Roll Tilt Psychophysics in Rhesus Monkeys
During Vestibular and Visual Stimulation

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Abstract

How does the brain calculate the spatial orientation of the head relative to gravity? Psychophysical measurements are critical to investigate this question, but such measurements have been limited to humans. In non-human primates, behavioral measures have focused on vestibular-mediated eye movements, which do not reflect percepts of head orientation. We have therefore developed a method to measure tilt perception in monkeys, derived from the subjective visual vertical (SVV) task. Two rhesus monkeys were trained to align a light bar parallel to gravity, and performed this task during roll tilts, centrifugation, and roll optokinetic stimulation. The monkeys accurately aligned the light bar with gravity during static roll tilts, but also demonstrated small orientation-dependent misperceptions of the tilt angle analogous to those measured in humans. When the gravito-inertial force (GIF) rotated dynamically in the roll plane, SVV responses remained closely aligned with the GIF during roll tilt of the head (coplanar canal rotational cues present), lagged slightly behind the GIF during variable-radius centrifugation (no canal cues present), and shifted gradually during fixed-radius centrifugation (orthogonal yaw canal cues present). SVV responses also deviated away from the earth-vertical during roll optokinetic stimulation. These results demonstrate that rotational cues derived from the semicircular canals and visual system have prominent effects on psychophysical measurements of roll tilt in rhesus monkeys, and therefore suggest that a central synthesis of graviceptive and rotational cues contributes to percepts of head orientation relative to gravity in non-human primates.
Introduction

When subjects move in a gravitational environment, the semicircular canals in the vestibular labyrinth sense angular head velocity and the otolith organs sense the vector sum of gravity and the inertial force produced by linear acceleration (gravito-inertial force, GIF). There is extensive evidence that the brain is able to use vestibular and other sensory cues to generate relatively accurate percepts of head orientation and motion (Merfeld and Zupan 2003), as well as appropriate oculomotor reflexes (Green and Angelaki 2003; Green and Angelaki 2004). To investigate the mechanisms used by the brain to accomplish these tasks, numerous studies have characterized vestibular-mediated eye movements in both human and non-human primates and tilt psychophysics in human subjects (see Guedry 1974 for a review). No psychophysical measurements of head tilt have been made in monkeys, although such studies could potentially utilize both standard motion protocols (e.g. tilt, translation, and centrifugation) and more invasive techniques (e.g. neural stimulation, ablation, and recording) that are not feasible in humans.

Psychophysical measurements are necessary to study the neural mechanisms used by non-human primates to estimate head orientation for several reasons: 1) Percepts of head tilt cannot be deduced from eye movement responses (Zupan and Merfeld 2005). Torsional eye movements, for example, include an angular VOR component that is independent of gravity as well as utricular contributions that do not reflect roll tilt of the GIF (Angelaki 1998; Paige and Tomko 1991; Merfeld et al 1996); 2) Recent work in human subjects suggests that qualitatively different neural mechanisms may be used by the brain to generate vestibular-mediated psychophysical (e.g. perceived tilt) and motor (e.g. eye movement) responses (Merfeld et al 2005a,b). This divergence between perception and action has been observed in other sensory systems (e.g. vision, Goodale and Westwood 2004), and implies that direct psychophysical measures are required to study the neural substrates underlying perceptual processes;
and 3) Substantial differences in vestibular-mediated eye movements have been described in monkeys (Angelaki and Hess 1994; Wearne et al 1999) and humans (Fetter et al 1992; Landsberg et al 1965; Merfeld et al 2001), such as the more pronounced alignment of vestibular and optokinetic eye movements with the GIF in monkeys. These well-documented differences in oculomotor responses suggest that psychophysical responses in human and non-human primates may also differ substantially.

Two principal hypotheses have been proposed to explain how the brain estimates the gravitational (tilt) and inertial (translation) components of the ambiguous GIF transduced by the otolith organs. It has been suggested that the GIF is disambiguated based on its frequency content (Paige and Tomko 1991; Telford et al 1997), with low-frequency shifts in the GIF interpreted as tilt and higher frequencies shifts interpreted as translation. Conversely, since head movements typically activate the canals and alter visual orientation cues, a second hypothesis is that the brain’s estimates of head orientation and motion are based on a central synthesis of gravito-inertial and non-otolithic afferent signals (Young 1984; Merfeld and Zupan 2003). In rhesus monkeys, numerous eye movement studies are consistent with the sensory synthesis hypothesis, as vestibular-mediated eye movements appear to result from an interaction between the rotational cues derived from the canals and the GIF information transduced by the otoliths (e.g. Angelaki et al 1999). While similar mechanisms appear to contribute to percepts of head tilt in humans (Merfeld et al 2001; Merfeld et al 2005 a,b), the neural processes that underlie tilt perception in monkeys remain unknown.

