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Kinesthetic estimation of the main orientations from the upright and supine positions

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Abstract

This work investigated the accuracy of the perception of the main orientations (i.e., vertical and horizontal orientations) with the kinesthetic modality—a modality not previously used in this field of research. To further dissociate the influence of the postural and physical verticals, two body positions were explored (supine and upright). Twenty-two blindfolded participants were asked to set, as accurately as possible, a rod to both physical orientations while assuming one of the two body positions. The horizontal was perceived more accurately than the vertical orientation in the upright position but not in the supine position. Essentially, there were no differences in the supine position because the adjustments to the physical vertical were much more accurate than they were in the upright position. The lower accuracy in the estimation of the vertical orientation observed in the upright position might be linked to the dynamics associated with the maintenance of posture.

PsycINFO classification: 2320
Keywords: Subjective vertical; Kinesthetic adjustments; Body orientation; *Z*-axis

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1. Introduction

With reference to human behavior, the concept of vertical includes the perception of body verticality (*subjective postural vertical*), the perception of the verticality of external objects via different sensory modalities (e.g., *subjective visual vertical* or *subjective haptic vertical*) (Guerraz, Luyat, Poquin, & Ohlmann, 2000; Luyat, Poquin, Isableu, Ohlmann, & Crémieux, 1999) and, according to Bronstein (1999), the preservation of orthogonality between the perception of verticality and horizontality. Consistent with this framework is the notion of frames of reference. [1] One of the broadest distinctions is made between egocentric (referenced to the participant's body) and allocentric (referenced to environmental features) spatial frames of reference (for a review see Wade, 1992). In the context of verticality, the *physical vertical* (the line through the mass centroid of the earth) is considered one of the primary allocentric reference frames, whereas the *postural vertical*, i.e., the actual orientation of the body and its parts to the earth-vertical (Mittelstaedt, 1998), constitutes one of the fundamental egocentric reference frames for spatial orientation.

Regardless of the type of vertical studied, an important and unresolved question concerns the mechanisms by which sensory information (visual, vestibular and somatosensory) is integrated to maintain or perceive a vertical orientation. Similar to the views of others (Bronstein, 1999; Luyat et al., 1999), we believe that the mechanisms underlying the subjective vertical (SV) can be specified by investigating various sensory modalities as well as the relationships among the different verticals.

The literature on the perception of the vertical is replete with studies involving the visual modality. The vertical and horizontal orientations (main orientations) are determined with an accuracy of about one degree when the participant is in an upright position and vision is available (Luyat, 1997; Luyat, Ohlmann, & Barraud, 1997; Mann, Berthelot-Berry, & Dauterive, 1949; Witkin & Asch, 1948; for review, see Howard & Templeton, 1966). However, body orientation influences this perception in systematic ways as evidenced by the Aubert and Müller effects which are SV deviations whose direction depends on the magnitude of body/head tilt (Asch & Witkin, 1948a, 1948b; Bauermeister, 1978a, 1978b; Luyat et al., 1997; Mittelstaedt, 1983, 1986, 1991, 1995).

The haptic modality had received less attention than the visual modality (Bauermeister, Werner, & Wapner, 1964) until recently (Guerraz et al., 2000; Wright & Glasauer, 2003). The haptic adjustments usually permit considerable tactile exploration as the participant adjusts the stimulus rod to the vertical orientation. In some studies (e.g., Mars, Popov, & Vercher, 2001; Wade & Curthoys, 1997), the amount of explo-

[1] From certain theoretical perspectives, subjective (sensory) frames of reference are irrelevant because the animal-environment interaction is thought to be directly and lawfully specified in ambient energy arrays (e.g., Stoffregen & Bardy, 2001). From this perspective, the direction of balance (a physical referent) would be the only referent useful for maintaining an orientation to the environment (e.g., Stoffregen & Riccio, 1988). In contrast, we believe that studying both objective and subjective frames of reference contributes to the elaboration of adapted spatial behaviors. Moreover, our methodology is not appropriate to test a reference like the direction of balance because our adjustment rod is self-balancing.

ration is reduced, although the hand fully envelops the stimulus rod during adjustments to the physical orientations. In contrast, in the current task, the haptic information is greatly reduced because participants are required to place a finger from each hand on either end of the rod. We refer to this task, which has not been used in previous research on the perception of verticality, as a "kinesthetic" task because tactile information is greatly diminished. The term "kinesthetic" is used in a restrictive way to refer to the receptors in the muscular–articular-link system that contribute to the conscious perception of movement and position (McCloskey, 1978). However, we should note that our use of the term kinesthetic is quite close to Pagano and Turvey's (1995) "dynamic touch," which they have 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 & Turvey, 1995, p. 1070).

It is surprising that such little work has been done on the perception of orientations using the kinesthetic modality given that kinesthetic information is so important to the maintenance of posture. In addition, muscular information not only provides information about the position of the limbs relative to each other, but it also has an exteroceptive function because it can be used to determine an object's orientation in the external world (Pagano & Turvey, 1992, 1995; Roll, 1994). As such, the first aim of this paper was to determine just how accurately participants could perceive the vertical and horizontal orientations using the kinesthetic modality.

