviation of the head's x-axis from the set infrared-emitting diode (λ) is plotted against the deviation of the head's x-axis from the objective horizon (pitch angle ν). The *solid line* is the deviation of the head's x-axis from the flashed target light-emitting diode. The overall regression line (*dotted line*), the individual coefficients of correlation and the threshold of perceived tilt (*black arrows*) are also reported. **B** The deviation of the estimated angle from accuracy (signed error Δ) plotted against the pitch angle ν and inter-individual standard deviation. Negative values of ν indicated a forward rotation, whereas positive values indicated a backward rotation of the platform. The overall regression line (*dotted line*) and the threshold of perceived tilt (*black arrows*) are also reported

Absolute errors in pointing to memorized targets

In order to compare the amplitude of errors according to the direction of the platform, absolute errors (unsigned errors) were computed. The ANOVA yielded no main effects of Direction and Angle (P>0.05) on the amplitude of the absolute errors. This suggested that the amplitude of errors in pointing to memorized targets does not depend on the direction of the tilt or on the amplitude of the tilt angle ν.

Discussion

These results suggested that, even though the subjects have a wrong representation of their whole-body orientation (see Teasdale et al. 1999), pointing movements towards memorized targets remain accurate. In such an egocentric task, subjects seemed to rely only on the position of the target and on the initial position of their pointing limb, independent of their body orientation (detected or not detected).

As suggested by Ito and Gresty (1997), there may be an apparent dissociation between processes responsible for estimating postural tilt and processes responsible for localizing and pointing memorized targets. In Experiment 1, only processes for pointing towards memorized targets were implied. However, in some other specific tasks, the subjects have to precisely take into account their body orientation. For example, adjusting or pointing to the subjective horizon may be defined as a geocentric task that is in direct relation to the position of the body and based on gravity forces (Paillard 1990). In an illuminated environment, subjects can perform geocentric judgments, such as indicating the eye level, by means of purely optical information, whereas in darkness, extraretinal, vestibular, and other proprioceptive information is necessary to determine this subjective direction (Stoper and Cohen 1989).

Experiment 2

Experiment 2 investigated the subjects' ability to determine accurately their subjective proprioceptive horizon (a geocentric task) when slow passive body rotations were imposed. In that task, subjects had to take into account both the change in the direction of the movement relative to the gravity vector (as in Experiment 1) and their own whole-body orientation to perform accurate judgments. Because a slow rotation of the structure induced errors in perceiving body orientation (Teasdale et al. 1999), significant errors in indicating the subjective proprioceptive horizon were expected.

Materials and methods

Subjects

Seven healthy human volunteers (two females and five males, mean age =27 years), naive to the purpose of the experiment, gave informed consent to participate. None of these had participated to Experiment 1. The experiment was carried out in compliance with the French Huriet Law.

Apparatus and task

The experimental apparatus was identical to that used in Experiment 1, except that the plotting board was not used. As in Experiment 1, arm-pointing movements were performed with the extended arm. More precisely, subjects were required to indicate their subjective horizon rather than pointing towards memorized targets. Precision of the movements was recorded as in Experiment 1 by means of the Hamamatsu infrared camera.

Procedure

Subjects were required to indicate as precisely as possible their subjective horizon with the extended arm. No visual cues were given to the subjects, the adjustments being performed in complete darkness. Subjects provided their answer at the go signal given orally by the experimenter. Subjects were not allowed final corrections and were required, as in Experiment 1, to validate verbally their final arm position. After the adjustment, subjects brought their arm back to its initial starting position while the structure continued to move slowly. Three pointing movements were executed during each trial at three different pitch angles, ν,of the rotating structure (2, 4, and 8°). As in Experiment 1, a training session of ten trials was followed by 18 experimental trials (six forward, six backward, and six blank trials) presented randomly.

Data analysis

For each subject, we first calculated the reference value for the subjective proprioceptive horizon, that is, the average final position of the pointing movements towards the subjective horizon realized during the blank trials. We then calculated the signed errors, Δ, expressed in degrees, by computing the algebraic difference between the reference value and the final positions measured during the rotation of the platform. A negative value indicated that the pointed subjective horizon was below the reference value, whereas a positive value indicated that the pointed horizon was above the reference. A 2 (Direction: forward and backward) × 3 (Angle: 2, 4, and 8°) ANOVA with repeated measures on both factors was applied to the data.