To investigate this problem, we have developed a method to measure tilt psychophysics in rhesus monkeys in the roll plane, based on the subjective visual vertical (SVV) task widely used in human studies (Bohmer and Rickenmann 1995; Strupp et al 2003; reviewed in Howard and Templeton 1966). Rhesus monkeys were trained to align a light bar parallel to the direction of gravity, and were tested with this task during a variety of motion paradigms. We hypothesized that in rhesus monkeys,
perception of head orientation in the roll plane depends at least in part on a synthesis of the GIF cues transduced by the otolith organs and rotational cues derived from semicircular canals and the visual system. We explicitly addressed this hypothesis by comparing SVV responses during three motion paradigms that shifted the GIF in the roll plane in a similar manner but provided substantially different canal rotational cues. Specifically, we compared SVV responses during roll tilt of the head (congruent roll canal cues), variable-radius centrifugation (no canal cues), and fixed-radius centrifugation (yaw canal cues orthogonal to the roll shift in GIF). We found that the rotational information provided by the canals had substantial effects on the SVV responses produced by roll tilt of the GIF. Furthermore, roll optokinetic stimulation also had a pronounced effect on SVV responses. Taken together, these results strongly suggest that a central synthesis of graviceptive and rotational sensory information contributes to neural estimates of head orientation with respect to gravity in rhesus monkeys. A preliminary description of a subset of these experiments has previously been published (Lewis et al 2005).

**Materials and Methods**

Experiments were performed in two 3.5 year-old juvenile rhesus monkeys (weights 3.6 and 3.9 kg) who had not participated in any prior experiments. All experimental methods were approved by the institutional animal care and use committee and were in accordance with USDA guidelines.

1) **General Methods:**

A head bolt was implanted in each monkey’s skull under general (pentobarbital) anesthesia using aseptic techniques in the hospital’s animal operating room. This appliance was necessary to immobilize the head during training and experiments. The head was held in a stereotactic frame, a triangular region of the scalp was removed, and the skull surface was cleaned carefully. 6-8 sterile, titanium screws were then placed in the skull in an inverted orientation (head of screw beneath the skull), and the skull surface was covered with dental acrylic. A fiberglass head bolt was then laid into the acrylic, oriented such that
the head was pitched forward approximately 18 deg with respect to the stereotactic zero when the head was immobilized in the monkey chair. This head orientation placed the lateral canals close to alignment with the earth-horizontal plane and the vertical canals close to the earth-vertical plane (Blanks et al 1985).

2) Subjective visual vertical training and testing:

The animals sat in the primate chair and grasped a small steering wheel attached to the front of the chair. The wheel provided no orientation information and was connected to a potentiometer that measured the amplitude of the wheel rotation. This signal was used to rotate in roll the orientation of a light bar presented on a LCD panel located 50 cm in front of the animal. To minimize visual orientation cues, the LCD panel and the entire visual surround were masked with black fabric, except for a circular aperture (27 cm in diameter) centered between the animal’s eyes, which contained the relevant visual display. This display was black except for the light bar and a visual reference bar that was used in the early stages of training. The visual displays were presented, and the animal’s behavioral responses recorded, with programs using the Virtual Reality Utilities (VRUT) software package. During all SVV training and testing, the monkey’s head was immobilized with the head bolt, but the rest of the body could move within the primate chair.

The monkeys were initially trained 4 days/week for approximately 6 months to align the light bar parallel to the direction of gravity, using the training paradigm described below. Throughout the subsequent periods of testing, the need for accurate performance on the SVV task was frequently reinforced. Once testing began, one full session each week was spent on the training task, and on testing days, each experiment was preceded by 5 min of training.