To address the relationships among the different verticals, we considered the suggestion that the perception of body orientation constitutes an elementary and pertinent reference for the estimation of the gravitational vertical (Luyat, Gentaz, Corte, & Guerraz, 2001; Luyat et al., 1999; Witkin & Asch, 1948) because the adjustments to the vertical, without visual reference, would amount to matching an external object with the perceived direction of the longitudinal axis of the body (i.e., subjective Z-axis). Indeed, with the matching of postural and physical verticals in the upright position, the vertical and horizontal axes are "sensory reinforced" by the convergence of various signals provided by the vestibular system, which codes the direction of equilibrium (Stoffregen & Riccio, 1988) and gravitational acceleration, the muscular and joint receptors, which regulate the balance of muscular tonus, and the cutaneous receptors, which record the relative pressures at the soles of the feet. One way to dissociate the postural vertical and the physical vertical, and therefore determine the relative contribution of the former to the estimation of the main orientations, is to test performance in the supine position. Most of the pertinent signals relevant to the egocentric vertical axis of reference are suppressed or greatly decreased in the supine position. For example, this body position does not allow coding of the head and/or the body in reference to the physical vertical. The various signals are diminished because the individual is not required to maintain his or her posture (Marendaz, 1998).

Previous studies on the estimation of the physical vertical or physical horizontal in the supine position are rare and often reveal contradictory results. Most studies have investigated the influence of the supine position on the accuracy of visual adjustments (Luyat et al., 1997; Parker & Poston, 1984; Templeton, 1973; Wade, 1970) and recently of haptic adjustments (Guerraz et al., 2000). A major difference among these experiments concerns the task itself: adjusting a stimulus to the physical vertical (Luyat et al., 1997; Parker & Poston, 1984) or orienting this stimulus in the direction of the *Z*-axis (Guerraz et al., 2000; Templeton, 1973; Wade, 1970). For the supine position, some authors have reported greater errors (Templeton, 1973), better performance in the presence of a tilted frame (Luyat et al., 1997), or no difference from the upright position (Wade, 1970). The consequences of a head or body tilt are also variable. For example, instead of finding an Aubert effect, Parker and Poston (1984) found a Müller effect. A similar effect was found by Guerraz et al. (2000) for egocentric haptic adjustments in both supine and upright positions when the head was titled, the Müller effect was greater in the supine than in the upright position. To our knowledge, this latter study is the only that used a non-visual modality in the supine position. Contrary to Guerraz et al. (2000), however, we investigated the perception of the physical orientations rather than egocentric perception. A comparison of performance in the supine and the upright positions should provide insight into the contributions of the sensory information associated with upright stance (vestibular and kinesthetic) to the estimation of verticality.

In summary, this study examined the kinesthetic perception of the main orientations when participants assumed either an upright or a supine position. Specifically, the present study aimed to answer three questions:

1. Are the kinesthetic estimations of the main orientations accurate? Because kinesthesia has been shown to provide both egocentric and exteroceptive information, the kinesthetic estimations of the main orientations were expected to be accurate.
2. Are the kinesthetic estimations of the physical vertical and the physical horizontal different from each other? Because our kinesthetic task permitted matching left and right arm positions during adjustments to the physical horizontal, we suspected that the horizontal judgments might be more accurate than the vertical judgments.
3. Is there a difference in the estimations as a function of the participants' body orientation? If the supine position interferes with the coding of the body and/or head position relative to the vertical and the horizontal, the estimations should be poorer in this position relative to the upright position.

2. Method

2.1. Participants

Twenty-two participants (mean age: 24 years-old, SD = 3.08) volunteered to participate in this experiment. Participant's laterality was tested with a simplified version of Edinburgh's inventory (Oldfield, 1971). Every participant obtained a score higher than 50 (mean = 85.22), reflecting a right preferential manual laterality. No participant reported perceptual, motor or postural deficits. Ten participants were assigned to a condition in which the task was performed in the upright position and the twelve remaining participants were assigned to a condition in which the task was performed in the supine position.

2.2. Task and apparatus

The task was to execute kinesthetic adjustments to both the vertical and horizontal orientations. The experimental device was composed of a carbon rod (36 × 0.5 cm) centered on an axis that permitted the rod to rotate in the frontal plane. The angular position of the rod was measured by a potentiometer attached to the axis of rotation. The standard position of the rod was the same for each participant, though height and distance were changed such that the participant could handle the rod comfortably with an outstretched arm (Fig. 1). The potentiometer was connected to a computer via a 12-bit A/D converter. The computer was used to control the experiment and record, reduce, and analyze the data. A customized software program (Verticale ©, by F. Jouen and R. Thouvarecq) was used to start and stop the trials and to permit visualization of the rod position on the computer screen (recording frequency: 36 Hz).

