Gravity and observer's body orientation influence the visual perception of human body postures

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Since human behavior and perception have evolved within the Earth's gravitational field, humans possess an internal model of gravity. Although gravity is known to influence the visual perception of moving objects, the evidence is less clear concerning the visual perception of static objects. We investigated whether a visual judgment of the stability of human body postures (static postures of a human standing on a platform and tilted in the roll plane) may also be influenced by gravity and by the participant's orientation. Pictures of human body postures were presented in different orientations with respect to gravity and the participant's body. The participant's body was aligned to gravity (upright) or not (lying on one side). Participants performed stability judgments with respect to the platform, imagining that gravity operates in the direction indicated by the platform (that was or was not concordant with physical gravity). Such visual judgments were influenced by the picture's orientation with respect to physical gravity. When pictures were tilted by 90° with respect to physical gravity, the human postures that were tilted toward physical gravity (down) were perceived as more unstable than similar postures tilted away from physical gravity (up). Stability judgments were also influenced by the picture's orientation with respect to the participant's body. This indicates that gravity and the participant's body position may influence the visual perception of static objects.

Keywords: posture, somatosensory cues, vestibular otolithic cues, subjective visual vertical, implied motion, inversion effect

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Introduction

Space perception and the control of body orientation require that the central nervous system detects gravitational acceleration and creates an internal model of gravity (Angelaki, Shaikh, Green, & Dickman, 2004; Merfeld, Zupan, & Peterka, 1999; Smetacek, 2002; Snyder, 1999). Human behavior on Earth therefore requires a representation of the *vertical* and the related *"up" direction* (Dyde, Jenkin, & Harris, 2006; Jenkin, Dyde, Jenkin, Howard, & Harris, 2003). The vertical on Earth is given by the *orientation* of the gravitational acceleration, enabling us to know, for instance, that the Tower of Pisa is leaning to one side. The "up" direction can be referred to as the *direction* from where the gravitational acceleration pulls: Newton's apple fell *down* under the terrestrial force of gravity. Both the vertical and the "up" direction are also elementary spatial concepts that may be part of the core spatial knowledge in human beings—despite semantic differences across cultures (Dehaene, Izard, Pica, & Spelke, 2006)—being skillfully manipulated by architects, bricklayers, sportsmen, and acrobats (Berthoz, 2000). Past research in experimental psychology and human physiology showed that perceiving the vertical and the "up" direction is based on multimodal integration of vestibular, somatosensory, and visual signals. Vestibular receptors located in the inner ear are directly sensitive to linear accelerations, and the vestibular system has been shown to play a crucial role in sensing

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the vertical (Böhmer & Mast, 1999; Bronstein, 1999; Mittelstaedt, 1991, 1992, 1999; Snyder, 1999; Zink, Bucher, Weiss, Brandt, & Dieterich, 1998; review in Lopez, Lacour, Ahmadi, Magnan, & Borel, 2007). Another reference for the perception of the vertical and "up" direction is a body-centered reference based on somatosensory information emanating from the receptors distributed in the muscles, joints, skin, and viscera (Lackner, 1988; Lackner & Dizio, 2005; Lopez, Lacour, Léonard, Magnan, & Borel, 2008; Mittelstaedt, 1992; Roll, Vedel, & Roll, 1989; Trousselard, Barraud, Nougier, Raphel, & Cian, 2004). Finally, spatial information about orientation originates from our visual environment (Dichgans, Held, Young, & Brandt, 1972; Dyde et al., 2006; Jenkin et al., 2003; Jenkin, Jenkin, Dyde, & Harris, 2004; Lopez, Lacour, Magnan, & Borel, 2006; Oman, 2003; Senot, Zago, Lacquaniti, & McIntyre, 2005; Witkin & Asch, 1948).

Empirical evidence for such a multisensory-based internal model of gravity arises from experiments conducted under normal gravity conditions (1G on Earth) as well as experiments conducted under microgravity conditions. During orbital space flights, crew members free-floating in weightlessness have been reported to loose the sense of the vertical and of the "up" direction (Oman, 2003; Young, Oman, Watt, Money, & Lichtenberg, 1984). During parabolic flights, inversion illusions of the spatial coordinates are commonly reported, depending on the visual references available (Lackner, 1992). These microgravity experiments have stressed the importance of vestibular otolithic signals, as well as tactile and visual cues for elaborating a representation of the vertical, of the "up" direction, and of self-orientation. In experiments run on Earth, important evidence for an internal model of gravity was found using time estimation of falling objects. Lacquaniti and colleagues found evidence that the brain encodes Newton's laws, as subjects accurately estimated the time to collision of a free falling ball (Indovina et al., 2005; Lacquaniti & Maioli, 1989; Senot et al., 2005; Zago et al., 2004, 2005; Zago & Lacquaniti, 2005). The existence of an internal model of gravity was further supported by data from McIntyre, Zago, Berthoz, and Lacquaniti (2001), showing that astronauts in weightlessness anticipate ball falling times based on a terrestrial model of gravity. Altogether, these studies demonstrated that, through experience, the central nervous system has internalized that terrestrial gravity accelerates objects downward at about 9.81 m s^{-2}.

Although most research on internal models of gravity has focused on the perception of *visual stimuli in motion*, it is very likely that representation of the vertical and "up" direction may modulate the perception of *static visual stimuli* as well. Indeed, perception of complex visual stimuli is strongly orientation-dependent. Turning this page around might lead to the perception of the letter "N" as a "Z". The perception of human faces and body postures is slower and less accurate when they are presented upside down or tilted (Reed, Stone, Bozova, & Tanaka, 2003; Reed, Stone, Grubb, & McGoldrick, 2006; Troje, 2003; Yin, 1969). Similar effects have been reported for biological motion perception (Troje, 2003; Troje & Westhoff, 2006). However, most previous studies only inverted the visual stimuli with respect to the observer's body, leading to an inversion of the picture with respect to gravity as well as the observer's body. Therefore, most previous studies have confounded the spatial reference with respect to which visual stimuli are oriented, so that the orientation-dependent mechanisms described for perception of visual stimuli might be due to gravity- and/or body-centered coding. In an attempt to dissociate the contribution of gravitational and bodily cues to visual perception, some authors tilted the body of the observer with respect to gravity, reporting varied results (depending on the visuospatial task). They found evidence for a contribution of gravity-centered coding (e.g., interpretation of reversible figures: Yamamoto & Yamamoto, 2006; perception of patch-light displays: Bingham, Schmidt, & Rosenblum, 1995; geometrical perception: Clément & Eckardt, 2005; Ferrante, Gerbino, & Rock, 1995), of retinocentric coding (e.g., face and biological motion perception: Troje, 2003), or of both gravity- and body-centered coding (e.g., visual vertical perception: Mittelstaedt, 1992; Van Beuzekom & Van Gisbergen, 2000; 3D perception of shape from shading: Jenkin et al., 2003, 2004; character recognition: Dyde et al., 2006, face perception: Lobmaier & Mast, 2007).