Results

Errors in adjusting the subjective proprioceptive horizon

The ANOVA showed a significant main effect of Direction [$F(1,6)=21.90$, $P<0.01$] and a significant interaction of Direction × Angle [$F(2,12)=5.67$, $P<0.05$] on the adjustment of the subjective proprioceptive horizon. The errors in indicating the horizon were directly dependent on the direction of the orientation of the platform (Table 2). As illustrated in Fig. 3, subjects systematically indicated their subjective proprioceptive horizon too high when rotated backward and too low when rotated forward, but in the range of a normal Aubert-effect.

Table 2 Mean deviation of the estimated angle from accuracy (signed error Δ) and standard deviation in adjusting the subjective proprioceptive horizon for the three angles and the two directions of tilt (ν)

Subjects		Forward			Backward		
		–2°	–4°	–8°	2°	4°	8°
1	Mean	–4.66	–2.79	–6.14	–0.33	2.32	2.48
	SD	1.72	1.82	2.79	2.73	2.37	4.15
2	Mean	–2.60	–1.57	–2.18	–1.38	–1.17	–2.16
	SD	2.99	3.74	–	2.76	3.44	–
3	Mean	–1.70	–1.63	–6.14	1.09	1.22	1.63
	SD	1.69	3.69	–	2.50	1.54	3.54
4	Mean	–1.63	–3.55	–2.50	0.63	2.07	3.69
	SD	2.56	3.26	2.30	2.47	2.61	2.45
5	Mean	–0.79	–1.41	–2.58	1.07	0.38	3.23
	SD	2.45	3.18	0.78	1.52	1.63	1.70
6	Mean	–1.13	–3.08	–4.87	0.59	1.68	1.60
	SD	3.69	2.87	3.31	4.57	2.45	4.91
7	Mean	–1.91	–0.32	1.40	–0.13	0.95	2.05
	SD	3.65	2.24	–	2.89	1.72	3.42
All subjects	Mean	–2.05	–2.05	–3.28	0.22	1.06	1.78
	SD	1.28	1.13	2.68	0.89	1.18	1.90