SVV Training: During each training trial, the bar appeared at a random orientation, the animal rotated the wheel until the bar was approximately upright, and a water reward was given. The light bar was
then extinguished and reappeared at another random orientation for the next trial. An angular “window” about the true earth-vertical (which was not visible to the monkey) was used during training, and the animals received water only if they correctly rotated the line into the window and kept it there for 0.8 s. The size of the window was gradually reduced over time (to a minimum of +/-4 deg) to increase the accuracy with which the animals oriented the bar. Initially the monkeys were trained with a visual reference line that indicated the true earth-vertical, and once this task was mastered, they were trained to align the light bar parallel to the earth-vertical without visual cues by gradually dimming and eventually eliminating the reference line.

To ensure that they learned to align the bar with respect to the earth-vertical rather than a head or retinal reference, early in the course of training we introduced different static head orientations along the roll axis, including trials with the head upright (yaw axis aligned with gravity) and trials with the head tilted statically to the left or right. In all head positions, the animals were rewarded for rotating the light bar into the earth-vertical orientation. When this task was carried-out accurately, they were trained while they were dynamically rotated about the roll axis.

**SVV Testing:** While the training paradigm required that the animal rotate the light bar into an angular window centered about the true earth-vertical, all data were acquired with a *testing* paradigm which did not impose any constraints on the placement of the light bar. We found by observing the animals’ behavior during the task that they would rapidly rotate the light bar close to their desired orientation, make several quick corrections, and then pause. To capture this behavior accurately but not impose any constraints on the monkey’s responses during data acquisition, we used a small tolerance window to determine when the pause associated with the desired response occurred. If the light bar remained within a small (typically 3 deg) window for a short interval (0.3 to 0.8 s), we concluded that the monkey had reached its desired response, and the bar orientation was written to the data file and the water reward
was provided. If the monkey was actively rotating the light bar, conversely, the bar would exit the 3 deg window before the time criteria elapsed, the window would re-center about the bar at its new orientation, and this process would continue until the time criteria was met, signaling the end of the trial. The bar then disappeared and reappeared at a random orientation. The appropriate time criteria were determined empirically for each motion paradigm by observing the animals’ behavioral responses while performing the SVV task. Longer time windows (e.g. 0.8 s) were used when the GIF orientation was stationary (e.g. static head tilts), while shorter time windows (e.g. 0.3 s) were used when the orientation of the GIF was changing (e.g. during centrifugation). Using this approach, we found that essentially all trials would terminate shortly after the monkey placed the bar in the desired orientation. During all data acquisition, therefore, the animals were free to rotate the bar into any orientation and were not forced by the paradigm to respond in any preconceived fashion. Since there was no feedback regarding the accuracy of performance, the testing paradigm did not provide information that could shape or influence the animals’ response to the SVV task.

While the monkeys were rewarded during the testing protocol each time they paused, they could not distinguish testing trials (which did not require a specific response) from training trials (which required that they align the light bar near the earth-vertical). If they were well motivated, they would pause only after they had rotated the light bar to their desired orientation. If the animal was not performing well on a given day, evidenced by erratic placement of the light bar during testing, the experiment would be terminated for the day to ensure that the learned behavior was not degraded by rewarding them for random responses.

3) Motion devices and paradigms:
For all motion paradigms, the angular and linear positions of the monkey chair were recorded in Labview. Since the animal’s head was fixed with respect to the chair, these measurements reflect the position of the head in three-dimensional space.

**Roll tilts:** The monkeys were rotated about the nasal-occipital earth-horizontal axis centered between the eyes. These rotations were not computer controlled and were generated by a small 10 N-m DC motor which was controlled directly by a human operator. Rotational velocities were always within +/- 15% of the desired velocities indicated below for each tilt paradigm.

**Static roll tilts:** The animals were maintained in different stationary head orientations for 30 s, and were tilted slowly between head positions at a low (about 2 deg/s) angular velocity. The head was positioned in a random manner at thirteen orientations, ranging from right-ear-down (RED) 30 deg to left-ear-down (LED) 30 deg in 5 deg increments. Typically 10-12 discrete SVV responses were obtained at each of the static tilt positions during each session. Tilt angles larger than 30 deg were poorly tolerated by the monkeys and therefore were not used.