The experimental device used for the kinesthetic adjustments in the supine position was identical to the one used for the adjustments in the upright position. However, in addition to the device itself, a wooden bench (195 × 26 × 45 cm) was used to

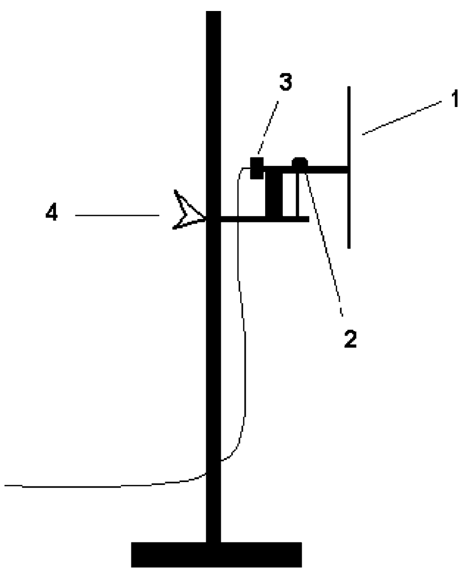

Fig. 1. Experimental device for the kinesthetic adjustments (lateral view): (1) carbon rod; (2) clip to stabilize the rod; (3) potentiometer; (4) clip to adjust the height of the rod.

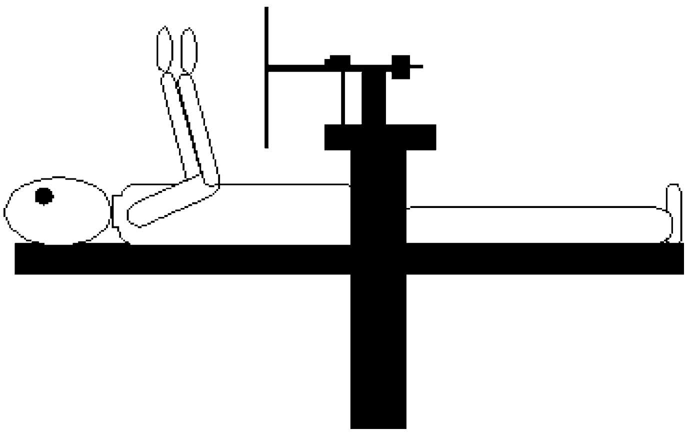

Fig. 2. Experimental device and postural position for the kinesthetic adjustments in a supine position.

maintain the participant in the prone position (see Fig. 2). The bench's dimensions were such that the entire dorsal surface of the body was in contact with it, yet the participant was still able to move the shoulders freely to execute the adjustments. On the sides of the bench, two adjustable brackets supported a wooden board (120 × 30 cm) that was positioned in the horizontal plane just above the body at the level of the pelvis. The experimental device was placed on the board so that it was in line with the participant's mid-saggital plane and extended to the center of the plexus. About 7 cm separated the end of the rod and the body of the participant to prevent the hand from touching the body during the adjustments. Finally, opaque goggles were used to exclude visual information during the adjustments in both experimental conditions.

2.3. Procedure

For both upright and supine experimental conditions, the procedure was the same. The experiment was performed in a dark and quiet room. After brief exposure to the experimental apparatus, the participant was invited to assume a position in front of the adjustment device; he/she stood in a Romberg position for the upright condition and lay on the back, with the head and legs in contact with the bench, for the supine condition. The rod was tilted either at 45° in the counter-clockwise direction or at 45° in the clockwise direction with respect to the physical orientation defined as the 0° position. Because the participant wore opaque glasses for the entire period of testing, 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 physical vertical or the horizontal orientation, according to the experimental condition, without exploring it and without temporal constraint. However, the participant was permitted to make as many corrections as necessary before releasing the rod. Each participant completed five attempts presented in a pseudo-random order and no feedback was given. The order of the experimental conditions (vertical and horizontal adjustments) was counterbalanced across the participants for each group (upright and supine). A 10-min break was allowed between the estimations of the main orientations. During this time, the equipment was recalibrated.

2.3.1. Data analysis and dependent variables

Data from the vertical estimations and the horizontal estimations were analyzed in the same way. Before any analyses, the recorded signal was fitted to a Boltzman equation. Two dependent variables were used to describe the participants' adjustments to both the vertical and horizontal orientations. 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: $CE = \sum(x_i - T)/n$, 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 & 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 overestimated, 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 counter-clockwise direction in relation to the physical vertical, this orientation was undershot. On the contrary, if the initial position of the rod was counter-clockwise and the final position clockwise, the physical vertical was overshot (Fig. 3). Thus, this variable gives information about both the magnitude and the direction of the angular error. The second dependent variable, the variable error (VE), measured the variability of the participant's adjustments with reference to his or her mean error. The formula for VE is: $VE = (\sum(x_i - M)^2/n)^{1/2}$ with x_i being the error on trial i, M, the mean adjustment error and n the number of trials that the participant executes (Schmidt & Lee, 1999). Consequently, this

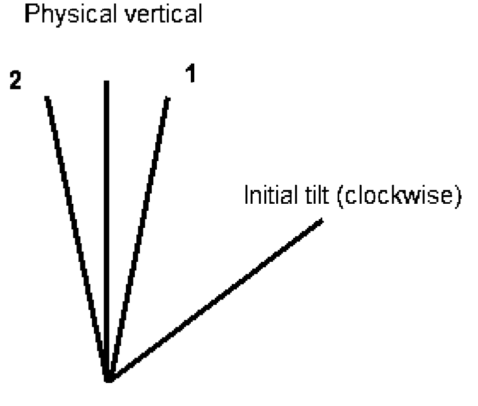

Fig. 3. Example of undershooting and a negative CE (the final position of the rod is in position 1) or of overshooting and a positive CE (the final position of the rod is in position 2) with reference to the initial position in the clockwise direction.