The present experiment was planned to investigate whether visual perception, using a paradigm requiring the visual judgment of the stability of human body postures (see Bonnet, Paulos, & Nithart, 2005), is influenced by physical gravity and the observer's body orientation. We used the presentation of static pictures with implied motion (e.g., Kourtzi & Kanwisher, 2000; Urgesi, Moro, Candidi, & Aglioti, 2006) where the movement of the body was not apparent, but suggested by the depiction of a body in gravity that was (or not) in the process of falling. We employed a design manipulating the observers' body orientation and the picture orientation with respect to physical gravity (Figure 1). Observers were shown pictures of a human body tilted in the roll plane. They judged whether or not the human body would fall over onto the platform when the pictures were presented in different orientations with respect to physical gravity (upright, upside down, right and left roll of 90°) and while they were themselves seated upright or lying right side down. This required that observers imagined gravity not with respect to physical gravity, but with respect to the direction of gravity concordant with the platform orientation (i.e., the "imagined gravity" was always orthogonal to the visual platform). In the case of an absence of an internal model of gravity, the observers' performance should be the same and not dependent on whether observers imagined gravity with respect to the platform that was oriented upright, upside down, or tilted clockwise

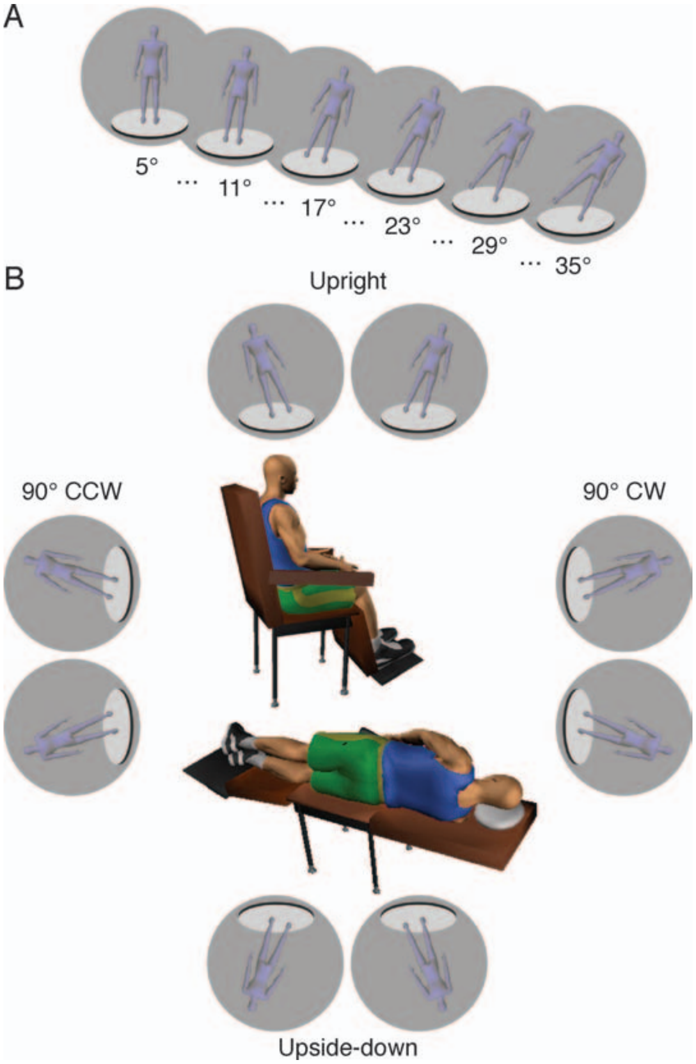

Figure 1. Experimental paradigm. (A) Visual stimuli were pictures representing a human body seen from the back and tilted either rightward or leftward on a platform. Sixteen amplitudes of human body roll were presented, ranging from 5° to 35°, by 2° steps. (B) Observers were tested upright and lying right side down. For each orientation of the observer, all visual stimuli were presented in four orientations *with respect to gravity*: upright, upside down, and rotated by 90° clockwise (CW) and counterclockwise (CCW).

and counterclockwise by 90°. We hypothesized that the internal model of gravity would influence such stability judgments. We further hypothesized that the internal model of gravity would influence the perception of static pictures with implied motion in a similar fashion as found for the perception of moving objects (Indovina et al., 2005; McIntyre et al., 2001). As body-centered references were shown to influence several aspects of visual perception (Dyde et al., 2006; Jenkin et al., 2003; Lobmaier & Mast, 2007), we hypothesized an additional, but functionally distinct, contribution of bodily cues to the perception of static pictures with implied motion. We expected visual judgments of the stability to be modulated in a direction-specific fashion depending on the orientation of the pictures of the human body with respect to the gravitational vertical and "up" (gravity effect) and, additionally, depending on the observer's body orientation (body effect).

Material and methods

Participants

The data were obtained from 17 healthy paid volunteers (10 men, ages: 22–32 years, mean ± *SD*: 25 ± 3 years). All of them had normal or corrected-to-normal vision and none reported a history of neuro-otological disorder. Fifteen participants were right-handed (mean score = +83 ± 13 at the Oldfield Edinburgh inventory test, Oldfield, 1971) and 2 were left-handed (−37 ± 33). Informed consent was obtained from all participants prior to their inclusion in the study. The study protocol was approved by the local ethics research committee at the University of Lausanne and was performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

Visual stimuli and procedures

The visual stimuli were pictures representing different postures of a human body standing upright on a platform (Figure 1A). The human body seen from the back was designed with Motion Builder 7.5 software for 3D character animation (Autodesk, USA). In order to insure realism of the postures, pictures were based on snapshots extracted from an in-house movie of a human falling laterally from a standing upright position onto a mattress. The human body was tilted on the platform either rightward or leftward (16 angles ranging from 5° to 35°; 2° steps, angle represents trunk roll). Human body orientation was defined as the amplitude of the trunk roll because the trunk contains the longest segment of the medial longitudinal body axis, the center of mass, and most of the body mass, and because it is an unpaired body segment defining the body axis uniquely (see Bonnet et al., 2005). For each picture, only one foot was in contact with the platform. The human body and the platform subtended ~13° vertically and ~9° horizontally of the visual field and they were presented on a light gray background. Pictures (1182 × 1024 pixels images) were presented on a 21-in flat-screen monitor (refresh rate of 60 Hz) using the E-Prime 1.1 software (E-Studio, Psychology Software Tools, USA). In addition, the screen was covered with a black circular frame in order to restrict the stimulated visual field to a circular area (25 cm in diameter, subtending ~17° of the visual field) and to exclude any vertical and horizontal references from the visual surrounding (see Lenggenhager, Lopez, & Blanke, 2008).