**Dynamic roll tilts:**

**Slow 30 deg tilts:** To approximate the shift in GIF orientation produced by the centrifugation paradigms (see below), roll tilts from upright to 30 deg LED and RED orientations were performed over a period of 10 s at an approximate rate of 3 deg/s. The tilted positions were maintained for 10 sec and then the animal was returned to upright over a 10 s period.

**Rapid roll tilts:** the monkeys were rapidly rotated (angular velocity of about 10 deg/s) from upright to 10, 20 and 30 deg LED and RED positions, held in each position for about 10 s, and then returned to upright.

**Roll optokinetic stimulation:** The animals viewed a clockwise (CW) or counterclockwise (CCW) roll optokinetic (OK) stimulus on the LCD panel, which also displayed the light bar for the SVV task. The
OK stimulus rotated at an angular velocity of 60 deg/s, spanned the central 30 deg of the visual field, and consisted of opaque circles (each spanning 1.8 deg) which were distributed randomly and filled 15% of the visual display. During OK stimulation, the monkeys were statically tilted in the roll plane from 20 deg LED to 20 deg RED in 10 deg increments. Data were acquired for intervals of 30 s while the head was statically tilted at each position.

**Centrifugation:** Centrifugation experiments were performed on a computer-controlled centrifuge, consisting of a linear track that rotated about the earth-vertical axis and a sled that translated along the track. In these experiments, the head was upright and oriented such that the centripetal acceleration aligned with the inter-aural (IA) axis. This system operated with the following specifications: 95 cm track length, 1.0 G maximum linear acceleration, and 360 deg/s maximum angular velocity.

**Sinusoidal variable-radius centrifugation:** To simulate the inter-aural acceleration produced by low-frequency sinusoidal IA translation, we employed the method of variable-radius centrifugation (Seidman et al 1998; Merfeld et al 2001). Specifically, the monkeys were slowly accelerated to an angular velocity of 230 deg/s about the earth-vertical axis, either CW or CCW when viewed from above. They were maintained at this constant velocity for five minutes with the chair centered at the rotational axis, allowing the yaw rotation cues derived from the semicircular canals to dissipate. Then the chair was translated *sinusoidally* at low frequencies (0.01 – 0.1 Hz) while the track continued to rotate. The amplitudes of translation (0.35 m for 0.01 Hz, 0.348 m for 0.05 Hz, and 0.342 m for 0.1 Hz translations) were chosen so that the net IA acceleration (centrifugal plus radial) modulated between right and left 0.58 g, with the centrifugal acceleration (\(r\omega^2\), where \(r\) is the displacement from the center of rotation and \(\omega\) is the angular velocity) providing the majority of the IA acceleration. This sinusoidal variable-radius centrifugation paradigm tilted the GIF in the roll plane over a range of right/left 30 deg, and mimicked the changes in inertial force that would be achieved with low frequency, large amplitude chair
translation. To avoid abrupt linear accelerations, the translational motion for the two higher frequencies included a ramp-up period (one-half cycle for 0.05 Hz, one cycle for 0.1 Hz).

The Coriolis accelerations \(2\omega \times v\), where \(\omega\) is the angular velocity and \(v\) the radial velocity) produced by these motion patterns (peak values: 0.02g [0.01 Hz], 0.09g [0.05 Hz], 0.17 g [0.1 Hz]) were always substantially smaller than the IA acceleration, and were below the human perceptual threshold (0.03g) for the lowest frequency (Melvill Jones and Young 1978; Travis and Dodge 1928). The Coriolis acceleration was also orthogonal to the IA acceleration that shifted the GIF in the roll plane, both spatially (as it was aligned with the naso-occipital axis) and temporally (as it was 90 deg out of phase with the IA acceleration). Furthermore, data were obtained with both CW and CCW angular velocities, which reversed the orientation of the Coriolis acceleration, but this did not influence the SVV responses. For these reasons, the Coriolis acceleration appeared to have a negligible influence on SVV responses in the roll plane during sinusoidal variable-radius centrifugation.

**Parabolic variable-radius and fixed-radius centrifugation:** These two centrifugation paradigms (Merfeld et al 2001), in association with the roll tilt experiments, allowed us to evaluate the effects of canal rotational cues on perceived tilt when the GIF rotates in the roll plane. Specifically, canal cues were coplanar with the roll shift in GIF orientation during roll tilt, were absent during parabolic variable-radius centrifugation, and were orthogonal (yaw axis) to the roll GIF shift during fixed-radius centrifugation. In both of these centrifugation paradigms, trials were obtained with the chair rotating CW or CCW (viewed from above), with the monkey seated so that its face or back was oriented towards the direction of motion.