Table 1
Means and standard deviations for the body orientation (upright, supine) and the physical orientation (vertical, horizontal)

Body orientation	Physical orientation	Constant error	Variable error
Upright	Vertical	−5.69 (2.68)	2.04 (1.15)
	Horizontal	−3.33 (0.88)	1.48 (0.67)
Supine	Vertical	−1.89 (2.01)	2.01 (0.64)
	Horizontal	−2.73 (2.1)	1.39 (0.45)

variable provides information about the consistency of performance. Note that both errors were expressed in degrees.

3. Results

With respect to the three questions raised previously, the results were organized in the following way: First, *t* tests were used to compare the constant error to the norm 0° (the physical vertical or horizontal) for each body position and for each physical orientation to determine if the kinesthetic adjustments were accurate. Because of the use of multiple *t*-tests to determine the accuracy of the kinesthetic orientations, we adjusted the *p* value to correct for the potentially inflated Type 1 error rate and the resulting significance level was 0.004. The descriptive results (means and standard deviations) are presented in Table 1 and not repeated for the subsequent analyses to avoid redundancy.

Second, a 2(body position) × 2(physical orientation) × 2(initial tilt of rod) ANOVA with repeated measures on the last two factors was performed to determine the influence of the body position on the accuracy of the estimations and to determine if the main orientations were kinesthetically perceived with the same accuracy. This inferential statistic was performed on both constant error and variable error.

3.1. Are the kinesthetic estimations of the main orientations accurate?

3.1.1. In the upright position

The descriptive results and comparisons relative to 0° revealed that the adjustments to the vertical orientation in the upright position were characterized by a significant undershooting of the physical orientation ($t(9) = -6.70$, $p < 0.004$). This undershooting was found for both initial directions of rod tilt (counter-clockwise: $M = -5.03$, $SD = 3.40$; $t(9) = -4.66$, $p < 0.004$ and clockwise $M = -6.35$, $SD = 2.92$; $t(9) = -6.87$, $p < 0.004$). In the same postural position, the adjustments to the horizontal orientation were also characterized by a significant undershooting of the physical orientation ($t(9) = -11.99$, $p < 0.004$). This undershooting was significant for the counter-clockwise and the clockwise initial tilts of the rod ($M = -3.90$, $SD = 1.41$; $t(9) = -8.70$, $p < 0.004$ and $M = -2.77$, $SD = 1.78$; $t(9) = -4.92$, $p = p < 0.004$ respectively) (Fig. 4).

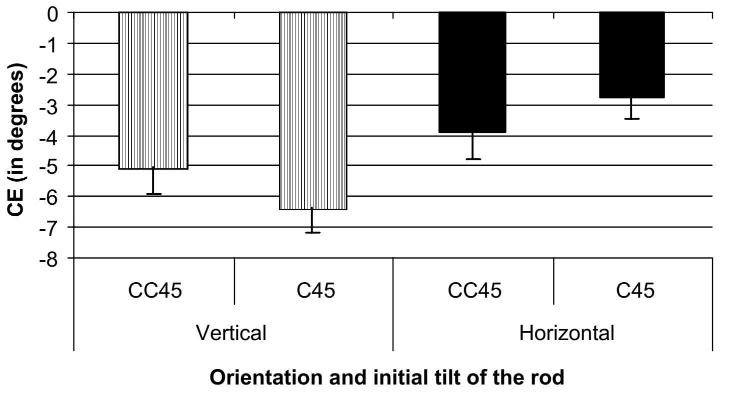

Fig. 4. Mean constant error CE (deg) during adjustments to the physical vertical and horizontal in the upright position from two initial positions of the rod (45C and 45CC: 45° respectively in the clockwise and the counter-clockwise direction in reference to the gravitational vertical).

3.1.2. In the supine position

At the 0.004 significance level, the undershooting of the physical vertical was not significant when the participants were in the supine position ($t(11) = -3.25$, $p = 0.010$). This undershooting was significant for clockwise initial starting positions of the rod ($M = -2.35$, SD = 2.32) ($t(11) = -3.51$, $p < 0.004$) but not for the counter-clockwise initial starting positions of the rod ($M = -1.42$, SD = 2.36) ($t(11) = -2.08$, $p = 0.067$). The kinesthetic adjustments to the horizontal orientation in the supine position did show a significant undershooting ($t(11) = -4.49$, $p < 0.004$). However, this undershooting was only significant for the initial positions of the rod in the counter-clockwise direction ($M = -4.49$, SD = 3.53) ($t(11) = -4.39$, $p < 0.004$); the error for the initial positions of the rod in the clockwise direction ($M = -0.97$, SD = 2.48) were not significant ($t(11) = -1.36$, $p = 0.207$) (Fig. 5).

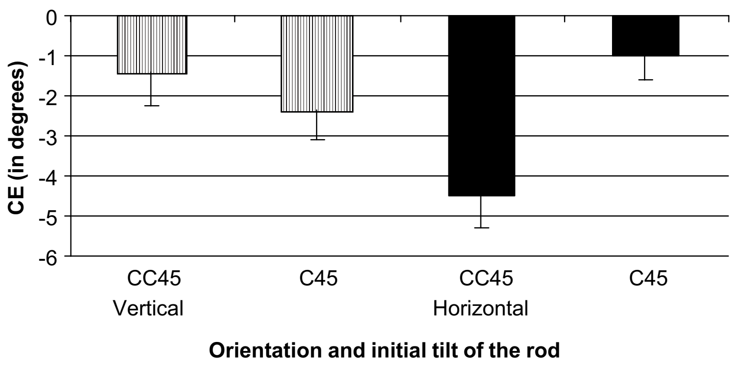

Fig. 5. Mean constant error CE (deg) during adjustments to the physical vertical and horizontal in the supine position from two initial positions of the rod (45C and 45CC: 45° respectively in the clockwise and the counter-clockwise direction in reference to the gravitational vertical).