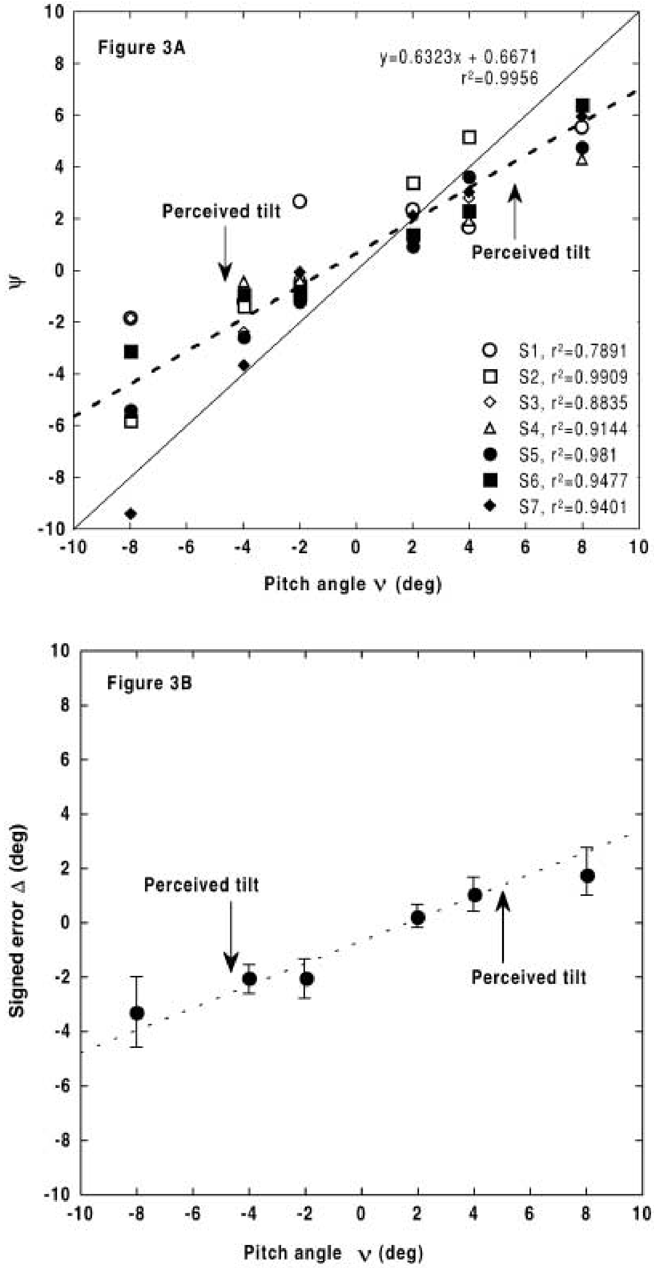


Fig. 3 **A** For each subject, the deviation of the head's x-axis from the subjective proprioceptive horizon (Ψ) is plotted against the deviation of the head's x-axis from the objective horizon (pitch angle ν). The overall regression line (*dotted line*), the individual coefficients of correlation and the threshold of perceived tilt (*black arrows*) are also reported. **B** The deviation of the estimated angle from accuracy (signed error Δ) plotted against the pitch angle ν and inter-individual standard deviation. Negative values of ν indicated a forward rotation, whereas positive values indicated a backward rotation of the platform. The overall regression line (*dotted line*) and the threshold of perceived tilt (*black arrows*) are also reported

Results showed that, when rotated slowly and passively, subjects, to some extent, performed inaccurate judgments of their subjective horizon. The errors were in the direction of body rotation. Interestingly, the threshold for tilt perception was at 5.35° on average, as indicated in Fig. 3, confirming results of Teasdale et al. (1999). A comparison of the errors made at 4° of pitch angle, ν, when body orientation was detected or non detected, did not show any significant effect, suggesting that the detection of body orientation did not affect subjects' behavior.

Absolute errors in adjusting the subjective proprioceptive horizon

The ANOVA yielded main effects of Direction [$F(1,6)=7.36$, $P<0.05$] and of Angle [$F(2,12)=14.18$, $P<0.001$] on the absolute errors. Absolute errors in adjusting the subjective proprioceptive horizon were greater when subjects were tilted forward than when they were tilted backward (2.59 vs. 1.51°). Furthermore, these absolute errors were also dependent on the pitch angle ν (1.4, 1.72, and 3.04° for 2, 4, and 8° of pitch angle, respectively).

Discussion

The results showed that, despite the possibility of using proprioceptive signals issued from the moving limb, subjects were inaccurate in adjusting their proprioceptive horizon. This suggests that information about arm position was not sufficient to precisely determine the subjective horizon. The fact that the subjects inaccurately detected and computed their whole-body orientation, leading to an altered adjustment of their subjective horizon, may explain the observed errors.

In the present task, subjects were asked to indicate their subjective horizon with the arm and without any visual cues. However, traditional adjustment tasks generally consist of adjusting a visual target on the subjective horizon, that is, defining the visually perceived eye level (VPEL) (e.g., Dizio et al. 1997; Matin and Li 1995; Raphel and Barraud 1994; Raphel et al. 1996). In such a task, subjects have to visually control and adjust online the position of a LED by manipulating a joystick. The use of arm proprioceptive information is generally reduced. Moreover, it has been shown that subjects mainly rely on vestibular and neck proprioceptive information (regarding the orientation of the head relative to gravity), extraretinal information (regarding the orientation of the eye relative to the head), and retinal information (to locate a visual target on the retina) to adjust the position of the LED (Matin and Li 1995). The absence of such retinal information may explain the errors observed in the present experiment.

Experiment 3

In Experiment 3, subjects performed a new geocentric task, in which they were required to adjust visually a LED to their subjective horizon, that is, the visually perceived eye level. Furthermore, they performed the task through the control of a joystick, in absence of any arm movement.

Materials and methods

Subjects

Seven healthy human volunteers (two females and five males, mean age =25 years) gave informed consent to participate. All subjects were naive as to the purpose of this experiment and did not previously participate to Experiments 1 and 2. The experiment was carried out in compliance with the French Huriet Law.