Observers were tested in a dark and noise-isolated room, the only source of light coming from the computer screen. Observers were shown visual stimuli and their performance was tested in two body orientations: sitting upright on a chair and lying right side down on a mattress (Figure 1B). In both orientations, they were facing the screen with their gaze aligned with the screen center at a viewing distance of ~85 cm. Half of the observers started in the sitting orientation, half in the lying orientation. The pictures were presented in four different orientations with respect to the gravitational vertical: upright (the platform was at the bottom of the screen), upside down (the platform was at the top of the screen), tilted 90° clockwise (the platform was on the left side of the screen), and tilted 90° counterclockwise (the platform was on the right side of the screen). Using such a paradigm, it was possible to match all picture orientations with respect to the observer (in a retinocentric reference frame) in the sitting upright orientation with all picture orientations when lying right side down.

Each of the 32 human body postures (16 roll angles × 2 directions of roll) was repeated nine times for each of the four picture orientations, giving a total amount of 1152 trials per observer orientation. The images were presented in random order in blocks of 96 images with the same orientation in space so that there were 12 blocks of trials for each observer orientation. For the sitting and lying orientations, the order of the blocks of trials was randomized within and between observers.

Each block started with the presentation of the platform followed by the apparition of the human body on the platform for 180 ms with an inter-stimulus interval of 1480 ms. The observers performed a two-alternative forced-choice task to judge whether the posture of the human body was stable or unstable, and they indicated their answer by means of a key press on a serial response box. The keys were counterbalanced across the observers: half of the observers used their right index finger to indicate a stable posture and their right medium finger to indicate an unstable posture, and vice versa for the other half of the observers. Observers were always explicitly required to judge the stability of the human body with respect to the platform, whatever its orientation, and never with respect to Earth's gravity. Thus, observers judged the stability of the human body and imagined gravity in the direction concordant with the visual platform (that was concordant or not with the direction of physical gravity). Two practice sessions were given at the beginning of the experiment to minimize training effects across the different blocks of trials.

Subjective visual vertical

To assess orientation perception in the different body orientations, we measured the subjective visual vertical (see Lenggenhager et al., 2008 for similar methods). A white dotted line (subtending ~10° of the visual field) was presented on the screen. The initial position in which the line was shown was either clockwise (5 trials) or counterclockwise (5 trials) at a randomly chosen angle. Observers were asked to move the line clockwise or counterclockwise by pressing a corresponding right or left keyboard button until they judged the line to be vertically oriented (aligned with their perceived gravitational vertical). There was no time constraint to perform the task.

Behavioral data and statistical analysis

For each trial, the dependent variables were the observer's answer (stable/unstable) and the response time (in milliseconds). For each observer orientation and each picture orientation, we analyzed the percentage of responses indicating an unstable posture (here called "percentage of instability") as a function of the amplitude and direction of the human body roll. The data were fitted with a sigmoid psychometric function using the least-squares regression (Matlab 7.6, MathWorks, Natick, MA, USA). The equation of the sigmoid function was

$$f(x) = \frac{1}{1 + e^{-b_1 x + b_2}}, \quad (1)$$

where x was the amplitude of the human body roll, and b_1 and b_2 were parameters determined by the regression performed on the individual observer data. Then we extracted from the individual data the "point of subjective instability" (PSI), namely the angle of human body roll leading to 50% of postures perceived as unstable (see Bonnet et al., 2005; Dyde et al., 2006 for similar approaches).

The percentage of instability and response time were analyzed using repeated measures analyses of variance (ANOVAs) with the observer orientation (body upright, body tilted), picture orientation (picture upright, upside down, tilted 90° clockwise and counterclockwise), direction of human body roll (leftward, rightward), and angle of human body roll (16 angles) as within-subjects factors. Post hoc paired t tests were used to further analyze the significant effects of the ANOVAs. Results were considered statistically significant for $p < 0.05$.

Finally, the mean subjective visual vertical (in degrees) was calculated by averaging the 10 consecutive values for each observer orientation. An ANOVA was performed on the mean subjective visual vertical with the variable observer orientation as a within-subject factor.

Results

Percentage of instability

The performance in the judgment of stability of body postures was measured as the percentage of "unstable" answers (or "percentage of instability"). A repeated measures ANOVA revealed that the picture orientation, the direction as well as the angle of the human body roll on the platform significantly influenced the stability judgments (see Table 1). Observer orientation modified stability judgments depending on picture orientation, angle, and direction of the human body roll (Table 1), suggesting an interaction of gravitational and bodily influences in stability judgments. This is illustrated in Figure 2, for upright observers, and in Figure 3, for observers lying right side down.

PSI, upright observers

When observers were upright, stability judgments were affected by the picture orientation as revealed by shifts of the psychometric curves representing the percentage of instability as well as changes in the mean PSI. When pictures were rotated by 90° from the gravitational vertical, we found that human postures tilted upward (away from gravity) were judged as more stable than the same pictures tilted downward (toward gravity). The percentage of instability was higher for human bodies tilted downward than upward for pictures rotated by 90° counterclockwise ($F_{1,16}$ = 6.66, $p < 0.05$). This can be seen in Figure 2C in a rightward shift of the psychometric curve and higher PSI for postures tilted rightward (i.e., away from gravity, Student's *t* test: $t_{16} = 2.3$; $p < 0.05$, see insert in Figure 2C). As predicted, the opposite was found when pictures were rotated clockwise, with higher PSI for postures tilted leftward (i.e., away from gravity: t_{16} = 2.2; $p < 0.05$; see insert in Figure 2D). By contrast, the mean percentage of instability was similar for rightward and leftward human body rolls on the platform when pictures were presented upright, i.e., with human bodies falling in a direction consistent with gravity ($F_{1,16} = 2.01$, $p = 0.18$; Figure 2A), and when pictures were presented upside down, i.e., with human bodies falling onto the platform in a direction that was visually opposite to gravity ($F_{1,16} = 0.68$, $p = 0.42$; Figure 2B).