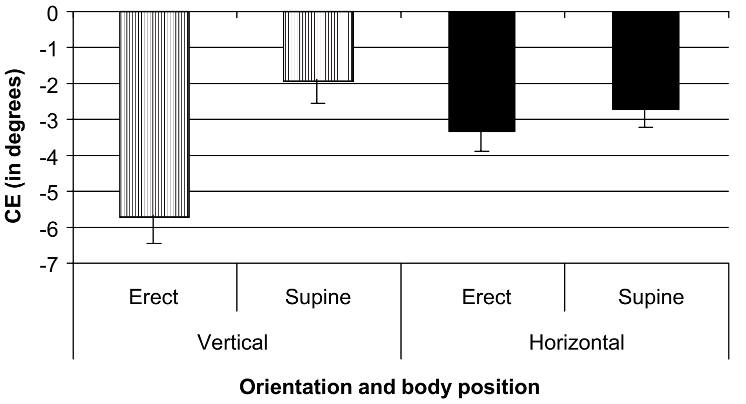

Fig. 6. Mean constant error CE (deg) for each orientation (vertical and horizontal) as a function of the postural position of the subject (upright versus supine).

3.2. Is there a difference in these estimations according to the body orientation of the participant?

The answer is positive since the ANOVA revealed a main effect of body position, $F(1,20) = 9.30, p < 0.05$, partial eta squared ($\eta^2 = 0.32$), with the adjustments in the supine position ($M = -2.31$, $\mathrm{SD} = 1.88$) being more accurate than those in the upright position ($M = -4.51$, $\mathrm{SD} = 1.40$). This effect was not linked to a higher variability in the adjustments because no significant difference in VE was found between both body positions $F(1,20) = 0.07$, $p = 0.794$, $\eta^2 = 0.003$.

Moreover, the accuracy of the kinesthetic adjustments depended on the physical orientation to which the adjustments were done, as evidenced by a significant interaction between body position and physical orientation $F(1,20) = 10.88$, $p < 0.05$, $\eta^2 = 0.35$. More specifically, the determination of the physical vertical was less accurate when the participant was in an upright position than in a supine position $F(1,20) = 14.43$, $p < 0.05$, $\eta^2 = 0.42$ (Table 1) whereas for the physical horizontal, no significant difference was observed as a function of body position $F(1,20) = 0.72$, $p = 0.406$, $\eta^2 = 0.034$ (Fig. 6).

3.3. Are the main orientations perceived with the same accuracy?

This question is qualified by the interaction previously mentioned. Despite no main effect for physical orientation $F(1,20) = 2.43, p = 0.134, \eta^2 = 0.11$, the interaction revealed that in the upright position, the physical horizontal was perceived more accurately than the physical vertical $F(1,9) = 6.87$, $p < 0.05$, $\eta^2 = 0.43$, whereas no significant difference was observed in the supine position $F(1,11) = 3.13$, $p = 0.104$, $\eta^2 = 0.22$ (Fig. 6).

The physical orientation also influenced the variability of the kinesthetic estimations as the mean VE was significantly greater for the vertical orientation ($M = 2.03$,

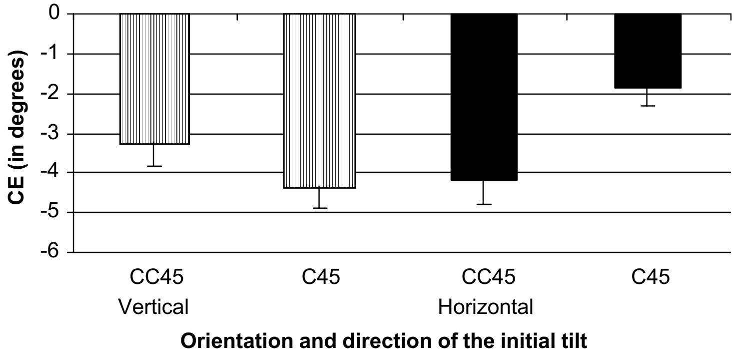

Fig. 7. Mean constant error CE (deg) for each orientation (vertical and horizontal) as a function of the initial tilt of the rod (C45: clockwise; CC45: counter-clockwise).

SD = 0.88) than for the horizontal orientation ($M = 1.44$, SD = 0.55), $F(1,20) = 7.67$, $p < 0.05$, $\eta^2 = 0.27$.

In addition to the previous results, a significant interaction between the physical orientation and the initial tilt of the rod, $F(1,20) = 12.30$, $p < 0.05$, $\eta^2 = 0.38$ was found (Fig. 7). The accuracy of the adjustments to the vertical was not affected by the initial tilt of the rod ($M = -3.06$, SD = 3.36 for the counter-clockwise direction and $M = -4.17$, SD = 3.26 for the clockwise direction) but the adjustments to the horizontal were more precise when the rod was tilted in the clockwise direction ($M = -1.79$, SD = 2.32) relative to the counter-clockwise direction ($M = -4.22$, SD = 2.74) (Fig. 7).