**Parabolic variable-radius centrifugation:** The animals were centered over the rotational axis and the chair was accelerated to an angular velocity of 230 deg/s over a period of 60 s. After 5 min of rotation at a constant velocity (which allowed the yaw rotational cue sensed by the lateral canals to dissipate), the
chair was translated along the IA axis from the center to an eccentricity of 0.35 m over a period of 10 s. The eccentric position (r) changed parabolically during the translation, introducing an IA centrifugal force (\( r^2 \)) that increased parabolically from 0 g to 0.58 g over 10 s (matching the IA force produced during fixed-radius centrifugation). The IA force shifted the orientation of the GIF in the roll plane from upright to 30 deg tilt towards the animal’s right or left ear, with the GIF tilt angle (equal to \( \tan^{-1}[r^2/g] \)) also shifting in an approximately parabolic manner. The chair remained at the eccentric position for 120 s and then returned to center over 10 s, removing the centrifugal force and returning the orientation of the GIF to upright. Recording of SVV responses began 15 s before the chair began to translate eccentrically and stopped 60 s after it returned to its centered position.

**Fixed-radius centrifugation:** The monkeys were first translated 0.35 m to the right or left of the rotational axis and were then rotated in yaw about an earth-vertical axis at an acceleration of 23 deg/s/s for 10 s to a constant velocity of 230 deg/s while their eccentric position remained constant. Like the parabolic variable-radius paradigm, this motion protocol provided a parabolic increase in IA centrifugal force which increased from 0 g to 0.58 g over 10 s, shifting the orientation of the GIF in the roll plane from upright to 30 deg tilted towards the right or left ear. After 120 s of constant-velocity rotation, the animals were decelerated in a symmetric manner to an angular velocity of zero. Recording of SVV responses began 15 s before the chair began to rotate and stopped 60 s after its angular velocity returned to zero.

**4) Data analysis:**

**Sign convention** (Fig. 1): Head tilts in the roll plane were defined as positive when the top of the head rotated towards the right and negative when it rotated towards the left. GIF tilts in the roll plane were defined as positive when the GIF rotated towards the right ear (e.g. consistent with a rightward head tilt) and negative when it rotated towards the left ear (consistent with a leftward head tilt). The SVV error
was defined as the angle between the light bar and the true earth-vertical, and was defined as positive when the top of the bar deviated to the left of the earth-vertical and negative when it deviated to the right. Similar to prior studies (e.g. Bortolami et al 2006), we refer to the sum of the head tilt (HT) angle and the SVV error as the *perceived head tilt (PT)*, although the exact relationship between the PT and the monkeys’ perception of head tilt is complex and considered extensively in the Discussion.

For roll head tilts, for example, if a 20 deg rightward (positive) head tilt resulted in a 3 deg leftward (positive) deviation of the SVV response, the PT was overestimated (20 + 3 = 23 deg). For the centrifugation paradigms, where the head remained upright (e.g. HT was zero), the PT was equivalent to the SVV error. For example, during centrifugation trials that rotated the GIF towards the right ear (positive deviation) the monkey would be predicted to rotate the light bar towards the left (positive SVV error), aligning it approximately parallel to the GIF.

**Roll tilts**: Since these motions were not computer-controlled, each rotation had slightly different dynamic characteristics. We therefore could not superimpose the PT responses as a function of time for multiple trials, and hence could only evaluate the dynamic characteristics of the PT responses in a qualitative manner. The quantitative analysis for the roll tilt experiments focused on the relationship between the actual and perceived head tilt while the head was stationary and in motion.

