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# Kinaesthetic and visual perceptions of orientations

Laure Lejeune, Régis Thouvarecq, David J Anderson, Jean Caston, François Jouen
Information, Organisation et Action, EA 4260, UFR STAPS, University of Caen Basse Normandie, 14032 Caen Cedex, France; e-mail: laure.lejeune@unicaen.fr
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**Abstract.** In the present study we compare the kinaesthetic and visual perception of the vertical and horizontal orientations (subjective vertical and subjective horizontal) to determine whether the perception of cardinal orientations is amodal or modality-specific. The influence of methodological factors on the accuracy of perception is also investigated by varying the stimulus position as a function of its initial tilt (clockwise or counterclockwise) and its angle (22°, 45°, 67°, and 90°) in respect to its physical orientation. Ten participants estimated the vertical and horizontal orientations by repositioning a rod in the kinaesthetic condition or two luminous points, forming a 'virtual line' in the visual condition. Results within the visual modality replicated previous findings by showing that estimation of the physical orientations is very accurate regardless of the initial position of the virtual line. In contrast, the perception of orientation with the kinaesthetic modality was less accurate and systematically influenced by the angle between the initial position of the rod and the required orientation. The findings question the assumption that the subjective vertical is derived from an internal representation of gravity and highlight the necessity of taking into account methodological factors in studies on subjective orientations.

## 1 Introduction

Most research on the subjective vertical involves the visual modality. A common task used to investigate the subjective visual vertical (SVV) consists of adjusting a luminous line to the physical vertical (a line through the mass centroid of the earth) in the frontal plane. Several studies have demonstrated that, without any contextual information, participants are able to adjust a luminous line to the vertical orientation with an error less than 1° (Bauermeister 1964; Howard and Templeton 1966; Luyat 1997, for review), suggesting that the SVV is very accurate. This accuracy decreases in patients with vestibular or cortico-parietal lesions, in whom the SVV significantly deviates from the physical vertical (Brandt and Dieterich 1994, for review). This accuracy also decreases when vestibular and proprioceptive inputs are modified by tilting the head and/or the body, that is to say when the physical vertical and the orientation of the body's longitudinal axis (or $Z$-axis) are uncoupled, or modified by centrifugation (Anastasopoulos et al 1997; Bauermeister 1964; Guerraz et al 1998; Lechner-Steinleitner et al 1979; Mittelstaedt 1991, 1995, 1999; Tardy-Gervet and Severac-Cauquil 1998; Yardley 1990; Zink et al 1998). Furthermore, the direction of the deviation of the subjective vertical (SV) depends on the magnitude of the body/head tilt as evidenced by the Aubert and Müller effects (called A and E respectively) (Asch and Witkin 1948a, 1948b; Bauermeister 1978a, 1978b; Luyat et al 1997; Mittelstaedt 1983, 1986, 1991, 1995).

Owing to gravity, the vertical and horizontal orientations are major physical references of the environment. They are sensorily 'over-reinforced' (Gentaz et al 2001) and described as main orientations (Appelle and Gravetter 1985; Jenkins 1985). The natural orthogonal relationship of these orientations leads many researchers to investigate one or the other interchangeably (Carriot et al 2008). While the preservation of orthogonality between horizontal and vertical is part of the concept of verticality (Bronstein 1999), the subjective horizontal has been poorly studied, except in relation to the vestibular modality to diagnose vestibular disturbances (Bergenius et al 1996; Betts and

Curthoys 1998; Tribukait et al 1996). In healthy participants standing upright, the visual subjective horizontal was found within the range $\pm 2.5°$ (mean value $= -0.21°$) by Tribukait and his colleagues (1996) and it appears as accurate as the visual subjective vertical (Tabak et al 1997).

As pointed out by Carriot et al (2008), when exploring the effects of roll tilt on horizontal estimations, the results obtained by Miller et al (1968) are similar to those of Bauermeister (1964) and show an alternation of A and E effects from the 90° counterclockwise body position to 90° clockwise body position. However, this subjective orthogonality is not systematic as only an increase of the A effect was found (Trousselard et al 2003). This orthogonality issue was extensively studied by Betts and Curthoys (1998) who showed that whole-body rotations interfere with the orthogonality of visual subjective vertical and horizontal. The discrepancy of results in the visual tasks stresses the necessity to investigate both vertical and horizontal orientations especially when exploring another modality (haptic, proprioceptive, or kinaesthetic). In the present study of participants standing upright we expected to observe a preservation of the orthogonality of the two subjective orientations.

Although vision is the preferred modality for studying the perception of spatial orientations and found to provide very accurate information about orientation, Wade and Curthoys (1997) have shown that, during whole-body roll tilt, ocular counter-roll alone can change the perceived orientation of a visual line. The implication is that the setting of a visual line cannot be used to infer perceived postural orientation directly (Wade and Curthoys 1997). As kinaesthesia is largely devoted to perception of the orientation of body segments but also has an exteroceptive function (Pagano and Turvey 1992, 1995; Roll 1994), the use of the kinaesthetic modality both resolves this weakness inherent in studies using the visual modality and contributes to a better understanding of the subjective vertical formation.

