

# The subjective visual vertical in a nonhuman primate

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We perceive the visual world as upright as our visual system used information on the orientation of the body to update the internal representation of the visual scene. In humans, this updating is not perfect, thus leading to distortions of the subjective visual vertical. For small roll-tilt angles ( $<60^\circ$ ), subjects overestimate the body tilt (E-effect), whereas for larger angles they underestimate it (A-effect). We wanted to know if monkeys show comparable perceptual distortions as they might help to identify the neural basis of a tilt-independent representation of visual objects at the level of single neurons. In order to answer this question, we trained two monkeys to align an arrow with an upright world-centered reference line whose visibility was varied between trials. Trials were performed at roll-tilt angles chosen from  $-90^\circ$  to  $90^\circ$ . The monkeys' responses were precise for trials in which the reference line was visible. However, for the trials in which there was no reference line, their responses reflected an overestimation of body tilt (E-effect-like) very similar to humans. Our ability to demonstrate similar visuo-vestibular illusions in monkeys and man is an important step towards understanding the neural mechanism responsible for the perception of an upright visual world.

Keywords: subjective visual vertical, Rhesus monkey, E-effect

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## Introduction

We perceive the world as stable and upright despite the fact that we continuously change our orientation as a consequence of our movements. This invariance of our percept of the world is one of the major foundations of successful spatial orienting and the development of useful behaviour directed at objects in the world. Despite its great ecological importance, the neural mechanisms leading to a veridical percept of an upright world remain largely unclear. Psychophysical studies suggest that the brain uses information on the orientation of the gravity vector, mainly mediated by the otolith system and probably supplemented by somatosensory signals, not only to assess the orientation of our body relative to the world but also to determine the orientation of visual structures with respect to the gravity vector (Klier, Angelaki, & Hess, 2005; Klier, Hess, & Angelaki, 2006; Van Gisbergen, Medendorp, & Van Pelt, 2005). Yet it is unclear where in the brain gravity-related signals are integrated into vision in order to convert the representation of visual structures from a retinal frame of reference

into a world-centered frame of reference. There are some hints that this integration may already occur—or at least start—at early stages of the cortical processing of visual information as single-unit recordings from areas V1 and V2 of cats and monkeys demonstrate tilt-dependent changes of orientation preferences in some of the neurons studied (40% of the neurons V2 and V3/V3A) (Horn & Hill, 1969; Schwartzkroin, 1972; Tomko, Barbaro, & Ali, 1981; Xavier, Sauvan, & Esther, 1999). Unfortunately, the lack of concomitant perceptual measurements prevents a reliable interpretation of these early observations.

As a first step to revealing the neural mechanisms responsible for the perception of an upright visual world, we therefore tried to develop a psychophysical paradigm allowing us to measure the percept of visual upright in monkeys. To this end, we adapted the classical psychophysical paradigm used to measure the perception of the orientation of the visual world in humans, the measurement of the subjective visual vertical (SVV) (Aubert, 1861), to the needs of monkeys. In human subjects, it is well known that the perception of the orientation of the visual world as expressed by the SVV is systematically influenced by the orientation of the body of the observer

(Aubert, 1861). If the observer is tilted about the roll axis, for small roll-tilt angles ( $<60^\circ$ ), subjects typically overestimate the roll tilt of the body (Müller- or E-effect) (Boff, Kaufman, & Thomas, 1986; Howard, 1982; Kaptein & Van Gisbergen, 2005) as expressed by opposite tilts of the SVV relative to the true vertical. Conversely, they tend to underestimate the body tilts for larger roll-tilt angles, pulling the SVV away from the true vertical in the direction of the tilted body (Aubert- or A-effect; Kaptein & Van Gisbergen, 2005). The E- and the A-effect must be understood as deviations from an ideal perception, obviously small enough to be tolerable ecologically. Importantly, they must reflect insufficiencies of the mechanism underlying the reinterpretation of visual orientation in the light of information on body orientation. Hence, if detectable also in species allowing single-unit recordings, these deviations might be exploited to identify the neural basis of a tilt-independent representation of visual structures as captured by the SVV.