4. Discussion

The aims of this study were to determine whether (1) the kinesthetic estimations of the main orientations are accurate, (2) the physical vertical and horizontal orientations are estimated with the same accuracy and, above all, whether (3) a disassociation between the physical and postural vertical influences the accuracy of the kinesthetic estimations.

Globally, the kinesthetic estimations of the main orientations were "inaccurate" because they differed significantly from the physical ones (i.e. 0°). In the upright position, the final position of the rod was significantly different from the physical orientations (vertical and horizontal). In the supine position, the same result was obtained for the horizontal orientation but the adjustments to the vertical orientation were very precise (i.e. not significantly different from the 0° norm). Regardless of body position, the inaccuracies were characterized by a systematic undershooting of the physical orientation along with some 2° of variability. In others words, the kinesthetic adjustments do not describe a specific location in the space as vertical but rather an area of verticality. This systematic underestimation leads us to believe that this is an inherent feature of the kinesthetic modality, at least in this type of task. Indeed, several replications of this study undertaken in our laboratory consistently showed that the adjustments to both orientations are characterized by underestimations of the physical orientations. In the literature, numerous studies on pointing movements in the horizontal plane and in three-dimensional space have revealed an undershooting of the targets and an increase in pointing errors with increasing target distances relative to the body (Fisk & Goodale, 1985; Medendorp, Van Asselt, & Gielen, 1999; Prablanc, Pelisson, & Goodale, 1986; Soechting & Flanders, 1989a). This underestimation appears to reflect an inaccurate transformation of target location, which is visually defined, to final fingertip position, which is based on proprioceptive information (Soechting & Flanders, 1989b). Obviously, this hypothesis does not apply to the present experiment because the task did not involve a visuo-kinesthetic transformation. Another hypothesis suggests that the constant error may reflect a perceptual bias in localizing the target (Prablanc et al., 1986; Wolpert, Ghahramani, & Jordan, 1994) or a tendency of the involved control system to generate undershoots towards peripheral objects as an efficient strategy for correcting the movements if more accurate information about the target position is available later (Gentilucci & Negrotti, 1996; Prablanc et al., 1986). This latter hypothesis might well account for the current findings. It is important for us to specify that this explanation does not mean that the resolution of the kinesthetic system is poor. Indeed, if that were the case, larger errors would be observed for both the estimations of the horizontal orientation and those in the supine position. The accuracy of the horizontal estimations actually provides an excellent example of the resolution of the kinesthetic system. The superior accuracy of the horizontal estimations relative to the vertical estimations also suggests that practice and familiarity play an important role in how well this type of adjustment task is performed. It is tenable to assume that participants have had much more experience matching the horizontal positions of their hands and arms than the vertical positions of their hands and arms. For example, horizontal matching is essential for successfully carrying objects such as large plates and trays, whereas carrying objects with one hand positioned above the other is far less common.

Body orientation had a clear effect on the estimation of orientation, though the effect was confined to the estimation of the physical vertical, where the precision of the adjustments was more accurate in the supine position than in the vertical position. This finding is contrary to the expectation that the supine position would disrupt perception of the physical vertical. Indeed, our results showed that the suppression of postural dynamics appeared to facilitate the estimation of the physical vertical (Stoffregen & Riccio, 1988; Stoffregen & Bardy, 2001). These results also call into question the notion that sensory information regarding the body's verticality makes a positive contribution to the estimation of the physical vertical (Marendaz, 1998).

How can the physical vertical be accurately perceived from the supine position when there is a disassociation between the Z-axis of the body and the plane of the rod? Although data from other experiments are difficult to compare directly with ours because of differences in methodology, the superior accuracy that we found

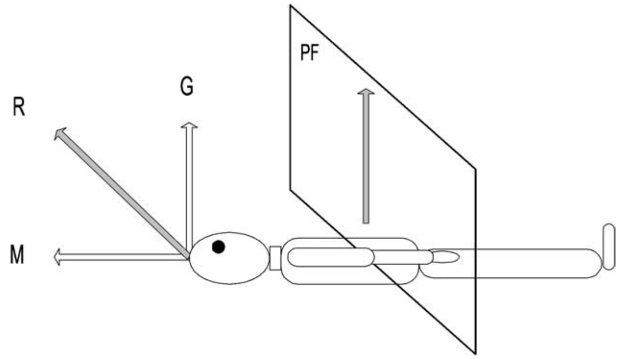

Fig. 8. Representation of the subjective vertical (grey arrow) as result of the idiotropic vector (M) and gravity vector (G) according Mittelstaedt's theory (1983). The projection in the frontal plane (PF) is confounded with the gravitational vertical.

in the supine position could be explained by the weight of the *Z*-axis (Luyat et al., 1997). Actually, both the idiotropic vector from Mittelstaedt's model (1983) and the subjective *Z*-axis (Luyat et al., 1997, 1999) provide potential explanations. In Mittelstaedt's model, the subjective vertical (SV) corresponds to the combination of the gravitational and idiotropic vectors (defined by the participant's own longitudinal *Z*-axis, and characterized by its variable weight from one participant to another). When the participant is in a supine position, the direction of the gravitational vector remains unchanged and the idiotropic vector is oriented in the *Z*-axis direction (i.e. orthogonal to the vertical plane). The resulting SV is therefore tilted in pitch with reference to the gravitational vector (Fig. 8). However, there is no reason to expect a positional bias in the frontal plane (i.e. plane of the adjustments) since the projection of the resulting SV is perfectly aligned with the physical vertical in the roll plane.