Surprisingly, the subjective kinaesthetic vertical (ie the adjustment of an object to the vertical by using kinaesthetic information only) has been rarely investigated. By 'kinaesthetic' we refer to the receptors in the muscular-articular link system that contribute to the conscious perception of movement and position (McCloskey 1978).[1] Most of recent research aimed at determining the coordinate system underlying kinaesthesia has shown that the kinaesthetic sensory system uses an earth-fixed gravitational axis (Darling and Hondzinski 1999; Flanders et al 1992; Soechting and Flanders 1989a, 1989b), similar to the visual system (Darling and Hondzinski 1997). In the same vein, the assumption of an earth-fixed gravitational axis has contributed, in large part, to the demonstration that the perception of upper-limb orientation is more accurate than the perception of shoulder and elbow joint angles (Soechting 1982; Soechting and Ross 1984; Worringham et al 1987). However, whereas these experimental tasks investigate the postural subjective vertical (ie the estimation of the physical vertical in setting the body or a part of the body to this orientation), our objective was to explore the kinaesthetic subjective vertical (ie the estimation of the physical vertical in setting an external object on the basis of kinaesthetic information) on the assumption that position sense is very accurate (2°–3°—Paillard and Brouchon 1968; Walsh et al 2006).

Until recently, the research on the perception of the physical vertical in a modality other than vision has been limited. In an earlier study, Bauermeister (1978a) examined how accurately participants could adjust a rod to the physical vertical during various body tilts and when considerable tactile exploration of the rod was permitted.

[1] Note that this definition is quite close to Pagano and Turvey's (1995) 'dynamic touch', which is defined as "different from cutaneous and haptic touch in that the sensitivity of the muscles plays a greater role in the detection of information than does sensitivity of the skin. Dynamic touch, in short, is the haptic subsystem most locked into the 'muscle sense'"(Pagano and Turvey 1995, page 1070).

He showed that perception of the vertical from the erect position was accurate, with a deviation from the physical vertical of approximately 2° towards the left. However, extensions of Bauermeister's work on the haptic modality have only been undertaken in earnest during the last decade (Bortolami et al 2006; Gentaz et al 2001, 2002; Guerraz et al 2000; Luyat et al 2001).

The main objective of this study was to investigate whether, similar to the visual modality, one could define a 'kinaesthetic subjective vertical' and a 'kinaesthetic subjective horizontal'. For this purpose, kinaesthetic estimation was tested by bimanual adjustments of a rod (as in experiments on the subjective visual vertical), rather than (i) by positioning a limb in a particular spatial orientation, as in experiments cited earlier concerning the postural subjective vertical (Darling and Hondzinski 1999; Darling and Miller 1995; Soechting 1982) or subjective horizontal (Carriot et al 2006) or (ii) by involving a major contribution of tactile inputs via active exploration of the external object, as in haptic tasks (Gentaz et al 2001, 2002; Guerraz et al 2000; Luyat et al 2001).

The first step of examining in detail the features of the kinaesthetic modality was to test the participants in their usual upright standing position, rather than in the seated position (and/or a tilted position) that is most commonly used in studies on the perception of verticality. The second step was to manipulate the initial orientations of the stimuli that had to be adjusted to the main orientations. As previous researchers have used only a single starting orientation, which differs across studies (Anastasopoulos et al 1997, 1999; Bauermeister 1964; Oltman 1968; Poquin et al 1998; Tardy-Gervet and Severac-Cauquil 1998), we investigated several oblique angles from the target orientation to determine if, as in the SVV studies, a single initial position of the rod can be chosen with the implicit assumption that starting position is not the main factor influencing the accuracy of the vertical estimation. One of the key questions in spatial perception is whether the brain has a unique internal representation of gravity that is generally accessible for various perceptual orientation tasks (Van Beuzecom and Van Gisbergen 2000). If this internal representation exists, the estimation of the vertical and horizontal directions should be constant (ie perceived at the same place) and independent of the initial position of the rod, for both modalities. By convention, the direction of the initial tilt (counterclockwise and clockwise) was also manipulated. Though we expected no effect of the direction of tilt between the two modalities, consistent with previous experiments on sedentary participants (Lejeune et al 2004a, 2004b), lower accuracy was expected in the kinaesthetic condition than in the visual condition.

## 2 Method and procedure

### 2.1 *Participants*

Ten volunteer students (five males/five females, mean age, $M = 27.8$ years, $\mathrm{SD} = 2.4$ years) were included in this study. All were right-handed, as determined by a score higher than 50 in the Edinburgh inventory [simplified version of Oldfield (1971)], the mean laterality score being 73. The dominant eye (ie the eye the participant reported he/she would use to look through a keyhole or into a microscope) was the right one in eight of the ten participants. The remaining two participants did not have a dominant eye.