Here we show that the SVV of rhesus monkeys can be measured reliably, and moreover, that rhesus monkeys indeed exhibit the same E-effect-like distortion as humans when trying to indicate their visual upright when roll-tilted by angles randomly chosen between  $-90^\circ$  and  $90^\circ$ .

## Materials and methods

### Subjects

We used two rhesus monkeys (*Macaca mulatta* L. M1, M2) in our experiments. All animal procedures followed the guideline as set by the NIH and national law and were approved by the local committee supervising the handling of experimental animals. The monkeys were seated in a primate chair. During the training and experimental sessions, the head of the monkeys were fixed with respect to the monkey chair and with respect to the rest of the body using a helmet. The body of the monkeys was restrained using a cushioned belt fixing the monkeys back to the primate chair. Additionally, foamed plastic was used to fill up the remaining empty space to minimize the trunk mobility in the chair. Although the trunk and the head of the monkeys were fixed, they were able to use their hands to manipulate a small rotating metal wheel (diameter 15 cm) fixed to the monkey's chair to indicate the SVV.

### Behavioral setup and training

The chair was placed on a two axis turn table with the monkey's naso-occipital axis aligned with the system's roll rotation axis. The visual stimuli were presented on a frontoparallel LCD screen (19 in., resolution:  $1280 \times 1024$ ) located at 50 cm in front of the monkey. The

monkey watched the screen binocularly through a circular aperture ( $30^\circ$  visual angle) preventing him from using any of the screen edges as orientation reference. The primate chair and the screen were surrounded by an opaque sphere (diameter 196 cm) dimming out the room around the monkey and effectively eliminating any visual cues that might have served as orientation landmarks from his surroundings.

The visual stimuli comprised a reference line (length:  $30^\circ$  width:  $2^\circ$  visual angle), whose contrast could be chosen from a fixed set of values (0%, 14%, 40%, 64%, 73%, and 81%) plus one additional contrast value of 68% (training trial line, see below). The contrast level was computed using the Michelson contrast formula (contrast level =  $100 * (\text{line luminance} - \text{background luminance}) / (\text{line luminance} + \text{background luminance})$ ). The reference line was centered on the screen and always oriented parallel to the direction of gravity. In addition to this reference line, a red arrow (length:  $28^\circ$ ; width:  $2^\circ$  visual angle; contrast 81%) was presented, whose orientation could be rotated by the monkey in the roll plane (angular resolution of the positioning  $0.27^\circ$ ). The edges of the reference line and the arrow were anti-aliased (Freeman, 1974) to prevent the monkey from using the orientation of individual pixels as basis for the judgment of the orientation of the arrow. The monkey controlled the orientation of the arrow by turning the steering wheel. Turning the steering wheel by  $30^\circ$  to the left closed an electronic contact, associated with a mechanical stopper, which led to a continuous counterclockwise rotation of the arrow at a constant velocity of  $15^\circ/\text{s}$ . Correspondingly, when the monkey turned the steering wheel by  $30^\circ$  to the right, the arrow started to rotate continuously in a clockwise manner at the same constant velocity. As soon as the monkey moved the steering wheel to a position in between the two extremes, the rotation of the arrow stopped. The monkey received a reward only if the angular deviation of the arrow from the reference line fell below a threshold fixed by the experimenter. Initially, the acceptable deviation was big ( $\pm 30^\circ$ ), but in the course of the training, gradually reduced to  $\pm 5^\circ$ . Note that the monkey had only one chance to meet the criterion per trial as no corrective adjustments of the arrow were allowed. If the arrow stopped outside the acceptable range, the monkey had to wait for the next trial in order to get a new chance.

### Experimental paradigm

Each experiment comprised a set of blocks of trials with each block characterized by a particular roll tilt, chosen at random from a range of  $-90^\circ$  to  $90^\circ$  in steps of  $10^\circ$  (the minus sign designating counterclockwise roll rotations and the plus sign clockwise roll rotations). From each block to the next, the monkey was moved into a new tilt position by rolling him slowly at a maximum angular