Apparatus, task, and procedure

The apparatus was similar to that used in Experiment 1. To eliminate the use of arm proprioception and focus on the influence of visual information, subjects were asked to indicate their subjective horizon by displacing an illuminated red LED on the plotting board through the manipulation of a joystick with the arm strictly immobile. The onset of the LED was the cue for the subjects to point to their subjective horizon. The LED was presented in three different positions relative to the physical eye level of the subjects (+20, 0, –20 mm). Position of presentation of this LED was counterbalanced across all trials. Subjects made three pointing movements per trial, triggered by the experimenter when the pitch angle, ν,reached 2, 4, and 8°. The subjects were asked to rapidly adjust the position of the LED by making no more than two corrective adjustments (reversing the direction of displacement of the LED). At the end of each adjustment, subjects were required to validate their position by clicking on the joystick. The session began with ten training trials followed by 18 experimental trials (six forward rotations, six backward rotations, and six blank trials) presented randomly. Rest periods were systematically provided during the return of the structure to the initial vertical position. For the blank trials, rest periods of approximately the same time were also provided.

Data analysis

The errors in indicating the subjective visual horizon were calculated as in the first two experiments. For each subject, we first calculated the reference value of the subjective horizon measured during the blank trials. The algebraic difference between the reference value and the actual horizon position pointed to corresponded to the signed error, Δ, in adjusting the horizon. As in the previous experiments, positive errors indicated an overshoot of the subjective horizon and negative errors an undershoot. A 2 (Direction: forward and backward) × 3 (Angle: 2, 4, and 8°) ANOVA with repeated measures on both factors was then applied to the subjective horizon-pointing errors.

Results

Errors in adjusting the subjective visual horizon

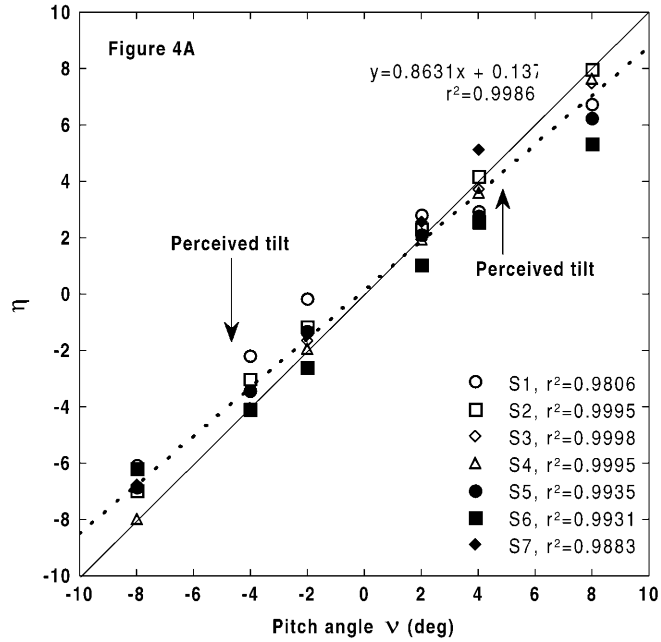
The ANOVA showed a main effect of Direction [$F(1,6)=15.15$, $P<0.01$] and a significant interaction of Direction × Angle [$F(2,12)=8.20$, $P<0.01$]. As illustrated in Fig. 4, subjects indicated their subjective visual horizon too high when they were slowly rotated backward and too low when they were rotated forward, but in the range of a normal Aubert-effect. This result showed that subjects misperceived their body orientation when rotated slowly and passively. Signed errors, Δ, in adjusting the visual horizon for each subject (means and standard deviations) are summarized in Table 3. Interestingly, the threshold for tilt perception was at approximately 4.7° on average, as indicated in Fig. 4. A comparison of the errors made at 4° of pitch angle ν, when body orientation was detected or non-detected, did not show any significant effect, suggesting that the detection of body orientation did not affect subjects' behavior.

Absolute errors in adjusting the subjective visual horizon

The ANOVA yielded no main effect of Direction ($P>0.05$), but a main effect of Angle [$F(2,12)=6.44$, $P<0.01$] on the absolute errors in adjusting the subjective visual horizon. As in Experiment 2, the absolute errors in adjusting the horizon were directly proportional to the pitch angle ν (0.55, 0.71, and 1.14° for 2, 4, and 8° of pitch angle, respectively).