**Sinusoidal variable-radius centrifugation**: Each trial consisted of multiple sinusoidal translations (3 cycles for 0.01 Hz, 10 cycles for 0.05 Hz, and 20 cycles for 0.1 Hz). For each trial, the cycles were superimposed and a sine wave was fit to both the motion stimuli (GIF tilt) and the PT responses, using a least-mean-square linear regression to the equation $x(t) = B + A_c \cos(\omega t) + A_s \sin(\omega t)$, where $B$ is the DC bias, $A_c$ is the amplitude of the cosine component, and $A_s$ is the amplitude of the sine component. $B$, $A_c$, and $A_s$ all have units of degrees. The values for these parameters were determined for each trial and then were averaged across multiple trials for each animal and specific motion parameters (frequency of
translation, direction of angular rotation). The gain and phase of the response was calculated from the averaged values, with the gain defined as \((1/30)(A_s^2 + A_c^2)^{1/2}\) and the phase defined as \(\tan^{-1}(A_s/A_c)\). The covariance matrix \(\begin{bmatrix} \sigma_s^2 & \sigma_{sc}^2 \\ \sigma_{sc}^2 & \sigma_c^2 \end{bmatrix}\) was calculated using standard methods that yield the variance of the sine \((\sigma_s^2)\) and cosine \((\sigma_c^2)\) component as the diagonal elements and the covariance \((\sigma_{sc}^2)\) of the sine and cosine components on the off-diagonal elements. The covariance ellipse, which is the two-dimensional extension of the one-dimensional confidence interval, was constructed using multivariate methods detailed elsewhere (e.g. Johnson and Wichern 1982). The standard deviation of the amplitude is the width of the ellipse in the radial direction and the standard deviation of the phase is the ellipse width in the perpendicular direction.

Parabolic variable-radius and fixed-radius centrifugation: For each trial, the tilt gain was defined as the peak perceived tilt (PT) while the IA force was present, normalized by dividing by the amplitude of the GIF tilt (30 deg); PT decay was the magnitude of the decline in PT while the IA force was maintained, expressed as a percentage of the peak PT; and the after-effect was the magnitude of the reversal in PT that occurred after the IA force was removed, expressed as a percentage of the peak PT. To characterize the temporal nature of the shift in PT during the trial, we determined the time required for the PT to shift to 0.63 of its maximal deviation. We chose this time to define the dynamics of the PT shift because there was considerable variability in the period needed for the PT shift to maximize; less variability was evident if we examined a point while the PT was changing fairly rapidly rather than the time required for the response to plateau. While the PT shifts were not consistently exponential and hence were not fit by a specific function, the time to 0.63 of peak corresponds to the time constant of an exponential function. To combine multiple centrifugation trials graphically, a linear interpolation was made between consecutive PT responses during each trial, allowing us to generate a continuous response variable, from which the mean and standard error of the PT over time could be calculated and plotted.
Results

Roll tilts:

Static roll tilts: When the monkeys were statically tilted in roll, their SVV responses aligned closely with the earth-vertical, yielding PT responses that closely approximated the actual HT as shown in the upper panels of Fig. 1 for a single test session. When the results of the eight static tilt sessions were combined for each monkey (Fig. 1, lower panels), it is evident that the SVV errors were quite small over the +/- 30 deg tilt range we tested. Both monkeys, however, overestimated the head tilt angle when the head was tilted 20 deg or less, and tended to slightly underestimate the head tilt angle for larger tilts, consistent with the Aubert and Muller effects observed in humans (Guedry 1974). While this position-dependent modulation of the SVV error was subtle, it was significant for each animal (monkey H: one-way ANOVA, p < 0.001, F=6.2, DOF = 12; monkey A: one-way ANOVA on ranks, p<0.001, H = 54.4, DOF = 12 ).

Slow tilts: When the monkeys were tilted 30 deg over a period of 10 s (average velocity of 3 deg/s), the PT responses closely aligned with the actual HT angle (Fig. 2). The monkeys’ responses were highly accurate while the HT angle was stationary at the upright or left/right 30 deg down positions, and were also accurate while the head was in motion between these static orientations. When all 15 slow tilt cycles were combined for each monkey (Fig. 3), the SVV errors while the head was head stationary at the three static positions were essentially indistinguishable from the SVV errors measured while the head was slowly tilting. For monkey H, linear regression of the static and dynamic SVV errors as a function of head position showed nearly identical offsets and slopes (static offset = -0.08, dynamic offset = 0.08; static slope = -0.01, dynamic slope = -0.002), and the static and dynamic responses were statistically indistinguishable (t-test on the means, p = 0.34; F-test on the variances p > 0.5). Similarly, for monkey A, linear regression yielded static and dynamic slopes that were nearly identical (static slope
= 0.02, dynamic slope = -0.03) and offsets that were similar (static = -0.07, dynamic = -0.28). Again, the static and dynamic SVV errors did not differ statistically (Mann-Whitney test on means, p = 0.38; F-test on variances, p > 0.1). These results demonstrate that during roll tilts with an angular head velocity of about 3 deg/s, the monkeys were able to accurately estimate the tilt angle while in motion, with no measurable lag between changes in head orientation and perceived head tilt.