velocity of  $2.1^\circ/\text{s}$ . In each block, the monkey was exposed to a series of trials chosen at random from two classes: *training trials* and *test trials*. In the *training trials* (which constituted 66% of all trials for M1 and 56% for M2), the monkey was asked to orient the indicative arrow upward by aligning it as precisely as possible with the clearly visible vertical reference line (contrast 68%, see Figure 1, situation A). The initial orientation of the arrow was randomized, and the velocity of the arrow orientation induced by the monkey was fixed to  $15^\circ/\text{s}$ . The orientation of the arrow adopted when its movement stopped for the first time for more than 2 s after trial onset was taken as the monkey's response. It was rewarded with a drop of apple juice, if the angular deviation between the arrow and the reference line fell below  $5^\circ$ . In the *test trials* (which constituted 34% of all trials for M1 and 44% for M2), in which the monkey experienced the same roll tilt as in the training trials, we chose the contrast level of the reference line with respect to the black background at random from 0%, 14%, 40%, 64%, 73%, and 81% (see Figure 1: situation B for 0% contrast, situation C for 73% contrast). Note that the contrast level of the reference line presented during the training trials (68%) was chosen from the range of contrast levels covered by the reference line in the test trials (i.e., 0–81%) in order to prevent that an odd contrast level might allow the monkey to distinguish the two classes of trials (training and test) and to adopt two different response strategies. A reward was provided in 60% of the *test trials* if the monkey stopped turning the arrow for at least 2 s at any time after the beginning of the

trial, irrespective of the angle chosen. At the end of each *training* or *test trial*, both the arrow and the reference line were extinguished and a visual mask, consisting of randomly plotted white dots, was turned on for 1 s to erase any orientation aftereffects. The interval between subsequent trials was 2 s. For each roll-tilt position, the animal performed around 25 arrow orientation settings. After altogether 320 s, the monkey was reoriented back to the upright position and allowed to rest for 15 s before being tilted into a new position.

A rest period of 15 s between different tilt positions seems sufficient to avoid tilt after effects as the time constants of the otolith and vertical-canal-derived signals underlying the sense of tilt are  $\leq 5$  s (otoliths responses: 5 s (Bockisch, Straumann, & Haslwanter, 2003); vertical canal responses: 5 s (Angelaki & Hess, 1994)). Correspondingly, Van Pelt et al. (2005) demonstrated that the SVV of humans as assessed by saccadic pointing is independent of the amount of rotation experienced on preceding trials. In summary, during a specific roll-tilt position, the monkey was asked most of the time to align the arrow with the visible upright reference line (training trials, contrast of 68%). Randomly inserting the few test trials with varying contrast levels of the reference line allowed us to measure the effect of the current static roll-tilt position on the perceived visual orientation of the arrow. Reducing the contrast level of the reference line in 6 steps from maximal to zero in these test trials allowed us to reveal an increasing influence of the vestibular signal on the monkey's percept of the arrow orientation.