Source of variation	*F*	*P*
Observer orientation	$F_{1,16} = 3.24$	0.0908
Picture orientation	$F_{3,48} = 4.57$	0.0068*
Direction of human body roll	$F_{1,16} = 11.16$	0.0042*
Angle of roll	$F_{15,240} = 197.07$	<0.0001*
Observer orientation × picture orientation	$F_{3,48} = 11.08$	<0.0001*
Observer orientation × direction	$F_{1,16} = 23.09$	0.0002*
Picture orientation × direction	$F_{3,48} = 7.44$	0.0003*
Observer orientation × angle	$F_{15,240} = 1.59$	0.0759
Picture orientation × angle	$F_{45,720} = 2.40$	<0.0001*
Direction of human body roll × angle	$F_{15,240} = 4.81$	<0.0001*
Observer orientation × picture orientation × direction	$F_{3,48} = 0.46$	0.7140
Observer orientation × picture orientation × angle	$F_{45,720} = 2.50$	<0.0001*
Observer orientation × direction × angle	$F_{15,240} = 4.94$	<0.0001*
Picture orientation × direction × angle	$F_{45,720} = 2.59$	<0.0001*
Observer orientation × picture orientation × direction × angle	$F_{45,720} = 1.90$	0.0005*

Table 1. Results of statistical analysis (repeated measures ANOVA) on the percentage of instability. Sources of variation: observer orientation (body upright, body tilted), picture orientation (picture upright, upside down, tilted 90° clockwise and counterclockwise), direction of the human body roll with respect to the platform (leftward, rightward), and angle of the human body roll (16 angles). *F*-statistics are reported with degree of freedom and probability level (*p*). *Note*: *Significant main effects and interactions.

PSI, tilted observers

When observers were lying right side down, performance differed from those in upright observers (Figure 3). In this body orientation, rightward and leftward human body rolls lead to different stability judgments when pictures were presented upright ($F_{1,16}$ = 20.13, $p < 0.0005$) or upside down ($F_{1,16}$ = 13.55, $p <$ 0.005). The mean PSI was significantly lower when the human postures were tilted on the platform leftward than rightward for pictures presented upright (Student's *t* test: $t_{16} = 20.24$; $p < 0.0005$; see insert in Figure 3A) as well as upside down ($t_{16} = 11.73$; $p < 0.005$; see insert in Figure 3B). For pictures rotated by 90° counterclockwise, i.e., presented in an upside-down position with respect to the observer's body, the human postures tilted downward (toward gravity) were judged as more unstable than those tilted upward (PSI: $t_{16} = 10.75$; $p < 0.005$, see insert in Figure 3C). Note that specifically when pictures were rotated by 90° clockwise, thus aligned with the observer's body axis, the percentage of instability was similar for postures tilted upward and downward ($F_{1,16} = 0.87$, $p =$ 0.36). Therefore, the mean PSI was similar for human bodies tilted toward and away from gravity ($t_{16} = 0.74$; $p = 0.4$; see insert in Figure 3D) suggesting that pictures perceived as upright in a body-centered reference frame are processed differently.

In order to disentangle the effects of picture orientation with respect to the observer's body and physical gravity, we summarized the PSIs in two polar plots keeping constant the orientation with respect to the body or physical gravity (Figure 4). The influence of the observer's body on stability judgments was revealed by changing the observer orientation while keeping constant the picture orientation with respect to gravity. This body effect is illustrated in Figure 4A. The data indicate that PSIs differ according to