Neither sensory, nor motor deficit was reported by the participants. Five participants wore corrective lenses for the visual experiment. Each participant completed four experimental conditions: the estimation of the vertical orientation with the visual and the kinaesthetic modality, and the estimation of the horizontal orientation with the visual and the kinaesthetic modality. The order of the four conditions was counterbalanced across participants.

## 2.2 *Apparatus*

For the kinaesthetic protocol, the experimental device was composed of a carbon rod (41 cm long with a 0.61 cm diameter) that was centred on a rotation axis perpendicular to the frontal plane and connected to a potentiometer that measured the angular position of the rod. The rod position could be adjusted to the participant's height (figure 1) and the participant–device distance was determined such that when the rod was horizontal, the angles between the trunk and the arm and between the arm and the forearm were approximately 15° and 115°, respectively.

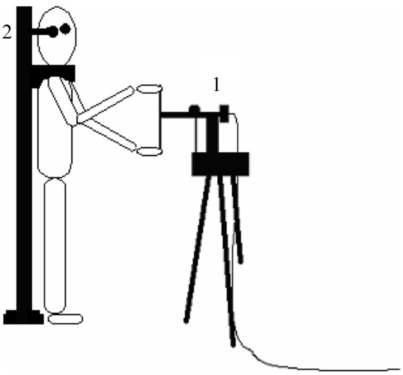


**Figure 1.** Schematic representation of the experimental device for kinaesthetic adjustments to the main orientations (1) and the device to constrain the participant (2).

The potentiometer was connected to a 12 bit A/D converter, then to a computer, which was used to control the experiment and record, reduce, and analyse the data. A program was used to start and stop the trials and it enabled visualisation of the rod position on the computer screen (recording frequency: 36 Hz).

For technical reasons, the apparatus used in the visual condition was not identical to the one used in the kinaesthetic condition. Here, the experimental device was composed of a computer screen placed at 1 m from the participant's eyes. On the black background of the screen, two points (one white, one red), 6 pixels large and approximately 14 cm apart, formed a virtual line that could rotate around its centre. The centre of the virtual rod was located at the level of the participant's eyes. An analogous program to that mentioned previously allowed the experimenter to place the line in the starting position, to displace the line around its centre and to record the data (recording frequency = 36 Hz). Note that the use of two luminous points at either end of the virtual line was designed to mimic the kinaesthetic condition in which participants had two points of contact when they placed the index finger from each hand at either end of the rod. The participant stood upright in a device that was designed to prevent head and shoulder oscillations. This device also allowed the participant to stand in a comfortable position with the arms unrestrained and designed to keep vestibular and neck muscle inputs constant during the whole experiment.

## 2.3 *Procedure*

The experiment was performed in a dark room. For each experimental condition, the rod or the two luminous points were placed in one of eight starting positions, characterised both by the angle (90°, 67°, 45°, 22°) with respect to the physical vertical or horizontal (taken as 0°), and the direction of initial tilt (clockwise or counterclockwise) with reference to each of these two physical orientations. For each starting position, the participant performed 10 trials. There was no temporal constraint and no feedback was available. The 80 trials were performed in random order, this order being the same for each experimental condition. A 10 min break was allowed in the middle of the session and after each completion of an experimental condition. In the kinaesthetic condition, the participant wore opaque glasses for the entire period of testing and also kept his/her eyes closed. The experimenter put the participant's index fingers at the ends of the rod (bimanual task) in such a way that during the whole experiment the participant's arms were never crossed. The task consisted of setting the rod to the vertical or to the horizontal orientation without exploring the rod. However, the participant was permitted to make as many corrections as necessary before releasing the rod. In the visual condition, the line was automatically placed in one of the eight starting positions already mentioned. The visual protocol was identical to the kinaesthetic protocol except that the participant was entirely passive to prevent the use of information from the muscular-articular link system. The experimenter rotated the line around its centre with a joystick. Once the participant estimated the virtual line to be vertical or to be horizontal, he/she indicated this verbally to the experimenter. If the participant realised that the initial estimate was wrong, he/she could ask the experimenter to turn the line back or forth as many times as necessary to correct the error. When the participant estimated that the virtual line was vertical or horizontal, he/she asked the experimenter to stop the trial. In each experimental condition, a calibration was done at the start of each testing session.

### 2.4 *Data analysis and dependent variables*

Typically, the algebraic mean is used to describe the deviation of the subjective vertical, SV. According to convention, deviations to the left (counterclockwise) are treated as negative and deviations to the right (clockwise) as positive. The SV value is determined by the mean of algebraic deviations computed over the trials. However, investigation of the kinaesthetic modality made us specify the constant error relative to the initial orientation of the rod: if the initial position of the rod was in the clockwise direction relative to the target orientation, then a terminal position of the rod that was clockwise relative to the target orientation was given a negative sign (ie it was deemed an undershoot) and a terminal rod position that was counterclockwise relative to the target orientation was given a positive sign (ie it was deemed an overshoot). For the visual modality, the errors were always in the counterclockwise direction with reference to the physical vertical, regardless of the direction in which the rod was initially positioned, and so not taking the initial orientation of the rod into account would have provided an accurate reflection of how participants performed on the task. However, in the kinaesthetic modality, the final position of the rod was always in the same direction as that in which the rod was initially positioned. Therefore, not taking the initial orientation of the rod into account drastically underestimates the errors in performance and hides some effects relevant to the spatial factors (eg angle and direction of the initial tilt) that were manipulated in the study. For this reason, the constant error, which determines the error with respect to the initial direction of tilt of the rod, appears to provide a more adequate description of performance (figure 2).