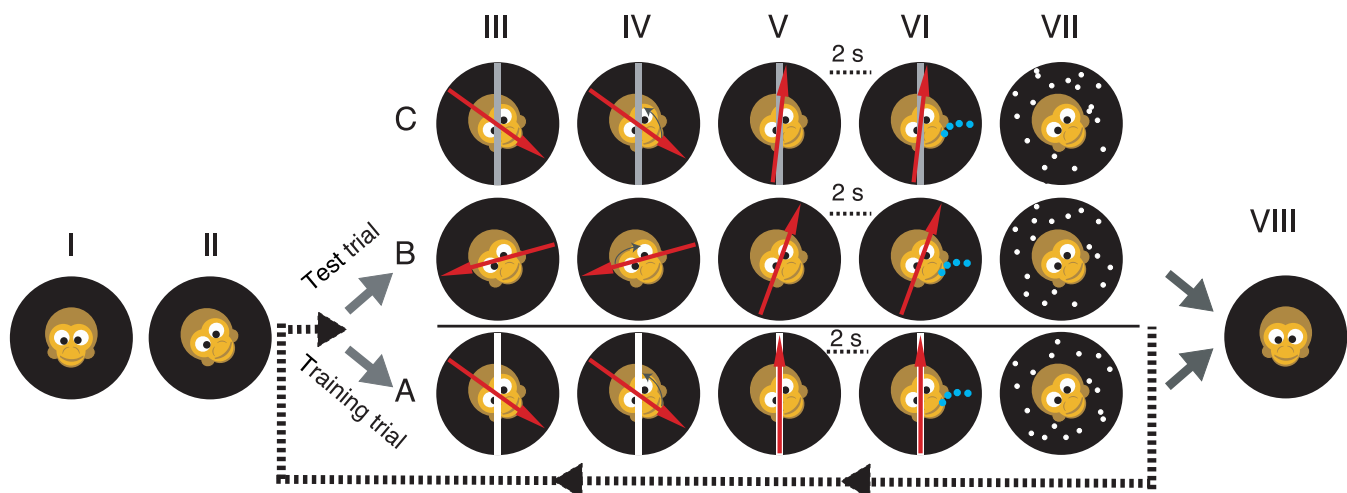


Figure 1. The paradigm. (I) The monkey is in an upright position. (II) The monkey is roll tilted into a randomly chosen orientation between  $-90^\circ$  and  $90^\circ$  (steps of  $10^\circ$ ). (III) When the roll position is reached, the type of the trial is randomly chosen: *training trial* (share of 66% for M1 and 56% for M2) or *test trial*. If a *training trial* is chosen, an upright reference line, at 68% contrast level, is plotted together with a red arrow indicating the monkey's SVV on a black background (A). If a *test trial* is selected, the contrast level of the reference line is chosen at random in 6 steps between maximal contrast of 81% and 0% contrast (B illustrates the 0% contrast level case and C the 73% contrast level case). (IV) The monkey rotates the arrow with the steering wheel in order to indicate his SVV. (V–VI) If the monkey stops the rotation of the arrow for 2 s, it gets a reward (see methods). (VII) A visual mask is flashed for 1 s. The dashed arrow indicates the start of new trial. For a given roll-tilt angle, the monkey could perform around 25 arrow orientation settings. (VIII) After 320 s, the animal is roll tilted back to the upright position.

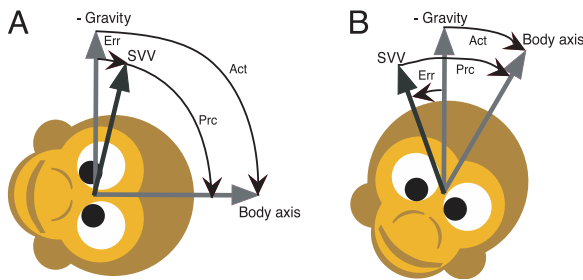


Figure 2. Sign conventions in the computation of the error of the perceived roll tilt: If the perceptual roll-tilt error ( $Err$  = the difference between the actual ( $Act$ ) and the perceived ( $Prc$ ) roll tilt) and the actual roll tilt ( $Act$ ) have the same sign, the roll tilt is underestimated (situation A, Aubert- or A-effect). If they have opposite sign, the roll tilt is overestimated (situation B, Müller- or E-effect).

## Conventions

The *perceptual roll-tilt error* ( $Err$ ) was computed as the difference between the actual tilt angle ( $Act$ ; Figures 2A–2B) and the perceived roll-tilt angle ( $Prc$ ). In Figures 3A–3G and 4A–4G, the error angles  $Err$  are shown as a

function of the roll-tilt angle according to the following sign conventions (described in Figures 2A–2B): Positive roll-tilt angles are clockwise roll rotations and negative ones are counterclockwise roll tilts from the monkeys' point of view. If  $Err$  and the actual roll tilt have the same sign, the roll tilt is underestimated (Figure 2A); conversely, if they have opposite signs, the roll tilt is overestimated (Figure 2B).

## Results

Figures 3 and 4 plot the mean perceptual roll-tilt error  $Err$ , the difference between actual and perceived roll tilt, as function of roll-tilt angle, separately for the two monkeys (Figure 3 for monkey M1, Figure 4 for monkey M2). In each figure, panel A shows the error for *training trials* (Figure 3A for M1, Figure 4A for M2), and panels B to G depict the errors for the *test trials*, ordered from the highest (B: 81%) to the lowest (G: 0%) reference line contrasts. M1 contributed  $n = 1790$  *training trials* and in total 926 *test trials*. M2 gave  $n = 1040$  *training trials* and