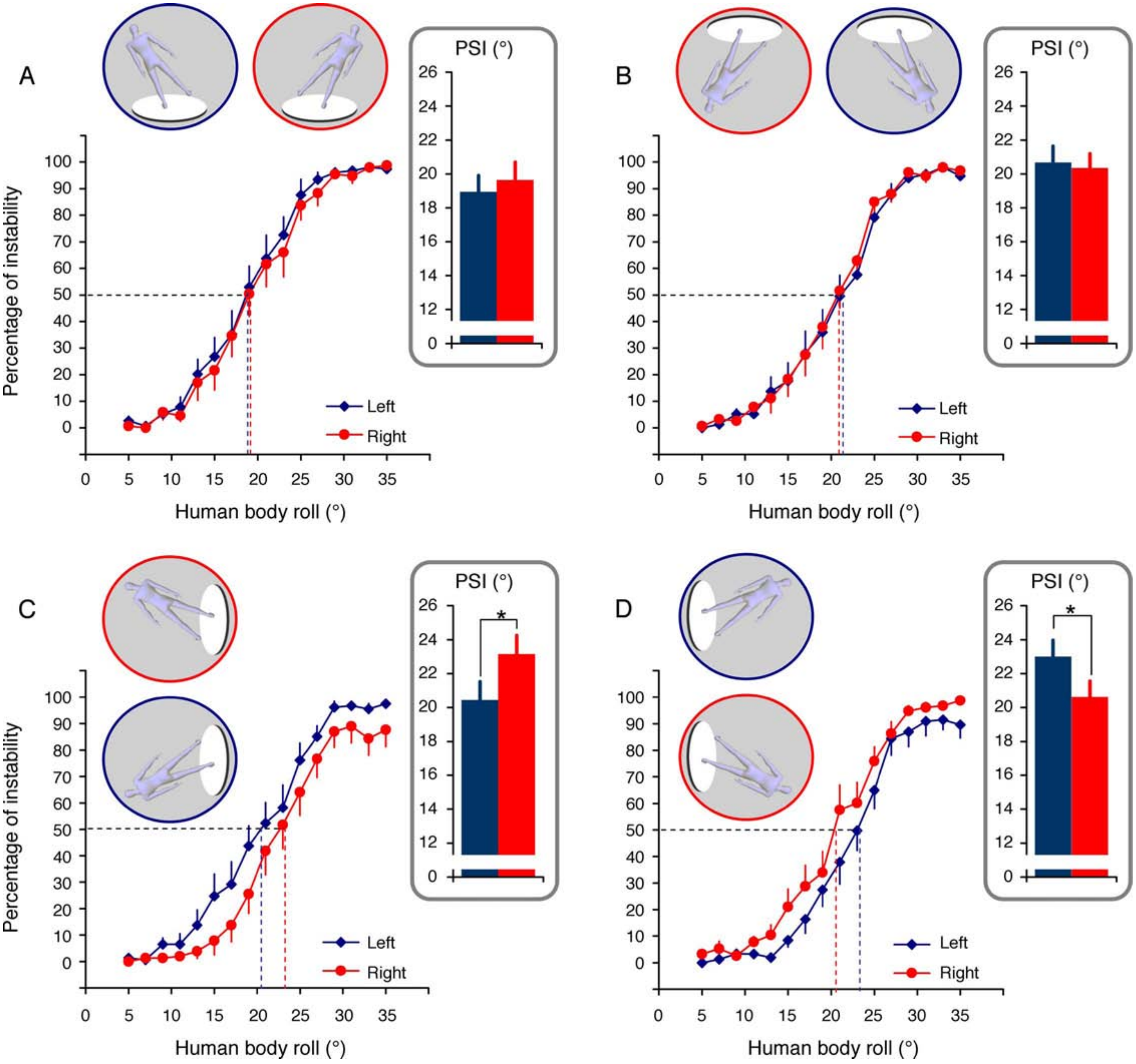

Figure 2. Judgment of the body stability with observers upright. Mean percentage of postures perceived as unstable is shown as a function of the amplitude and direction of the human body roll [leftward roll (*blue curves*) vs. rightward roll (*red curves*), roll with respect to the platform]. The angle of the human body roll always refers to the amplitude of the trunk tilt with respect to the platform and not to gravity (the "zero degree" angle would then refer to a trunk orthogonal with respect to the underlying platform). Note that similar sigmoid curves were evidenced for rightward and leftward human body rolls when pictures were presented (A) upright and (B) upside down, but that significant shifts of the curves were observed when pictures were rotated by 90° (C) counterclockwise and (D) clockwise with respect to gravity. The histograms in the inserts represent the mean point of subjective instability (PSI). *Note*: *Significant difference ($p < 0.05$) between leftward (blue) and rightward (red) rolls of the human body with respect to the platform. Vertical bars represent the standard error to the mean.

the picture orientation with respect to the observer's body. For example, the PSIs for pictures presented upright differed significantly for observers upright and lying right side down (leftward roll, $t_{16} = 2.38$; $p < 0.05$; rightward roll, $t_{16} = 4.43$; $p < 0.001$). The influence of physical gravity on stability judgments was revealed by

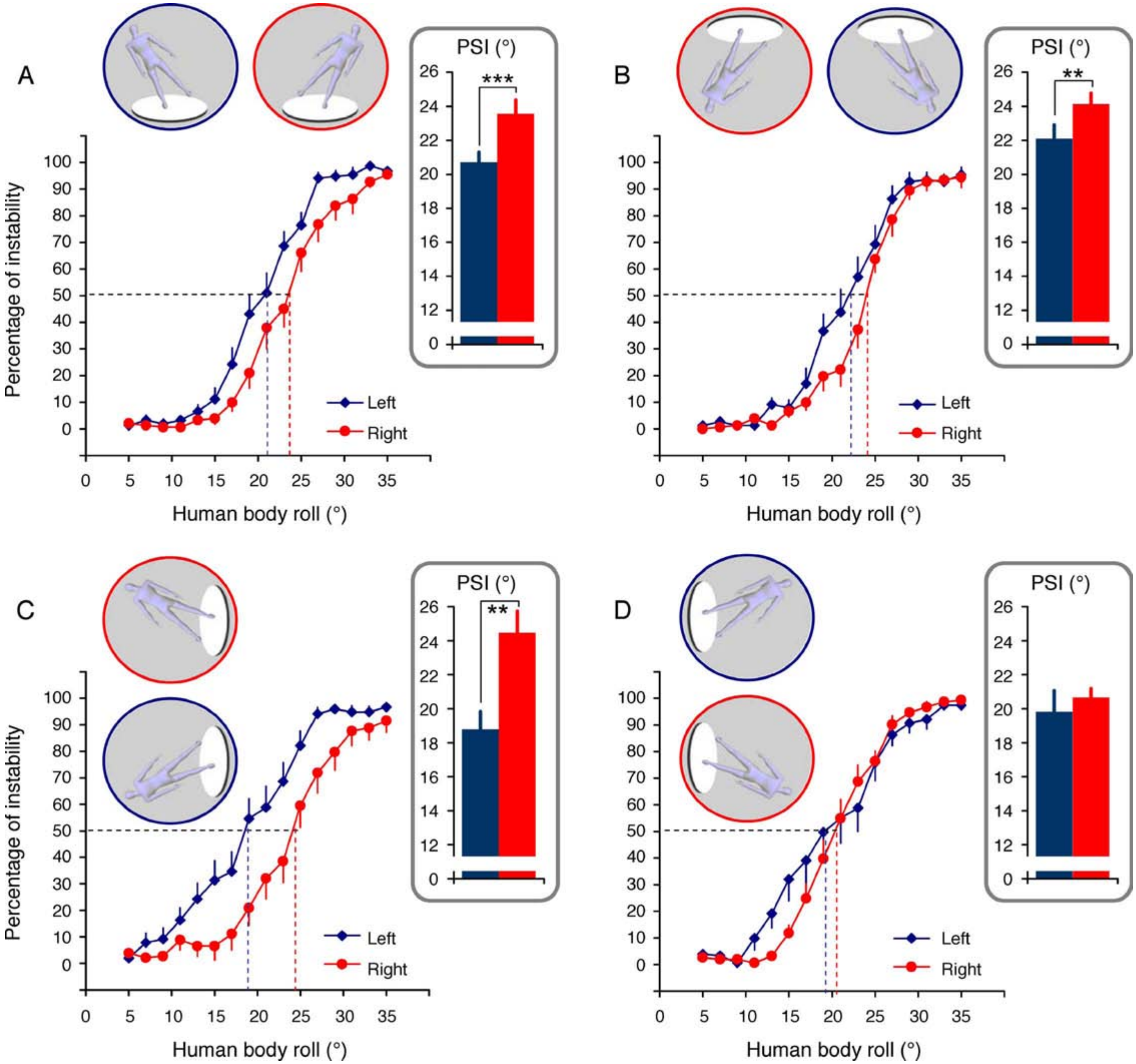

Figure 3. Judgment of the body stability with observers lying right side down. Mean percentage of postures perceived as unstable is shown as a function of the amplitude and direction of the human body roll [leftward roll (*blue curves*) vs. rightward (*red curves*) roll with respect to the platform]. The histograms in the inserts represent the mean point of subjective instability (PSI). Picture orientations represented in (A)–(D) reflect the actual orientation with respect to gravity (same conventions as in Figure 2).