Luyat and colleagues (e.g., Luyat, 1997; Luyat et al., 1999) have argued that the estimation of verticality involves predominantly the subjective *Z*-axis. In the supine position, the participant would execute a projection of the *Z*-axis in the frontal plane and would use the perception of body orientation (subjective *Z*-axis) to execute correct judgments of verticality, independently of his postural vertical. The perception of verticality can therefore be precise in the supine position—an idea that is reinforced by the work of Spidalieri and Sgolastra (1997), who have shown that participants in a supine position can point with great accuracy toward the median line of the trunk on the basis of a "mental representation."

Though the above explanations can explain how the vertical can be estimated accurately from the supine position, they cannot explain the superior accuracy of the kinesthetic adjustments in the supine position. One possible explanation for this observation is that postural instability in the upright position interferes with estimations of the vertical. On the contrary, in the supine position, the individual is more stable because the base of support is larger and the center of gravity is much closer to the base of support and consequently is more easily maintained within it. The postural sway typically observed in the upright position (or associated noise from the vestibular and/or somatosensory system) might interfere with the accurate establishment of a SV, such that the area in which the participant perceives his body in the vertical orientation is increased. This notion is to parallel to what Bisdorff, Wolsley, Anastasopoulos, Bronstein, and Gresty (1996) described as a cone of sensitivity to the vertical in the subjective postural task. An appropriate way to test this explanation would be to correlate postural stability (data for which was not collected in the current experiment) with the accuracy and variability of estimations or to assess performance on the task with and without artificial postural support in the upright position.

An important question emerges from this study: Is the systematic undershooting of the physical vertical related to the sensitivity with which participants can determine the position of the *Z*-axis in reference to the physical vertical on the basis of kinesthetic information? A way to answer this question would be to investigate in the same experiment the Subjective Kinesthetic Vertical and the Subjective Postural Vertical. If the previous interpretation is right, we would expect a strong correlation between the cone of verticality found by Bisdorff et al. (1996) and the area of verticality found in this type of experiment. This approach to the perception of the vertical, which focuses on kinesthetic information, suggests a new way to establish the relations among the different verticals.

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References

Asch, S. E., & Witkin, H. A. (1948a). Studies in space orientation: I. Perception of the upright with displaced visual fields. *Journal of Experimental Psychology, 38*, 325–337.

Asch, S. E., & Witkin, H. A. (1948b). Studies in space orientation: II. Perception of the upright with displaced visual fields and with body tilted. *Journal of Experimental Psychology, 38*, 455–477.

Bauermeister, M. (1978a). Differences between right versus left lateral body tilt in its effect on the visual and tactual perception of verticality. *Psychological Research, 40*, 183–187.

Bauermeister, M. (1978b). Perception of the visual horizontal during lateral body tilt: Right–left asymmetries. *Perceptual and Motor Skills, 47*, 715–720.

Bauermeister, M., Werner, H., & Wapner, S. (1964). The effect of body tilt on tactual-kinesthetic perception of verticality. *American Journal of Psychology, 77*, 451–456.

Bisdorff, A. R., Wolsley, C. J., Anastasopoulos, D., Bronstein, A. M., & Gresty, M. A. (1996). The perception of body verticality (subjective postural vertical) in peripheral and central vestibular disorders. *Brain, 119*(Pt 5), 1523–1534.

Bronstein, A. M. (1999). The interaction of otolith and proprioceptive information in the perception of verticality. The effects of labyrinthine and CNS disease. *Annals of the New York Academy of Sciences, 871*, 324–333.

Fisk, J. D., & Goodale, M. A. (1985). The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral visual space. *Experimental Brain Research, 60*(1), 159–178.

Gentilucci, M., & Negrotti, A. (1996). Mechanisms for distance reproduction in perceptual and motor tasks. *Experimental Brain Research, 108*(1), 140–146.

Guerraz, M., Luyat, M., Poquin, D., & Ohlmann, T. (2000). The role of neck afferents in subjective orientation in the visual and tactile sensory modalities. *Acta Otolaryngologica, 120*, 735–738.

Howard, I. P., & Templeton, W. B. (1966). *Human spatial orientation*. New York: John Wiley.

Luyat, M. (1997). Verticale subjective versus verticale posturale: Une note sur l'étude de la perception de la verticale. *L'Année Psychologique, 97*, 433–447.

Luyat, M., Gentaz, E., Corte, T. R., & Guerraz, M. (2001). Reference frames and haptic perception of orientation: Body and head tilt effects on the oblique effect. *Perception & Psychophysics, 63*(3), 541–554.

Luyat, M., Ohlmann, T., & Barraud, P. A. (1997). Subjective vertical and postural activity. *Acta Psychologica, 95*(2), 181–193.