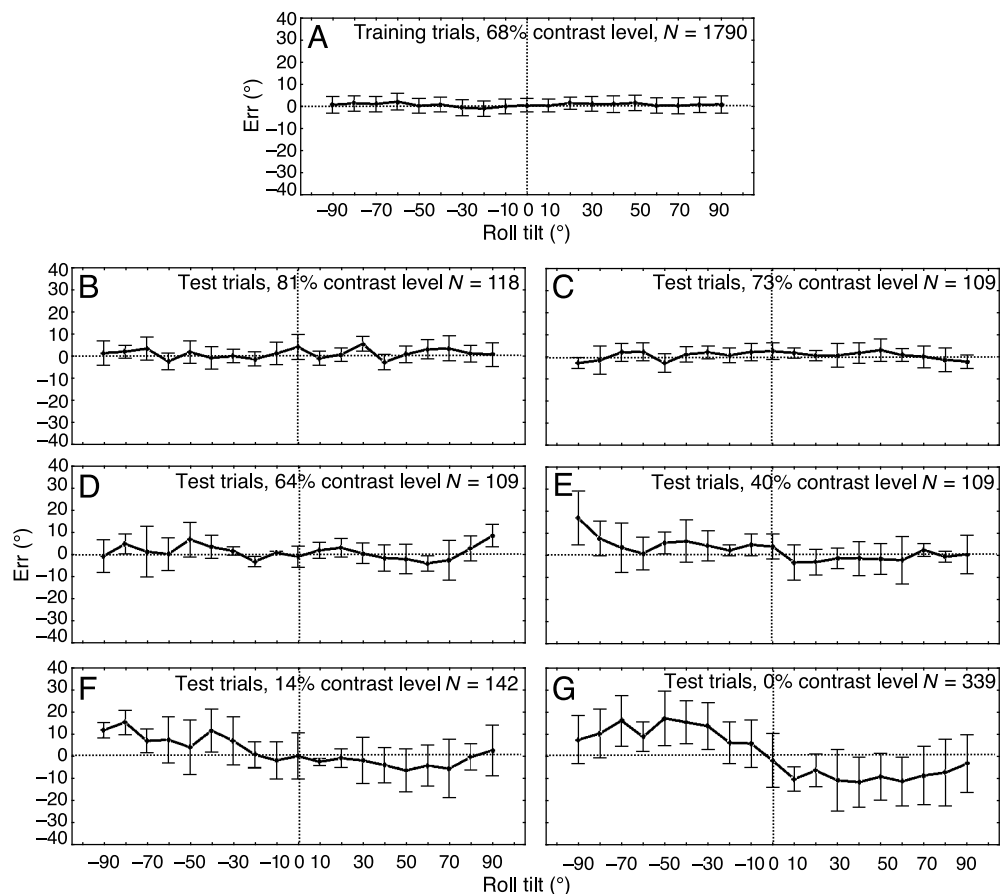


Figure 3. Plots of mean  $Err$  (difference between perceived and true roll tilt; see Figure 2) as function of roll-tilt angle for *training* (A) and *test trials* (B–G) for monkey M1. In the *test trials*, the contrast level of the reference line was randomly chosen from 0%, 14%, 40%, 64%, 73%, and 81%. The vertical bars indicate the standard deviations.