manipulating the picture orientation with respect to gravity, while keeping the picture orientation constant with respect to the observers. This gravity effect is shown in Figure 4B. The data indicate that PSIs differ according to the picture orientation with respect to gravity. For example, the PSIs measured with pictures upside down with respect to the observers differed significantly for observers upright and lying right side down (leftward roll, $t_{16} = 2.71$; $p < 0.05$; rightward roll, $t_{16} = 3.46$; $p < 0.005$).

Concerning the perception of the *visual vertical*, observers judged accurately the orientation of the gravitational vertical when tested upright (mean: 0.5° ± 0.2°). By contrast, the subjective visual vertical was deviated clockwise by 8.7° ± 1.7° on average when observers were lying right side down (significantly different from the

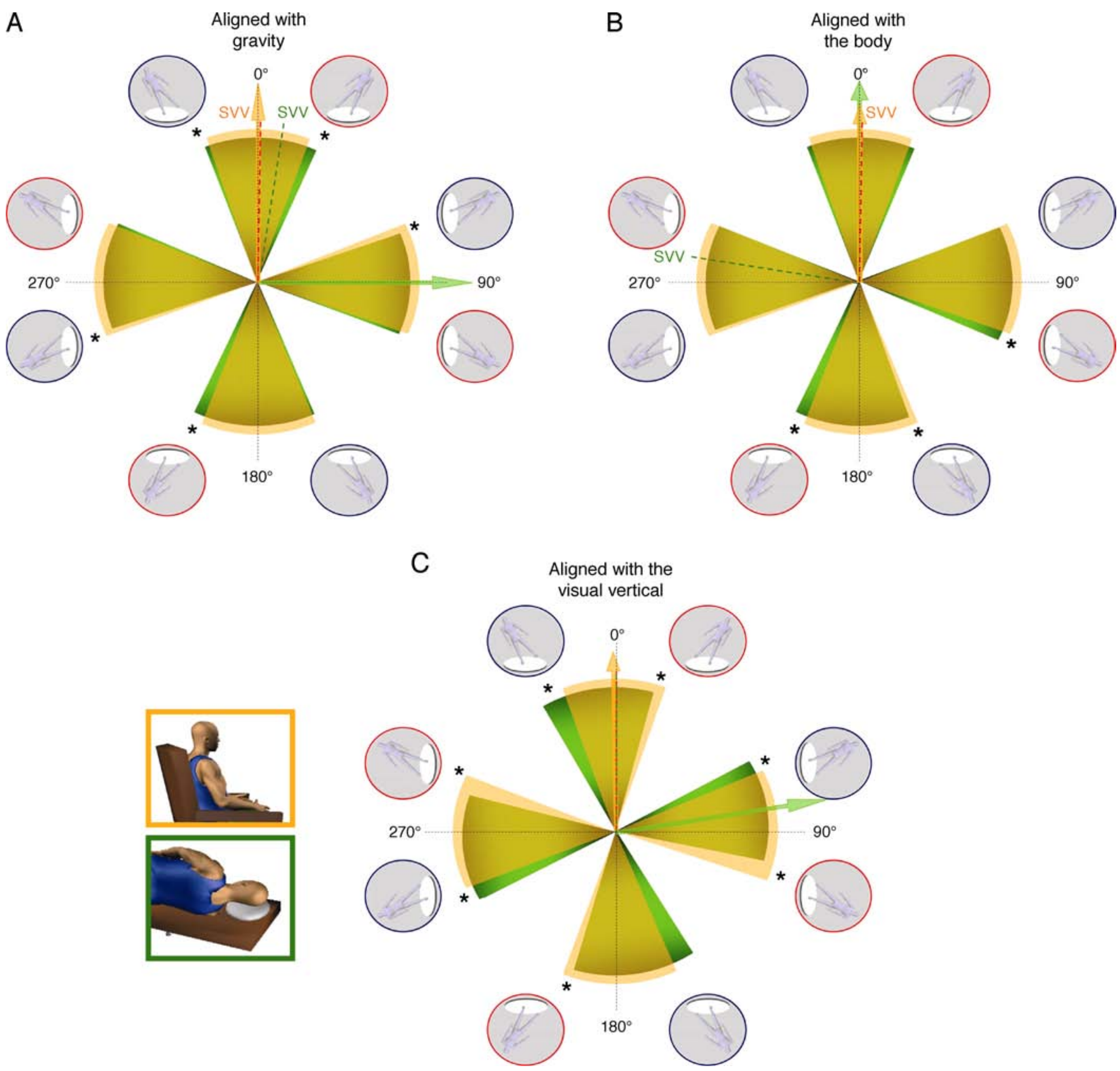

Figure 4. Polar plots of the performance in the stability judgment task with respect to three different types of coordinates: with respect to (A) Earth (0 degree is the gravitational vertical), (B) the observer's body (0 degree is the observer longitudinal body axis), and (C) the subjective visual vertical. The colored areas represent the mean extent of the zone of subjective stability (the postures within the indicated areas were perceived as stable >50% based on the mean point of subjective instability, PSI). The postures outside these areas were perceived as unstable >50% according to the mean PSI. This is shown for leftward and rightward rolls of the human body on the platform. The orange and green areas refer to the zone of subjective stability in the upright and right side down positions, respectively. The mean subjective visual vertical (SVV) is represented as orange (upright observers) and green (right side down observers) dotted lines. The orange and green arrows represent the orientation of the observer's body axis when upright and lying right side down, respectively. *Note*: *Significant difference ($p < 0.05$) between the mean PSIs in both observer orientations, revealing (A) the body effect and (B) the gravity effect.

subjective vertical measured when sitting upright; $t_{16} = 4.7$; $p < 0.0005$), corresponding to the classical Aubert effect. To investigate whether performance in the stability judgment task was related to performance in the visual vertical task, we correlated the PSI with the visual vertical of each observer. The performance in the visual vertical task was not correlated with the stability judgments for upright or right side down observers (range of the

Pearson's correlation coefficients, *r*: −0.34–0.40; range of *p*: 0.107–0.953). This can also be seen in Figure 4C showing the performance in the stability judgments after data were corrected for the bias in the vertical perception. Statistical analysis of the PSI after the data were corrected indicated a significant main effect of the picture orientation ($F_{3,48} = 4.86$, $p < 0.005$), direction of human body roll on the platform ($F_{1,16} = 21.85$, $p < 0.0005$), as well as a significant observer orientation × picture orientation interaction ($F_{3,48} = 10.0$, $p < 0.0001$). Post hoc analyses revealed that the PSIs differ according to the observer orientation. This shows that aligning the data to the perceived visual vertical did not suppress the effects of the picture and observer orientations.