**Rapid roll tilts:** Even during relatively fast roll tilts the PT tilt responses closely aligned with the actual HT (Fig. 4). For monkey H, eight full trials were analyzed (each consisting of tilts from upright to right or left 10, 20, and 30 deg and back to upright), resulting in 281 SVV error measurements with a root mean squared (RMS) value of 1.96 deg. Seven trials were analyzed for monkey A, yielding 304 SVV error measurements with a RMS value of 1.86 deg.

**Roll optokinetic stimulation:** When the monkeys viewed a roll OK stimulus in the absence of visual orientation cues, their SVV errors deviated in the direction of the OK motion. Monkey H viewed a CCW stimulus and the SVV errors deviated to the left, consistent with an illusion of roll tilt to the right. Monkey A viewed a CW stimulus and the SVV errors deviated to the right, consistent with an illusion of roll tilt to the left (Fig. 5: diamonds = OK stimulus present, squares = OK stimulus absent). The influence of the OK stimulus on the SVV error was significant for each monkey (p < 0.001 [Mann-Whitney rank sum test]) when pooled data with and without OK stimulation for each animal were compared. For both monkeys, the magnitude of the illusionary tilt produced by the OK stimulus was larger when the head was statically tilted in the direction opposite the illusionary tilt, and was smaller when the head was tilted in the same direction as the illusionary tilt (Fig. 5). For monkey H, the illusionary tilt towards the right was largest with the head tilted leftward. While a linear regression of the SVV error without OK stimulation in this monkey had a small rightward bias (1.4 deg) and a slope close to zero (0.02), a regression of the
responses with the OK stimulation present yielded a much larger rightward bias (12.4 deg) but also a non-zero negative slope (-0.11). Similarly, for monkey A, the illusionary tilt was towards the left and was largest in magnitude with the head tilted rightward. For this monkey, linear regression of the SVV errors without OK stimulation yielded no bias (0 deg) and small positive slope (0.04) while regression of responses during OK stimulation showed a large leftward bias (-4.5 deg) and a substantial negative slope (-0.2) (Fig. 5). 2-way ANOVA confirmed that the effect of the OK stimulus on the SVV errors was dependent on head orientation (p <0.001 for the interaction between OK state and head tilt angle for each monkey).

**Centrifugation:**

**Sinusoidal variable-radius centrifugation:** Perceived tilt aligned relatively closely with the GIF tilt for 0.01 Hz translations (gains near 0.8, phase shifts close to zero (Fig. 6, Table 1). As the frequency of the sinusoidal translations increased, the amplitude of the PT declined somewhat (gains near 0.7 for 0.05 Hz, 0.6 for 0.1 Hz) (Table 1). Since the timing criteria used for SVV data acquisition (see Methods) introduced a delay of 0.3 s for each SVV response, an obligate phase lag (1.1 deg [0.01 Hz], 5.4 deg [0.05 Hz], and 10.8 deg [0.1 Hz]) was introduced. Correcting for the phase lag associated with the SVV task (Table 1) yields fairly small phase shifts for the three translational frequencies we tested (0 to 5.0 deg for 0.01 Hz, -13.0 to -3.7 for 0.05 Hz, and -9.1 to 1.8 deg for 0.1 Hz, with negative values indicating a lag). The bias for all trials was positive (towards the left), consistent with a small misperception of roll tilt towards the right for both animals during all stimulus conditions.

**Parabolic variable-radius centrifugation:** When IA force was added during parabolic variable-radius centrifugation, perceived head tilt shifted rapidly towards alignment with the GIF but clearly lagged behind the change in GIF orientation (Fig. 7). While the GIF tilt reached 63% of its maximum after 6.3 s, PT did not reach 63% of its peak shift until 9-15 s (Table 2). PT approached but did not reach the 30
deg tilt of the GIF for any direction of rotation (CW or CCW) or head orientation (facing motion, back-to-motion). The tilt gains (peak PT/30 deg) ranged from 0.90 to 0.94 when the PT was towards the right-ear-down orientation (positive values) and were somewhat smaller (range 0.65 to 0.74) when the PT was towards the left-ear-down orientation (negative values) (Fig. 7, Table 2).