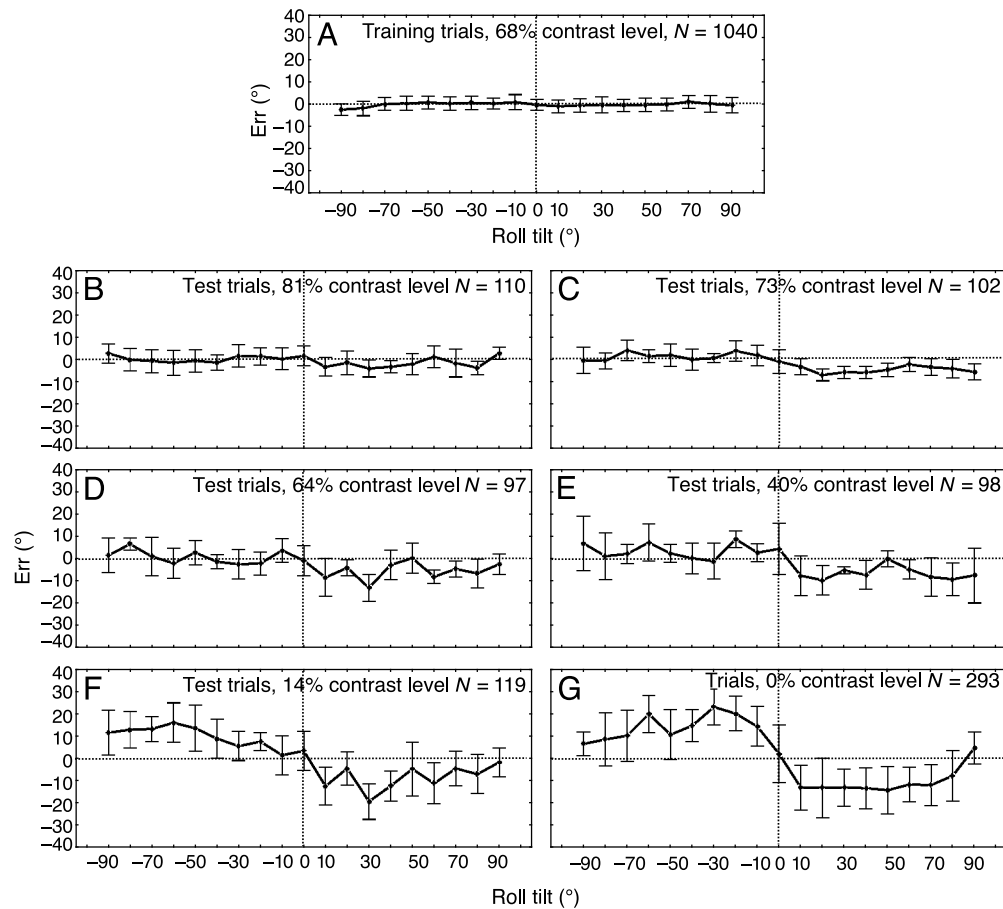


Figure 4. Plots of mean *Err* (difference between perceived and true roll tilt; see Figure 2) as function of roll-tilt angle for *training* (A) and *test trials* (B–G) for monkey M2 (same notation as in Figure 3).

in total  $n = 819$  *test trials*. Visual examination of the plots suggests that in both monkeys, reducing the visibility of the reference line had two effects: First, the variability of the perceptual roll-tilt error *Err* increased with decreasing reference line contrast. Actually, for 0% contrast level *test trials*, the standard deviations of the error measures were about 5 times as large as those for the *training trials*. Secondly, systematic tilt-dependent deviations of *Err* seemed to build up with decreasing visibility of the reference line. While clearly absent for *training trials* and for higher reference line contrast *test trials* and questionable for medium contrast *test trials*, both monkeys showed clear tilt-dependent deviations of *Err* in the absence of any reference line (0% contrast; Figures 3G and 4G), a deviation which becomes even more compelling after pooling data from both monkeys (Figure 5). In order to test the validity of a systematic influence of roll-tilt angle on the perceptual roll-tilt error *Err*, gated by decreasing contrasts of the reference line, we subjected the *test trials* data to a two-way ANOVA with the factors *contrast* and *roll-tilt angle*, separately for the two monkeys. Note that this analysis was applied to  $z$ -transformed data in order to account for the contrast-dependent differences in standard deviations alluded to before. Consequently, ANOVA

indicated that the effect of reference line contrast on *Err* was not significant ( $p > 0.05$ ), neither for M1 nor for M2. On the other hand, the effect of the roll-tilt angle on *Err* was highly significant for both M1 ( $F(18,828) = 4.8644$ ,

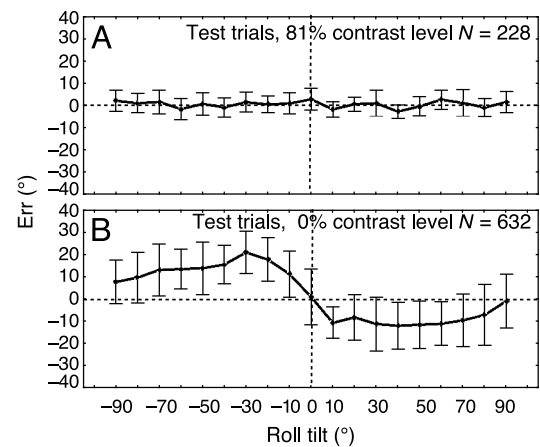


Figure 5. Mean of *Err* for data pooled from M1 and M2, as function of roll-tilt angle for *test trials* with 81% contrast of reference line (A) and 0% contrast (B). Vertical bars indicate the standard deviations of *Err*.