Two dependent variables were consequently preferred to describe the participants' adjustments (Schmidt and Lee 1999), each being computed in the same manner for both modalities. The first variable, the constant error (CE), was used as an indicator of bias (undershooting or overshooting of the physical orientation). It is defined by the following formula: $\mathrm{CE} = \Sigma(x_i - T)/n$, where $x_i$ is the score for trial $i$, $T$ is the target, and $n$ is the number of trials executed by the participant (Schmidt and Lee 1999). The sign of the CE depends on the type of error made by the participant. It was negative when the vertical or the horizontal was undershot and positive when it was overshot, with respect to the starting position of the rod. For example, for vertical adjustments, if the initial and final positions of the rod were both in a counterclockwise direction in relation to the physical vertical, this orientation was undershot. Conversely, if the initial position of the rod was counterclockwise and the final position clockwise, the physical

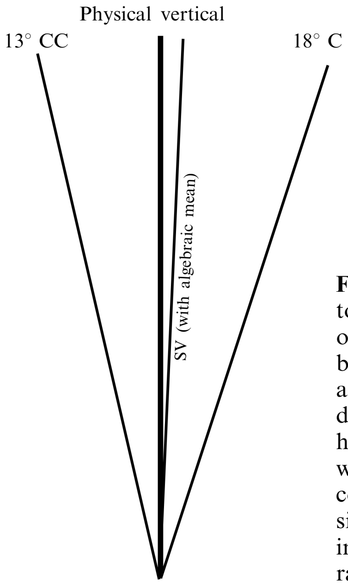


**Figure 2.** The typical behaviour in the kinaesthetic modality is to undershoot the physical vertical from counterclockwise (CC) or clockwise (C) initial positions of the rod. Typically, the algebraic mean corresponds to the mean of the final errors coded as negative when in the CC direction and positive in the C direction in reference to the physical orientation (vertical or horizontal). However, the limitations are readily apparent, where it can be seen that the small error in the kinaesthetic condition (here 2.5°) is a function of the large errors on either side of the physical vertical cancelling each other out (13° and 18° in the CC and C directions, respectively). Note that the values are randomly chosen for graphic reasons.

vertical was overshot. This variable gives information about both the magnitude and direction of the angular error (figure 2).

The second dependent variable, the variable error (VE), measured the variability of the participant's adjustments with reference to his/her mean error. The formula for VE is: $\mathrm{VE} = [\Sigma(x_i - M)^2/n]^{1/2}$ with $x_i$ being the error on trial $i$, $M$ the mean adjustment error, and $n$ the number of trials that the participant executed (Schmidt and Lee 1999). Consequently, this variable measured the inconsistency in movement outcome. It represented the participant's variability about his/her mean constant error. All errors were expressed in degrees.

Statistical analyses consisted of 2 (modality: kinaesthetic, visual) × 2 (orientation: vertical, horizontal) × 2 (direction: clockwise, counterclockwise) × 4 (angle: 90°, 67°, 45°, 22°) ANOVAs on mean constant errors and mean variable errors. Comparisons in reference to 0° (the physical orientation) were performed on CEs by using a $t$-test to determine the accuracy of the kinaesthetic and visual estimations (regardless of the direction and the angle). A posteriori comparisons were done with Tukey's a posteriori tests. The significance level was 0.05 for all analyses.

## 3 Results

### 3.1 *Constant errors*

The descriptive results (means and standard deviations) are presented in table 1.

The analysis of variance on the CE revealed that the visual modality was significantly more accurate than the kinaesthetic one ($M = -0.04$, SD $= 0.18$, and $M = -3.4$, SD $= 2.6$, respectively) ($F_{1,9} = 17.42$, $p < 0.05$). In addition, the horizontal was globally perceived with greater accuracy than the vertical orientation ($M = -0.81$, SD $= 2.18$, and $M = -2.64$, SD $= 4.28$, respectively) ($F_{1,9} = 7.71$, $p < 0.05$).