Discussion

According to Matin and Li (1992), three kinds of information are useful to adjust precisely VPEL in darkness: (1) extraretinal infor-



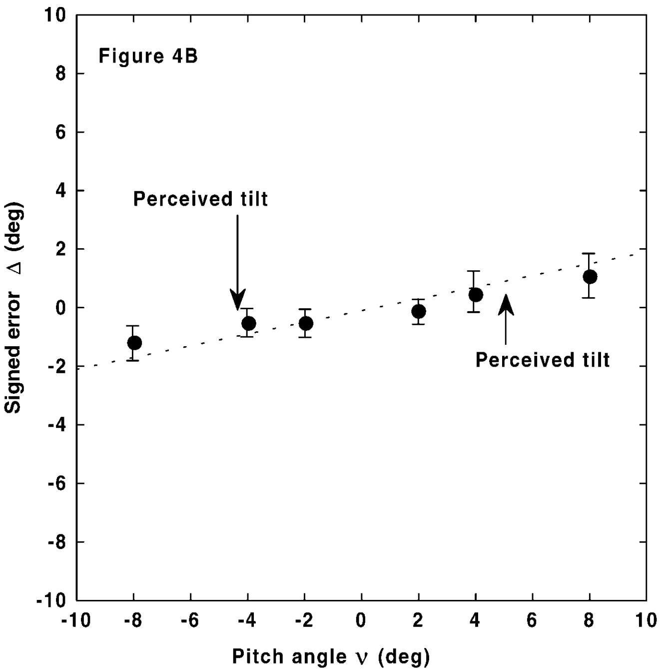


Fig. 4 **A** For each subject, the deviation of the head's x-axis from the subjective visual horizon (η) is plotted against the deviation of the head's x-axis from the objective horizon (pitch angle ν). The overall regression line (*dotted line*), the individual coefficients of correlation and the threshold of perceived tilt (*black arrows*) are also reported. **B** The deviation of the estimated angle from accuracy (signed error Δ) plotted against the pitch angle ν and inter-individual standard deviation. Negative values of ν indicated a forward rotation, whereas positive values indicated a backward rotation of the platform. The overall regression line (*dotted line*) and the threshold of perceived tilt (*black arrows*) are also reported

Table 3 Mean deviation of the estimated angle from accuracy (signed error Δ) and standard deviation in adjusting the subjective visual horizon for the three angles and the two directions of tilt (ν)

Subjects		Forward			Backward		
		–2°	–4°	–8°	2°	4°	8°
1	Mean	–1.82	–1.82	–1.92	–0.83	1.08	1.27
	SD	1.07	1.04	1.63	0.80	1.66	1.18
2	Mean	–0.84	–0.98	–1.03	–0.31	–0.19	0.03
	SD	0.50	0.90	0.74	0.44	0.78	0.62
3	Mean	–0.33	–0.56	–1.10	0.06	0.28	0.52
	SD	0.59	0.47	0.56	1.00	0.48	0.98
4	Mean	–0.07	0.15	–0.04	0.07	0.41	0.37
	SD	0.31	0.96	0.71	0.28	0.44	0.29
5	Mean	–0.67	–0.57	–1.13	–0.09	1.24	1.75
	SD	1.15	0.69	0.37	0.67	1.41	1.80
6	Mean	0.58	0.09	–1.80	0.97	1.43	2.66
	SD	0.57	0.28	1.74	0.79	1.78	1.71
7	Mean	–0.55	0.06	–1.24	–0.57	–1.12	1.10
	SD	0.81	0.46	–	0.78	1.42	–
All subjects	Mean	–0.52	–0.51	–1.18	–0.09	0.44	1.1
	SD	0.73	0.71	0.61	0.57	0.90	0.90

mation regarding the orientation of the head relative to gravity, (2) extraretinal information regarding the orientation of the eye relative to the head, and (3) information regarding the location of a visual target onto the retina. Alteration of one of these types of information may generate specific modifications of VPEL. Our results showed a decrease of the accuracy level in indicating VPEL. Contrary to Experiment 2, retinal information was available through the illumination of the LED. However, this retinal signal did not give information about target position with respect to gravity, but only about target position with respect to eye-fixed coordinates. Extraretinal information regarding the orientation of the eyes with respect to the head was also preserved. Thus, the observed errors in indicating VPEL were probably due to a misperception of the orientation of the head relative to gravity. This observation confirmed results obtained by Teasdale et al. (1999) on the role of the otolithic organs. In the present study, subjects were unable to indicate precisely their VPEL, as if they did not precisely detect their own orientation or could not rely on otolithic signals to implement a cognitive coding.