Finally, the ANOVA for response times revealed a significant main effect of angle of human body roll ($F_{15,240} = 18.11$, $p < 0.0001$). There was no main effect of the observer orientation ($F_{1,16} = 1.51$, $p = 0.24$) or the picture orientation ($F_{3,48} = 0.16$, $p = 0.92$), and the interaction of observer orientation × picture orientation did not reach statistical significance ($F_{3,48} = 1.24$, $p = 0.31$). The time to judge the stability of the posture was affected by the roll of the human body on the platform, and on average, task difficulty was similar in both observer orientations.

Discussion

We asked observers to judge the stability of different human body postures in the roll plane while systematically manipulating the orientation of a picture of the human body and the observer's body. Although observers could base their stability judgments entirely on visual cues available in the pictures, we found that visually identical postures may be perceived differently depending on their orientation with respect to gravity and with respect to the observer's body.

Visual judgments of the stability of human body postures

Human body postures were shown as if the body was standing on a platform and we asked observers to judge the stability of the human body with respect to the platform. The overall performance mainly depended on visual references provided by the platform, which indicated the orientation of the "imagined gravity" (that was always orthogonal to the platform). The present data show that observers were able to refer to the orientation and direction of the imagined gravity (indicated by the orientation of the platform); they easily performed the visual stability judgment task and were able to judge the stability of the human body postures even for directions that were not concordant with the direction of physical gravity. This was reflected in response speed showing that stability judgments had the same speed for the different picture and observer orientations. That observers reliably referred to visual references depicted in the images is in line with previous reports that visual references, such as visually polarized backgrounds, may modify the perception of letters (e.g., the letter "p" versus "d"; Dyde et al., 2006) or the perceived direction of illumination (Jenkin et al., 2003, 2004).

Our data also show that the visual form of the human body significantly contributed to the stability judgments and that observers reliably referred to this information to perform the task. Observers consistently reported the instability of the body postures as a function of the angle of the human body roll, in line with previous data on the visual judgment of the stability of postures tilted in the pitch plane (see Bonnet et al., 2005). The human body postures we used contained visual information of whether the depicted person was falling onto the platform or not because these body postures were realistic and because they reflected the gravitational constraints on the body segments (Bonnet et al., 2005; Bouisset & Do, 2008). Observers may have used this important information about gravitational constraints to solve our task, as earlier reports suggest that observers refer to their previous knowledge of biomechanical constraints to interpret body pictures (Bonnet et al., 2005; Petit & Harris, 2005). That observers consistently interpreted the body configuration may be related to the fact that the human visual system is highly tuned to the perception of body configuration and body motion (Blake & Shiffrar, 2007; Reed et al., 2003). The present data also indicate that the stability of a human body can be judged on the basis of pictures in which the movement of the body is not apparent but implied. This is in line with the notion that human movements, including postural control, may be recognized and judged based on static pictures (Kourtzi & Kanwisher, 2000; Urgesi et al., 2006).

Stability judgments of body postures are influenced by physical gravity

Our data show that pictures of a human body that is tilted in the direction opposite to physical gravity ("up") are judged as more stable than pictures of a body that is tilted in the direction of physical gravity ("down"). This was observed when pictures were rotated by 90° clockwise and counterclockwise from the physical vertical with observers in an upright orientation (Figures 2C and 2D), and when pictures were rotated by 90° counterclockwise with observers lying right side down (Figure 3C). Although observers were instructed to perform the stability judgment with respect to the platform and imagine gravity according to the depicted visual cues (the "imagined gravity" was orthogonal to the platform), they were not able to ignore the influence of the physical gravitational acceleration. This finding speaks in favor of an internal representation of gravity (or of Newton's laws) in the brain that biases the judgment of static pictures with implied motion. In other words, our data suggest that visual stability judgments are biased by the inference made from our everyday experience of gravity that objects, including human bodies, always fall "down" and this even if conflicting visual cues are provided. As humans have evolved under constant gravitational acceleration, they may have internalized the "up" and "down" directions along the axis of gravity, as well as the effects of gravity on objects (Hubbard, 1995). This is also compatible with human developmental data in newborns and infants showing that sensitivity to gravitational effects on visual perception of moving objects develops early and gradually in childhood. Thus, Kim and Spelke (1992, 1999) found that, by the age of 5 to 7 months, infants consider that it is more "natural and familiar" for a downward moving object (i.e., in the direction of gravity) to be accelerating than decelerating. Early anchoring of visual perception in a gravity-centered reference may account (at least partly) for our findings that observers cannot fully ignore physical gravity (even when explicitly required to do so). This is also in line with previous reports that gravity constrains visuospatial imagery (e.g., Grabherr et al., 2007).

The present data extend previous findings that an internal model of gravity influences visual perception of moving objects such as a falling ball (Indovina et al., 2005; McIntyre et al., 2001; Senot et al., 2005; Zago et al., 2004, 2005; Zago & Lacquaniti, 2005). These authors reported performance differences when observers estimated the manual interception of a ball either moving upward or falling downward. Performance was consistent with an anticipation of gravitational effects on the objects (see Senot et al., 2005). Our data suggest that physical gravity also influences visual stability judgments, even when physical motion of the visual stimulus is absent and is only implied. This may be comparable with findings showing that the representation of physical forces such as gravity, friction, or centripetal forces may affect the representation of object movement, based on viewing a series of static pictures that induce "representational momentum" (Freyd, 1983, 1987; Freyd, Pantzer, & Cheng, 1988; Hubbard, 1995, 1997, 2005; Vinson & Reed, 2002). Experiments on the effects of physical forces on representational momentum involve the presentation of multiple pictures depicting a picture sequence of a human body (e.g., a person jumping off a wall; Freyd, 1983) or of a displaced object (e.g., a plant hanging from a hook; Freyd et al., 1988). By contrast, our data show that the presentation of a single static image was sufficient to reveal the influence of gravitational forces on visual perception. We also note that although studies on representational momentum found an effect of gravity on visual perception (so-called "representational gravity", Hubbard, 2005), these studies did not dissociate gravitational and bodily influences, because, as far as we know, they did not manipulate the orientation of the picture and the observer in space.