A significant interaction between modality and orientation ($F_{1,9} = 7.23$, $p < 0.05$) highlighted that the vertical was estimated with less precision ($M = -5.23$, SD $= 1.39$) than the horizontal ($M = -1.62$, SD $= 0.54$) in the kinaesthetic modality ($F_{1,9} = 7.52$, $p < 0.05$), but not in the visual modality ($F_{1,9} = 0.20$, ns) (with $M = -0.06$, SD $= 1.50$, and $M = -0.01$, SD $= 1.41$ for the vertical and the horizontal orientation, respectively). The comparison of the CE to the physical vertical (0°) indicated that the overall undershooting obtained in the kinaesthetic adjustments ($M = -5.2$, SD $= 4.4$) was significantly

**Table 1.** Constant errors (CE in degrees) as a function of the initial tilt (CC: counterclockwise; C: clockwise) and the angular distance for each experimental condition. SDs are shown in parentheses.

| Modality | Orientation | Initial tilt/° | | Angle/° | | | |
|---|---|---|---|---|---|---|---|
| | | CC | C | 90 | 67 | 45 | 22 |
| Kinaesthetic | vertical | −5.12 (3.83) | −5.35 (5.33) | −5.67 (5.11) | −6.23 (5.18) | −5.47 (4.54) | −3.56 (3.28) |
| | horizontal | −0.64 (2.33) | −2.60 (2.33) | −1.93 (2.49) | −2.13 (2.62) | −1.85 (2.56) | −0.57 (2.26) |
| Visual | vertical | −1.07 (1.20) | 0.95 (1.05) | −0.10 (1.63) | −0.05 (1.49) | −0.07 (1.46) | −0.03 (1.58) |
| | horizontal | −0.49 (1.39) | 0.47 (1.30) | −0.06 (1.43) | 0.07 (1.42) | −0.10 (1.54) | 0.04 (1.40) |

different from 0° ($t_9 = -3.76$, $p < 0.05$), contrary to the CE in the visual adjustments ($M = -0.06$, $SD = 0.3$) ($t_9 = -0.66$, ns). For the horizontal orientation, the overall undershooting was again significantly different from the 0° norm when the adjustments were performed with the kinaesthetic modality ($t_9 = -2.9$, $p < 0.05$), but not with the visual modality ($t_9 = -0.18$, ns).

A significant interaction between modality and direction ($F_{1,9} = 5.48$, $p < 0.05$) revealed that the error between counterclockwise and clockwise initial directions of the rod ($M = -2.87$, $SD = 3.84$, and $M = -3.97$, $SD = 4.29$, respectively) was not significantly different in the kinaesthetic modality ($F_{1,9} = 2.92$, ns) but that a trend occurred between counterclockwise and clockwise initial directions of the rod in the visual modality (with $M = -0.78$, $SD = 1.31$, and $M = 0.70$, $SD = 1.18$, respectively) ($F_{1,9} = 4.49$, $p = 0.06$) (figure 3). More specifically, the CE observed in the kinaesthetic modality was oriented in the direction of the initial tilt of the rod, whereas for the visual modality the CE was located in the counterclockwise direction with reference to the physical vertical or horizontal regardless of the initial direction of the rod. The interaction between orientation, modality, and direction was not significant.

An interaction between orientation and direction was also found ($F_{1,9} = 9.49$, $p < 0.05$). Specifically, when both modalities were combined, counterclockwise initial directions of the rod led to greater errors in the vertical ($M = -3.09$, $SD = 3.45$) than in the horizontal orientation ($M = -0.56$, $SD = 1.89$) ($F_{1,9} = 9.99$, $p < 0.05$), on the contrary, constant errors for the clockwise initial directions of the rod were not significantly different between vertical and horizontal orientations ($M = -2.20$, $SD = 4.93$, and $M = -1.06$, $SD = 2.41$) ($F_{1,9} = 3.95$, ns) (figure 4).

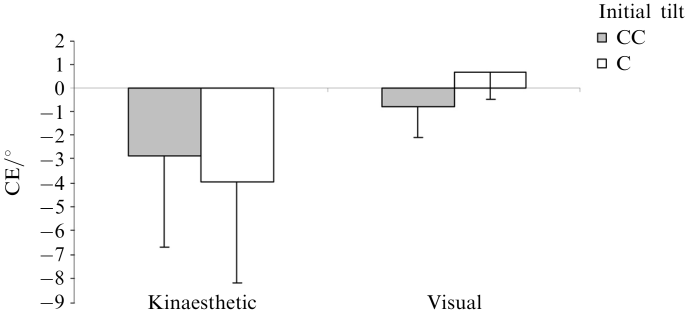


**Figure 3.** Constant error (CE) as a function of the initial tilt of the rod (CC: counterclockwise; C: clockwise) and the modality.

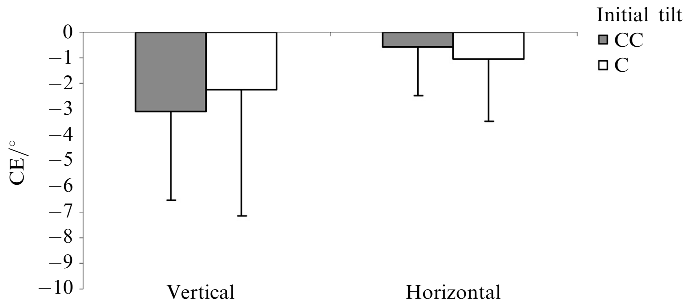


**Figure 4.** Constant error (CE) as a function of the initial tilt of the rod (CC: counterclockwise; C: clockwise) and the orientation.