Luyat, M., Poquin, D., Isableu, B., Ohlmann, T., & Crémieux, J. (1999). Existe-t-il des processus communs impliqués dans l'estimation de la verticalité et dans le contrô le de la posture?. In M. Lacour (Ed.), *Posture et equilibre. Entrées sensorielles, méthodes d'exploration et applications* (pp. 55–72). Montpellier: Sauramps Médical.

Mann, C. W., Berthelot-Berry, N. H., & Dauterive, H. J. (1949). The perception of the vertical: I. Visual and non-labyrinthine cues. *Journal of Experimental Psychology, 39*, 538–547.

Marendaz, C. (1998). Nature and dynamics of reference frames in visual search for orientation: Implications for early visual processing. *Psychological Science, 9*(1), 27–32.

Mars, F., Popov, K., & Vercher, J. L. (2001). Supramodal effects of galvanic vestibular stimulation on the subjective vertical. *Neuroreport, 12*(13), 2991–2994.

McCloskey, D. I. (1978). Kinesthetic sensibility. *Physiological Reviews, 58*(4), 763–820.

Medendorp, W. P., Van Asselt, S., & Gielen, C. C. (1999). Pointing to remembered visual targets after active one-step self-displacements within reaching space. *Experimental Brain Research, 125*(1), 50–60.

Mittelstaedt, H. (1983). A new solution to the problem of the subjective vertical. *Naturwissenschaften, 70*(6), 272–281.

Mittelstaedt, H. (1986). The subjective vertical as a function of visual and extraretinal cues. *Acta Psychologica, 63*(1–3), 63–85.

Mittelstaedt, H. (1991). The role of the otoliths in the perception of the orientation of self and world to the vertical. *Zool. Jb. Physiol., 95*, 419–425.

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

Mittelstaedt, H. (1998). Origin and processing of postural information. *Neuroscience and Biobehavioral Reviews, 22*(4), 473–478.

Oldfield, R. C. (1971). The assessment and analysis of handedness. The Edinburgh inventory. *Neuropsychologica, 9*, 97–113.

Pagano, C. C., & Turvey, M. T. (1992). Eigenvectors of the inertia tensor and perceiving the orientation of a hand-held object by dynamic touch. *Perception & Psychophysics, 52*(6), 617–624.

Pagano, C. C., & Turvey, M. T. (1995). The inertia tensor as a basis for the perception of limb orientation. *Journal of Experimental Psychology: Human Perception and Performance, 21*(5), 1070–1087.

Parker, D. E., & Poston, R. L. (1984). Tilt from head-inverted position produces displacement of visual subjective verticale in the opposite direction. *Perception & Psychophysics, 36*, 461–465.

Prablanc, C., Pelisson, D., & Goodale, M. A. (1986). Visual control of reaching movements without vision of the limb. I. Role of retinal feedback of target position in guiding the hand. *Experimental Brain Research, 62*(2), 293–302.

Roll, J. P. (1994). Sensibilités cutanées et musculaires. In M. Richelle, J. Requin, & M. Roberts (Eds.), *Traité de psychologie expérimentale* (1, pp. 483–542). Paris: Presses Universitaires de France.

Schmidt, R. A., & Lee, T. D. (1999). *Motor control and learning: A behavioral emphasis* (3rd ed.). Windsor: Human Kinetics.

Soechting, J. F., & Flanders, M. (1989a). Sensorimotor representations for pointing to targets in three-dimensional space. *Journal of Neurophysiology, 62*(2), 582–594.

Soechting, J. F., & Flanders, M. (1989b). Errors in pointing are due to approximations in sensorimotor transformations. *Journal of Neurophysiology, 62*(2), 595–608.

Spidalieri, G., & Sgolastra, R. (1997). Psychophysical properties of the trunk midline. *Journal of Neurophysiology, 78*(1), 545–549.

Stoffregen, T. A., & Bardy, B. G. (2001). On specification and the senses. *Behavioral and Brain Sciences, 24*, 195–261.

Stoffregen, T. A., & Riccio, G. E. (1988). An ecological theory of orientation and the vestibular system. *Psychological Review, 95*(1), 3–14.

Templeton, W. B. (1973). The role of gravitational cues in the judgment of visual orientation. *Perception & Psychophysics, 14*(3), 451–457.

Wade, N. J. (1970). Visual orientation during lateral head tilt when upright and supine. *Quarterly Journal of Experimental Psychology, 22*, 420–422.

Wade, N. J. (1992). The representation of orientation in vision. *Australian Journal of Psychology, 44*, 139–145.

Wade, S. W., & Curthoys, I. S. (1997). The effect of ocular torsional position on perception of the roll-tilt of visual stimuli. *Vision Research, 37*(8), 1071–1078.

Witkin, H. A., & Asch, S. E. (1948). Studies in space orientation: III. Perception of the upright in the absence of a visual field. *Journal of Experimental Psychology, 38*, 603–613.

Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1994). Perceptual distortion contributes to the curvature of human reaching movements. *Experimental Brain Research, 98*(1), 153–156.

Wright, W. G., & Glasauer, S. (2003). Haptic subjective vertical shows context dependence: Task and vision play a role during dynamic tilt stimulation. *Annals of the New York Academy of Sciences, 1004*, 531–535.