Our observation that stability judgments are influenced by the picture orientation with respect to gravity is also in agreement with behavioral studies suggesting that gravity influences the perception of other types of pictures: the perceived "up" direction influences various geometrical visual illusions such as Rock's diamond/square and the Ponzo illusions (Clément & Eckardt, 2005), perception of right angles (Ferrante et al., 1995), character recognition (Dyde et al., 2006), perception of shape from shading (Jenkin et al., 2003, 2004), as well as interpretation of reversible figures (Yamamoto & Yamamoto, 2006). Finally, the importance of physical gravity in visuospatial processing gains further support from experiments using artificial stimulation of the vestibular receptors by caloric and galvanic vestibular stimulations. These stimulations—which modify the perceived orientation of gravity as well as the perceived body orientation with respect to gravity—were shown to impair various aspects of visual imagery (Lenggenhager et al., 2008; Mast, Merfeld, & Kosslyn, 2006).

Stability judgments of body postures are influenced by the orientation of the observer's body

Our data demonstrate that visual judgments of the stability of human body postures are also influenced by the picture orientation with respect to the observers' body, because performance in the right side down condition differed from performance in the upright condition (Figure 3). Importantly, the picture orientation with respect to physical gravity was kept constant in these conditions. When observers were lying right side down, we found different PSIs for rightward and leftward human body rolls when pictures where presented upright, upside down, or rotated by 90° counterclockwise with respect to gravity. This was not the case when pictures were rotated by 90° clockwise (i.e., when aligned with the observer's body).

Thus, pictures aligned with the observer's body (i.e., visually upright in a retinocentric reference frame) seem to be processed differently. We propose that this effect may be due to the fact that visual stimuli (especially other people's bodies) are, in daily life, usually aligned with the observer's body axis. Additionally, the ability to process body postures on the basis of prior knowledge of the human biomechanical constraints (Bonnet et al., 2005) might be impaired when pictures are rotated with respect to the observer's body. Indeed, numerous studies have pointed to impaired processing for the visual perception of faces, bodies, and biological motion when pictures are in a non-canonical orientation (Lobmaier & Mast, 2007; Reed et al., 2003, 2006; Troje, 2003; Troje & Westhoff, 2006;

Yin, 1969). The importance of the body-centered reference frame for the perception of the human face and biological motion was stressed by Troje (2003), who suggested that the inversion effect depends on the picture orientation with respect to the retinocentric reference frame and not with respect to the gravitational reference. However, other studies on the inversion effect demonstrated an additional influence of the gravitational reference. Lobmaier and Mast (2007), using a large range of body rolls, observed an influence of the observer orientation on human face perception, and Gaunet and Berthoz (2000) found a small effect of the observer's body orientation on the perception of visual scenes. Nevertheless, despite the combination of gravity- and body-centered references, these studies showed that the inversion effect was based mainly on the pictures' orientation with respect to the observer's body, and such a body-centered reference seems to be present early in life (Kushiro, Taga, & Watanabe, 2007).

Subjective visual vertical

A final factor that may have influenced task performance is the perceived orientation of gravity (the subjective visual vertical) and of the "up" direction that differed in both observer orientations. Whereas observers accurately estimated the orientation of the gravitational acceleration when sitting upright, the perceived visual vertical was deviated by ~9° toward the body axis in the tilted orientation. This deviation of the perceived visual vertical, also known as the Aubert effect (Aubert, 1861; Mittelstaedt, 1983; Van Beuzekom & Van Gisbergen, 2000), is probably due to an increased weighting of the body-centered reference frame when observers are in a lying orientation, leading to a reorientation of the perceived vertical toward the observer's body axis (Luyat, Ohlmann, & Barraud, 1997; Mittelstaedt, 1991, 1992, 1999). We tested whether the tilted visual vertical influenced, or was associated with, the present stability judgments, hypothesizing that human bodies tilted rightward (for upright pictures) and leftward (for upside-down pictures) were judged as more stable than human bodies tilted in the opposite direction, because they were perceived as being more upright with respect to the erroneous "up" direction (that was reoriented toward the observer's body axis). We did not find any significant correlations between the subjective visual vertical and individual PSIs. To summarize, our data suggest that the central nervous system combines gravitational, bodily, and visual (indicated by the platform) cues to elaborate a representation of the vertical and "up" direction affecting the perception of static pictures with implied motion. Our data are also in line with previous experiments suggesting that the perceived vertical and "up" direction interfere with the perception of more basic visual stimuli such as shape-from-shading perception (Jenkin et al., 2004) or character recognition (Dyde et al., 2006).

Conclusion

The present study indicates that, in addition to the prominent influence of the visual references provided by the platform and the visual form of the human body, the visual judgment of the stability of a human body is influenced by the orientation of the picture with respect to gravity as well as the observer's body. Thus, although visual references such as the platform and human body indicate the direction of the imagined gravity, the present gravity effect demonstrates that physical gravity cannot be ignored and influences the perception of pictures devoid of any explicit movement or representational momentum (Freyd, 1983; Freyd et al., 1988; Hubbard, 1995). We also demonstrate that such visual judgments are also influenced by the orientation of the observer's body axis (body effect); this is probably related to the fact that pictures of human bodies are usually upright and aligned with respect to the body of the observer. The data also suggest that the vertical and "up" direction are spatial concepts that, even when not explicitly required, may influence our visual perception of the external world. Collectively, the present data point to the highly adaptive role of the representation of the vertical and "up" direction and that humans constantly update this representation on the basis of multisensory cues, not only to maintain balance for standing upright or achieving acrobatic feats (Berthoz, 2000; Smetacek, 2002) but also for accurate visual perception. This may also affect more sophisticated spatial skills such as those required for geometry and architecture (Clément & Eckardt, 2005; Ferrante et al., 1995).

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