General discussion

Teasdale et al. (1999) recently showed that subjects were inaccurate in consciously detecting slow passive body rotations when only the otolithic signal was informative, that is, when proprioceptive signals were severely reduced and when visual cues were not available. The purpose of the present experiments was to investigate the capability of precisely pointing to specific targets in similar pseudo-static conditions. More precisely, it was to investigate the influence of whole, passive body orientation on subjects' level of accuracy. This body orientation may be a source of inaccuracy for pointing movements. Subjects performed two different types of task during slow and passive whole-body rotations. In Experiment 1, subjects were asked to perform pointing movements towards visually memorized targets (egocentric task). In Experiments 2 and 3, they were asked to perform adjustments of their subjective horizon (geocentric tasks) using either a proprioceptive (Experiment 2) or a visual signal (Experiment 3). The results were different according to the nature of the task. When subjects performed an egocentric task, the accuracy of the pointings was not altered by a slow passive orientation of the body. Conversely, when performing a geocentric task (Experiments 2 and 3), subjects made larger errors in adjusting their subjective horizon. This was true whatever the sensory cues available (arm proprioceptive signals in Experiment 2 and visual cues in Experiment 3), suggesting that these errors were mainly due to a shift in the perception of the body relative to the gravity vector.

This observation confirms that signals issued from various receptors have to be integrated in a multi-modal reference frame (Lipshits and McIntyre 1999; Mittelsteadt 1983) to compute body orientation and determine the subjective horizon. In Experiments 2 and 3, however, different sources of information were severely reduced and did not allow this dynamic multisensory integration. Indicating the proprioceptive subjective horizon or similarly adjusting the VPEL is related to a horizontal plane orthogonal to gravity. A misperception of the orientation of gravity may lead to an inaccurate coding of the horizon. Previous studies using modifications of the gravito-inertial force have shown elevator and oculogravic illusions (Dizio et al. 1997; Raphel and Barraud 1994). In these experiments, the new gravitational force induced a modification of the coding of the orientation of the head relative to gravity. This modification was responsible for the errors made in adjusting the VPEL, when subjects were aware of the new force as well (Dizio et al. 1997). Welch and Post (1996), studying hand pointing movements in pitched visual environments, concluded that both a small change in the perceived visual localization and a larger shift in the perception of the gravity vector contributed to VPEL shifts.

As previously emphasized, indicating the subjective proprioceptive horizon with the outstretched arm (Experiment 2) or indicating the subjective visual horizon via a LED (Experiment 3) led to errors. Interestingly, when arm proprioception was available, the errors were greater than when vision of the LED was provided (see Figs. 3 and 4 and tables 2 and 3). In Experiment 3, the process in the subjects' brain controlled, by means of motor commands to the hand moving the joystick, the deviation η ($\eta=\nu-\Delta$) of the LED from the head's x-axis, which is represented by both retinal and extraretinal signals. ν is the pitch angle and Δ the deviation of the visual indicator of the subjective horizon (i.e., the deviation of the estimated angle from accuracy). The system, therefore, must adjust η to the deviation ν of the head's x-axis from the objective horizon, which is computed by means of otolithic signals. According to a theory of the subjective visual vertical that has since stood many tests (Mittelstaedt 1983), these computations can, in the present case of pure pitch, be represented as follows:

$$\eta=\arctan\left(\sin\nu/((Fz/Fx)\cos\nu+NM)\right)$$

where Fz/Fx is the proportion of the z- to the x-components of the otoliths, N is the square root of the sum of ($\sin\nu$) squared plus [$(Fz/Fx)\cos\nu$] squared, and M is the amount of the idiotropic vector, a tilt-independent internal input that tends to rotate the visual subjective horizon into the x-y plane of the head. In an adaptation of the parameters of the theory to the data of Udo de Haes (means of 13 Ss, 1970), Fz/Fx was determined as 0.54/0.7=0.771 and M=0.48. Inserted into the equation above, these parameters fit the results of Experiment 3 rather well. The parameters can also be fitted to the result of Experiment 2, either with Fz/Fx=0.771 and M=0.9 or Fz/Fx=1.0 and M=0.48, or many push-pull variations between these two boundary-values of Fz/Fx and M, provided the constant bias of about 0.6° is subtracted from η in the initial equation. This suggests that the subjective proprioceptive horizon in Experiment 2 differs from the subjective visual horizon in Experiment 3 by an enlarged gain of the z-axis component, Fz, or an enlarged idiotropic vector, M, or both. The use of the trunk-bound arm may induce the z-axis component of the truncal graviceptors (Mittelstaedt 1992) or may increase the tendency to assume that head and body are still upright (Mittelstaedt 1999) or may increase both effects.

This result underlines the possible contribution of the proprioceptive signal in the adjustment of the subjective horizon. Moreover, this proprioceptive information may also allow the subjects to partly adjust on line their arm position by positioning the arm perpendicularly to the gravity vector. However, it is noteworthy that this information is not sufficient for performing the adjustments without making errors. On the other hand, this difference between the two experiments stresses the weak contribution of the visual cue in improving the accuracy of the adjustment. This result may be explained by the fact that visual cues, contrary to proprioceptive information, does not directly inform the subjects about the direction of the gravity vector. Moreover, only objectively horizontal or vertical visual structures could help to orient the subjective visual horizon, yet not a single mobile LED. The different contribution of proprioceptive and visual cues in indicating the subjective horizon may induce that the simultaneous existence of both signals may improve the accuracy of the adjustments of the subjective horizon. On one hand, the proprioceptive signal may inform the subjects about the position of their arm relative to gravity. On the other hand, as suggested by Blouin et al. (1995), visual cues (that is retinal information) may be essential for the calibration of the position of the eye in its orbit. This suggestion will be tested further.

Finally, it is also important to underline that the errors made in adjusting the subjective horizon (with the extended arm or only through the joystick) were systematically smaller than the amplitude of the body orientation. For example, when the subjects' body was inclined 8° from vertical, subjects made errors of 1.2° on average. This suggested that, also in a geocentric task, subjects partially took their body orientation into account even though they were not always conscious of the rotation of the platform. Some compensatory mechanisms may exist in the adjustment of the subjective horizon, suggesting that sensorimotor processes (with respect to cognitive processes) took place. Two kinds of explanation may account for this particular result. On the one hand, changes in the otolithic information used to adjust the subjective horizon took place too slowly to allow a complete and accurate adjustment. On the other hand, other kinesthetic and tactile sensations (e.g., variations of pressure on different parts of the body) were used. Matin and Li (1992) confirmed the possible contribution of such information to the specification of head and body orientation relative to gravity. More generally, results showing that the perceived vertical is based on multisensory information (Lipshits and McIntyre 1999; Mittelstaedt 1983) could also explain why, in the present experiment, subjects made errors smaller than the angle of tilt in estimating their proprioceptive or visual subjective horizon. In the present experiments, however, this information was considerably reduced (e.g., limited and slow variations of pressure, since the subjects were attached with large belts and the platform rotated slowly and head fixed).

In summary, two main insights emerged from the present results. First, subjects were able to take the angle of tilt into account to perform accurate movements, even though they were unaware of their whole-body orientation (Experiment 1). However, the comparison of Experiment 1 with Experiments 2 and 3 emphasized the differentiation between a pointing task that can be performed at a sensorimotor level (egocentric task) and judgment tasks (geocentric tasks) that can be considered to be more complex tasks requiring a computation of sensory information to extract a cognitive answer. The perception of the visual and the perception of the postural vertical seem to be based on different, only partially overlapping, inputs and are formed by different central nervous algorithms (Mittelstaedt 1983, 1999). In the present study, the perception of the proprioceptive (Experiment 2) and visual horizon (Experiment 3) was present, whilst that of tilt was missing. Furthermore, these perceptions changed as a single, smooth, and monotonic function of tilt, independent of whether the perception of body orientation was present or not.

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