$p = 0.0000$ ) and for M2 ( $F(18,705) = 20.537$ ,  $p = 0.0000$ ), and also the interaction between the two factors, roll-tilt angle and reference line contrast, was significant for both M1 ( $F(90,828) = 2.4485$ ,  $p = 0.0000$ ) and M2 ( $F(90,705) = 1.8278$ ,  $p = 0.00002$ ).

Subjecting data pooled from the 2 monkeys for the *test trials* with contrast level 81% (clearly visible reference line) and 0% (invisible reference line) (Figure 5) to the same analysis (2-way ANOVA of  $z$ -transformed error measures with factors *contrast level* and *roll-tilt angle*) replicated the finding of a nonsignificant ( $p > 0.05$ ) main effect of contrast level, significant main effect of roll-tilt angle ( $F(18,822) = 11.749$ ,  $p = 0.0000$ ), and a significant interaction of the two ( $F(18,822) = 8.1874$ ,  $p = 0.0000$ ).

## Discussion

This report describes a behavioral procedure we designed in an attempt to measure the percept of vertical in a species, the rhesus monkey (*M. mulatta*), unable to deliver verbal reports of subjective insights based on introspection, arguably also attainable to nonhuman primates. As any attempt to capture subjective experiences in monkeys and other animals, also assessing the percept of vertical therefore requires the observation of nonverbal behavior and the demonstration that the observed behavior shows features that in humans are known to be associated with specific subjective states. Humans can be asked to indicate their subjective visual vertical by adjusting the orientation of a line in darkness in the absence of any visual landmarks. This is basically also what our two monkeys were asked to do in the 0% contrast level *test trials* of our experiments. But why should we be allowed to assume that the monkeys indeed tried to associate the orientation of the arrow chosen by them with their percept of upright? Actually, there are two arguments supporting the validity of the conclusion that the monkeys were indeed trying to indicate their subjective visual vertical (SVV). The first one is based on the behavioral framework constraining the arrow setting behavior of the monkeys, and the second one is based on the consistent and nontrivial patterns of responses obtained, which fully correspond to those exhibited by human subjects tested under similar conditions. With behavioral framework, we refer to the fact that the monkeys were trained to orient the arrow relative to a reference line, clearly visible in training trials, which stayed vertical relative to the world independent of the monkey's orientation. We hoped that rewards delivered in response to successful alignments of the arrow and the world-centered reference line would facilitate the development of an association of desired arrow orientation and the vertical, which at some point would become independent of the availability of the visual reference as in 0% level test trials. Of course, the monkeys

might have chosen to orient the arrow relative to the visual vertical reference—if available—but to prefer to make random choices or idiosyncratic choices in the absence of useful visual landmarks, i.e., in 0% level *test trials*. However, clearly, the choices made in *test trials* were neither random nor idiosyncratic, the latter in the sense that they would be noninterpretable. Rather they consistently reflected the orientation of the external world, actually with the same systematic roll-tilt-dependent distortions exhibited by humans, known as the E-effect. Roll-tilting the body away from the gravitational vertical in humans leads to an overestimation of the perceived tilt as indicated by a rotation of the arrow, the measure of the subjective vertical, in the opposite direction. In humans, this E-effect typically peaks around 60° of roll tilt, and its peak size is on the order of 15° (Jaggi-Schwarz & Hess, 2003). Although the monkey data lacked similarly sharp peaks also the monkey E-effect was largest around 60° and had a similar order of magnitude (around 12°). Actually, these numbers may only be approximative as we cannot rule out small compensatory eye and head movements our monkeys may have been able to make. Rather than using implanted head holders, as described in the [Materials and methods](#) section, the head of the monkeys was immobilized with respect to the body by using a helmet attached to the chair, probably leaving room for minimal (<2°) head movements, partially compensating the roll tilt of the body. The same holds for ocular counter roll not controlled in our experiments, which is usually estimated to be <10% in monkeys for the body tilt angles used (Cabungcal, Misslisch, Scherberger, Hepp, & Hess, 2001). As these counter movements would in any case reduce the efficient tilt, the true E-effect would be even larger than estimated based on the body tilt applied.