The angle between the initial position of the stimulus and the main orientation was also found to influence the accuracy of the adjustments ($F_{3,27} = 15.49$, $p < 0.05$). Tukey's a posteriori comparisons revealed that the CE for the 22° angle was significantly smaller ($M = -1.03$, $\mathrm{SD} = 0.286$) than for the other angles ($p < 0.05$), and the CE observed for each of the three latter positions [ie 90° ($M = -1.94$, $\mathrm{SD} = 0.50$), 67° ($M = -2.08$, $\mathrm{SD} = 0.48$), and 45° ($M = -1.87$, $\mathrm{SD} = 0.44$)] was not significantly different. Moreover, a significant interaction between modality and angle ($F_{3,27} = 13.11$, $p < 0.05$) revealed that this angle effect on the participants' performances was found in the kinaesthetic modality only ($F_{1,9} = 17.25$, $p < 0.05$); with no significant effect of angle on CE being found for the visual modality ($F_{1,9} = 0.41$, ns) (figure 5).

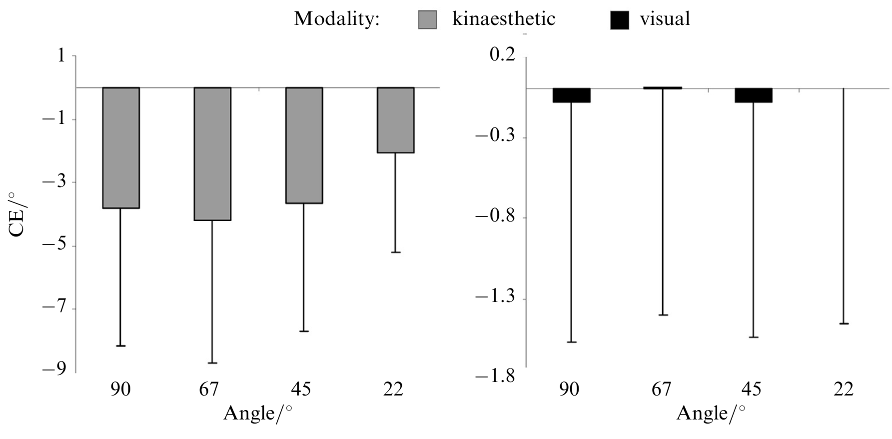


**Figure 5.** Constant error (CE) as a function of the angle of the rod (90°, 67°, 45°, and 22°) and the modality. Note that the SD bars appear excessively large in the visual condition because of the small scale.

Tukey's a posteriori comparisons revealed that only the mean constant error for the 22° angle was smaller ($M = -2.07°$, $\mathrm{SD} = 0.57$) than that measured with the 90° ($M = -3.80°$, $\mathrm{SD} = 0.99$), 67° ($M = -4.18°$, $\mathrm{SD} = 0.96$), and 45° ($M = -3.67°$, $\mathrm{SD} = 0.81$) angles ($p < 0.05$); this error being not significantly different between 45°, 67°, and 90° positions.

### 3.2 *Variable errors*

A similar ANOVA performed on the variable error revealed that this error was greater in the kinaesthetic modality ($M = 2.50$, $\mathrm{SD} = 0.11$) than in the visual modality ($M = 1.04$, $\mathrm{SD} = 0.04$) ($F_{1,9} = 115.59$, $p < 0.05$). No other significant main or interaction effects were found.

### 3.3 *Individual differences*

Even though our goal was to study the mean accuracy of the perception of the main orientations, it is interesting and important to mention that in the kinaesthetic modality and for the vertical orientation the accuracy varied among participants. Indeed, five of the ten participants presented a global error inferior or equal to 3° ($M = -1.36°$, $SD = 1.09$), the remaining participants were, in contrast, inaccurate with errors ranging from 6° to 10.8° ($M = -9.11°$, $SD = 1.91$) (figure 6). Of these five participants, three estimated the kinaesthetic vertical and horizontal with a CE inferior to 1° but showed the greatest error in the visual modality ranging from 0.21° to 0.46° ($M = 0.37°$, $SD = 0.11$), whereas the visual constant error for the seven other participants was 0.03° ($SD = 0.07$). For the horizontal orientation, such a heterogeneous profile was not observed as out of ten participants, nine showed constant errors inferior or equal to 3°. Thus, the kinaesthetic estimation of the vertical orientation appears to be more sensitive to interindividual differences than the kinaesthetic estimation of the horizontal orientation.

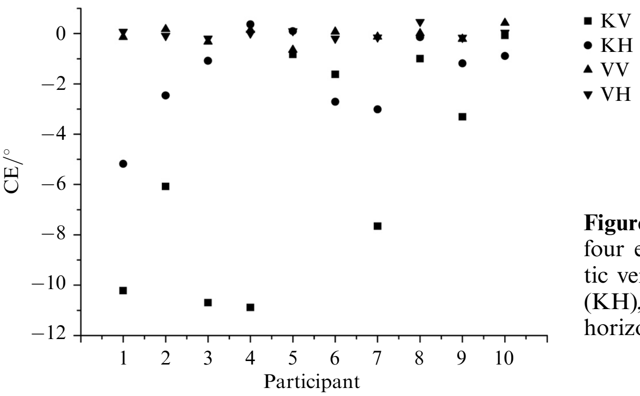


**Figure 6.** Individual constant error in the four experimental conditions [kinaesthetic vertical (KV), kinaesthetic horizontal (KH), visual vertical (VV), and visual horizontal (VH)].

## 4 Discussion

We investigated here how accurately the main orientations (vertical and horizontal) are perceived with the kinaesthetic modality and compared how the main orientations were estimated with the kinaesthetic modality in comparison to the visual modality.

### 4.1 *Visual adjustments*

Concerning the visual modality, the adjustments for both vertical and horizontal orientations were very accurate and thus support previous findings (Anastasopoulos et al 1997, 1999). However, these results are also unique because, until now, studies of the SVV have generally used a luminous line as a stimulus and not two luminous points, as in the present experiment. The current results suggest that minimal visual information is sufficient to perform the task with accuracy.

The adjustments in the visual modality, to the vertical as well as to the horizontal, deviated in a consistent direction from the main orientations. Indeed, the participants undershot the main orientation when the starting position of the rod was in the counterclockwise direction and overshot the main orientation when the starting position was in the clockwise direction. It appears that the SVV consistently deviated in a counterclockwise direction from the physical vertical, a result reported earlier by Bauermeister (1978a).

### 4.2 *Kinaesthetic adjustments*

The kinaesthetic adjustments for both orientations revealed an undershooting clearly different from the actual physical orientation (5.2° and 1.6° for the vertical and horizontal orientations, respectively). The significant difference in accuracy between estimation of the vertical and horizontal orientations with the kinaesthetic modality does not support the traditional idea that the two dominant directions of our environment are perceived equivalently. Moreover, the difference in accuracy revealed that the orthogonality of the subjective vertical and horizontal is not preserved in this kinaesthetic task, despite the upright position of the participant. As mentioned previously, few studies have examined both vertical and horizontal orientations, complicating the comparison between our results and the literature. In our opinion, the study by Gentaz et al (2002) on haptic estimation of the vertical, horizontal, and oblique orientations in the frontoparallel plane is the closest in procedure to our study. For initial tilts of a rod of 20° in the counterclockwise and clockwise directions, Gentaz and colleagues found a significant overestimation of the vertical orientation whereas the estimation of the horizontal orientation did not differ significantly from 0°. For a similar population (young adults), the constant error was 3.8° ($SD = 2.8$) and 3.1° ($SD = 1.5$) for the left and right hemispaces, respectively, for the vertical orientation and $-1°$ ($SD = 3.5$) and $-1°$ ($SD = 3$) for the left and right hemispaces, respectively, for the horizontal orientation. Despite the different nature of the tasks (ie large tactile-kinaesthetic exploration of the rod with one hand versus bimanual adjustments with limited tactile cues), the similarity of the biases observed for the vertical and horizontal orientations in the study of Gentaz et al (2002) and our study suggest that the differences are reliable. Of course, this conclusion will need to be verified with further investigations.

One explanation, specific to our kinaesthetic adjustment task, is that the vertical and horizontal orientations require different strategies. Adjustments to the horizontal necessitate identical positions of both arms. Thus, as the participant adjusted the rod to the horizontal, the perception of postural matching of the position of the arms very likely constituted an important source of information. This explanation is supported by experimental findings showing that the error obtained in our horizontal task was close to the accuracy of forearm matching in the vertical plane at 30° and 60°, when the arms were unsupported ($2.7° \pm 0.5°$—Walsh et al 2006). Furthermore, the same authors have proposed that the perceived effort of fighting against gravity would provide a positional cue during unsupported matching of the arms. This better accuracy is therefore linked to the tested orientation per se which in ecological conditions requires arm matching. In contrast, such advantageous arm matching was not available for adjustments to the vertical orientation because the arms were configured asymmetrically.

Within the haptic modality and with the head in an upright position, the SV deviated from the physical vertical by approximately 2° towards the left (Bauermeister 1978a), 0.06° toward the right (Guerraz et al 2000), and 0.71° toward the right ($SD = 1.56$) (Luyat et al 2001). These values for the SV are smaller than the one we found in the present task. Recently, Bortolami et al (2006) assessed the SV on the basis of haptic adjustments and verbal reports. They found that the intercept of the median value of the haptic errors was $-4.96°$, a value quite close to the one we found for the subjective kinaesthetic vertical in the present study.

For each of the test orientations in the kinaesthetic modality the magnitude of the errors was influenced by different factors, but for both an undershooting, which depended on the angle, was noted. The constant error was larger for the 90°, 67°, and 45° angles than for the 22° angle. In a previous study involving kinaesthetic adjustments from the same angles, but performed with one hand by soccer players and sedentary participants, the constant error linearly increased as the angle from the physical orientation increased (Lejeune et al 2004a). Whatever the origin of these findings, they are consistent with the present findings and strongly suggest that the angle factor has to be taken into account when comparing nonvisual studies on the perception of the physical orientations and/or developing valid and reliable clinical tests involving the kinaesthetic modality.