While our demonstration of a consistent E-effect in monkeys is in accordance with observations on humans, it is not fully compatible with the only previous attempt to measure tilt perception in monkeys, we are aware of. In a study by Lewis, Haburcakova, and Merfeld (2005) monkeys were statically roll tilted (up to 30°) and asked to align a light bar in the direction of the vector of gravity. While the monkeys seemed to show occasional tilt overestimation, the average performance was accurate, lacking a systematic difference between the actual and the perceived roll-tilt angle. The reasons for this discrepancy remain unclear. One speculative possibility is that the behavioral paradigm used actually prompted the monkeys to report their actual body tilt rather than the SVV, which—at least in humans—lacks the systematic distortions characterizing the former (Van Beuzekom & Van Gisbergen, 1999, 2000). A further discrepancy between the Lewis et al. study and ours seems to relate to the existence of adaptation of the SVV. In humans, the reports of the SVV do not depend on the time subjects have spent in a particular tilt position (Jaggi-Schwarz & Hess, 2003), at least for periods of up to 90 s. On the other hand,

Lewis et al. (2005) observed in their study of monkeys adaptation of the SVV, in the sense that the SVV seemed to slowly move towards the body axis if an off-vertical position was maintained for around 40 s. Correspondingly, the monkeys occasionally displayed a bias in the opposite direction, an adaptation after effect, when the monkey was returned to the upright position. Although we did not compare different tilt durations in our study, our results seem to speak against significant adaptation and adaptation after effects in monkeys. The reason is that our estimates of the SVV were based on responses distributed over periods of 320 s in which monkeys stayed in a given off-vertical position. Nevertheless, the SVV measured corresponded—at least approximately—to those measured in humans for much shorter tilt durations.

As mentioned in the introduction, human subjects exhibit a second type of deviation of the SVV, the A-effect, typically observed for tilt angles exceeding 60° and maximal for angles of 130°. In contrast to the E-effect, it is characterized by an underestimation of the actual body tilt. In our experiments, we could occasionally observe an A-effect-like deviation if monkeys were tested at 90° roll tilts. This tendency towards an A-effect might have become clearer if we had been able to roll tilt our monkeys even further. However, unfortunately, as yet our attempts to reach larger tilt angles have failed as monkeys typically stop working at angles exceeding 90° body roll tilts.

Defining the orientation of the subjective vertical in the absence of visual landmarks requires information on the orientation of the vector of gravity provided by the vestibular system and probably supplementary gravitation-dependent somatosensory signals (Mittelstaedt, 1995). Surprisingly, these gravity-related signals indispensable for the reconstruction of the subjective vertical in *test trials* seemed to influence the monkeys' choices even in the presence of suitable visual reference lines, in which the monkeys could have chosen the orientation of the arrow exclusively with respect to the visual reference. That the monkey did not resort to a purely visual strategy is indicated by the emergence of weak E-effect like deviations for low contrast *test trials* and by the linear increase of the variance of the monkey's perceptual choices with decreasing contrast of the visual reference line, including the 0% contrast *test trials*. This linear dependency suggests that the monkeys estimated their subjective vertical by combining the visual information provided by the reference line with vestibular information in a statistically optimal manner (Ernst & Banks, 2002), giving progressively less weight to the vestibular signal, when the visibility of the reference line increased.

In summary, we describe a behavioral procedure that allowed us to reliably measure the SVV in nonhuman primates and to establish that monkeys' SVV shares a key feature of the human SVV. In principle, the behavioral procedure we exploited may easily be extended to test other types of interactions between vision and graviception. Importantly, the ability to reliably measure perception

based on visuo-graviceptional interactions in monkeys will ultimately allow us to address the question of how graviceptional information is incorporated into neuronal representations allowing us to perceive a stable visual world.

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