Unexpectedly, the direction of the initial tilt of the rod influenced the estimation of the horizontal orientation. The undershooting was (in addition to the angle effect) smaller when the rod was initially in the counterclockwise direction. This finding is quite puzzling because it was not observed in a previous study on the estimation of the physical orientations where the participant stood upright without the device (Lejeune et al 2004b). However, a similar direction of the initial tilt effect was observed when the subject's body was constrained because of a supine position (Lejeune et al 2004b). Also, other investigations using the same procedure showed that the adjustments to the horizontal orientation, but not the vertical orientation, were associated with a significant backward displacement of the body when the head and/or trunk were not restrained (eg Thouvarecq et al 2005). Thus, the direction of initial tilt effect was observed only for the horizontal adjustments when the body was in some way restrained and not when it was free to move. It therefore seems that the effect of the initial direction of rod tilt on the horizontal adjustments was an artifact of the current device that was designed to keep vestibular and neck muscle inputs constant and which prevented postural adjustments from occurring.

### 4.3 *Modality specific mechanisms?*

It is important to note that analyses of the constant errors showed that the kinaesthetic modality is characterised by a significant undershooting—this was not the case for the visual modality—and confirms the assumption that the kinaesthetic system is less accurate than the visual system in this task of orientation perception. Moreover, for both orientations, the greater variability of the adjustments in the kinaesthetic modality reflects either the large number of inputs this modality has to deal with for determining the orientation of external objects, or the fact that the kinaesthetic task is less familiar because there are fewer opportunities to judge how objects are aligned relative to the physical orientations with the kinaesthetic modality than there are with the visual modality.

Depending on the modality, the accuracy of the adjustments was influenced by different spatial factors. The interaction between the direction of the initial tilt and modality revealed that constant error was oriented in the direction of the initial tilt for the kinaesthetic modality, whereas it was oriented in the counterclockwise direction, regardless of the initial direction of the rod, for the visual modality. In the same way, the interaction between angular distance and modality in the case of constant errors suggests a differential sensitivity to angular distance for the visual and kinaesthetic modalities. Smaller constant error was obtained for the 22° angle than for the other angles (45°, 67°, and 90°) in the kinaesthetic modality, whereas in the visual modality no significant effect of the angle on the constant error was observed. This interaction was observed both for the adjustments to the vertical and to the horizontal orientations, further confirming that kinaesthetic adjustments to these orientations are governed by similar processes. These two 'spatial factors' (the direction of the initial tilt and the angle) highlight the specificity of the visual and kinaesthetic systems. Overall, these findings challenge the traditional assumption in the literature that perception of verticality depends on a unique internal representation of gravity. In contrast, our findings suggest that the subjective vertical (or horizontal) depends on the perceptual modality involved (Bronstein et al 2003). Consequently, whether or not the vertical and horizontal orientations are two fundamental spatial references, modality-specific mechanisms are involved in the processing of both references (Bronstein 1999; Bronstein et al 2003). In addition, the findings have relevance to the clinical domain, where subjective orientation tests are used to diagnose vestibular and cortical/parietal lesions

(Böhmer et al 1996; Friedmann 1970; Gresty et al 1992; Tabak et al 1997), because they show that methodological factors influence participant's performance and must therefore be taken into account if the tests are to provide useful information.

## 5 Conclusion

This study showed that the accuracy of perception of the main orientations by the kinaesthetic and visual modalities is different. Furthermore, 'spatial factors' have different effects depending on whether the visual or kinaesthetic modality is used to determine orientation. Vertical and horizontal orientations are determined accurately as spatial fixed points when the visual modality is used. When the kinaesthetic modality is used, the orientations are systematically undershot, suggesting determination of an area of subjective verticality and horizontality, respectively.

These differences highlight specific mechanisms inherent to each modality and they show that no common process exists for the two modalities in the perception of orientations. Nevertheless, we can't strictly affirm that the stimuli had comparable salience and pertinence in our adjustment tasks. Further experiments, in which visual and kinaesthetic information is delivered together, would provide precision about the mechanisms of integration.

Use of the 'constant error' revealed that the kinaesthetic modality was characterised consistently by undershooting and an 'angle' effect, and that both orientations were processed by similar mechanisms. Further investigation is required to explain the particular status of the 22° angle. The main differences observed between the vertical and horizontal orientations in the kinaesthetic adjustments were the direction of the initial tilt effect and the magnitude of errors. The first could be explained by the influence of gravitational cues on the hand – arm system during the adjustment. The second could be due to the accurate position sense in a task whose ultimate objective is related to arm matching in the horizontal orientation. Adjustments to the vertical orientation would not benefit from arm matching and the accuracy of the vertical estimation would depend on the accuracy with which the kinaesthetic system estimates the $z$-axis or the gravitational vertical.

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