The PT decayed substantially during sustained tilt of the GIF (Fig. 7). The amount of PT decay ranged from 35% to 68% of the peak PT (Table 2). A substantial reversal in the PT (after-effect) occurred when the IA force was removed (Fig. 7), ranging from 23% to 55% of the peak PT (Table 2).

**Fixed-radius centrifugation:** Unlike the parabolic variable-radius protocol, when IA force was added during fixed-radius centrifugation, PT shifted very slowly, lagging well behind the shift in GIF orientation (Fig. 8). PT did not reach 63% of its peak value until 33-46 s (Table 2), substantially longer than the time-frame associated with parabolic variable-radius centrifugation (9-15 s). The PT had similar gains in the fixed and parabolic variable-radius protocols (Table 2), although less difference was evident between positive (right-ear down) and negative (left-ear-down) directions of illusionary tilt in the fixed-radius paradigm (Fig. 8, Table 2). Finally, no meaningful decay or reversal of the PT occurred with the fixed-radius paradigm.

**Discussion**

We have developed and implemented a method to measure percepts of head tilt in rhesus monkeys using a task derived from the subjective visual vertical, and have measured SVV responses during a number of motion paradigms that rotated the head or the GIF in the roll plane. As discussed in detail below, our principal finding is that psychophysical measurements of roll tilt in rhesus monkeys, like humans, appear to depend on a central interaction between the gravito-inertial cues sensed by the otolith organs and the rotational cues sensed by the canals and the visual system. We will first discuss a
number of issues that relate to the psychophysical task we employed in the monkeys, and then will discuss the significance of our results.

1) Measuring tilt psychophysics with the subjective visual vertical: A principal tenent of this study is that the placement of the light bar during the SVV task provided an indication of the monkey’s perceived head orientation in the roll plane. A number of issues must be considered regarding this contention, including factors that are specific to the training and testing methods we employed in non-human primates, and factors that pertain to the subjective visual vertical test more generally.

a) SVV task in monkeys: When the SVV is used to test human subjects, they are instructed to align the light bar so that they perceive it to be parallel to the earth-vertical. The principal constraint with non-human primates is that we cannot provide similar verbal instructions and hence must rely on a training paradigm to teach them how to perform the SVV task. Since we cannot know the monkeys’ actual perception of the earth-vertical, we utilized a training paradigm that rewarded the monkeys when they aligned the light bar close to the true earth-vertical during static and dynamic roll tilts of the head. It is quite clear that the monkeys were trained to orient the light bar with respect to the earth-vertical rather than some other reference frame. While their SVV responses closely approximated the true earth-vertical with the head upright or tilted in roll (Fig. 1), other potential reference frames, such as the longitudinal axis of the body or the retinal vertical (Suzuki et al 1997) rotated away from the earth-vertical during roll tilts.

A discrepancy existed between the training task (e.g. rotate the light bar parallel to gravity) and the desired task (e.g. rotate the light bar parallel to the perceived direction of gravity), and this may have affected our results. The training approach made the implicit assumption that during roll tilts the perceived earth-vertical was relatively close to the true earth-vertical. Two observations support this contention: 1) since human subjects orient the light bar close to the earth-vertical when they are tilted in
roll over the relatively small range we employed in our study (+/- 30 deg), we hypothesized that monkeys would also have a close correspondence between the perceived and actual direction of gravity during roll tilts; and 2) during training the gravitational vector appeared to be a stable, reproducible reference for the monkeys, and there was never evidence that they were learning to suppress or overcome any bias that would reflect a significant disparity between the perceived and actual earth-vertical.

These observations suggest a relatively close correspondence between the perceived and actual direction of gravity during roll tilts of the head but they do not indicate that these two orientations are identical. For example, during the testing paradigm (which placed no constraints on the animals’ responses), the monkeys showed small orientation-dependent misperceptions of the earth-vertical during roll tilt (see Fig. 1). It is possible that these errors may have been larger in the naïve monkeys and were reduced by training. Although the monkeys’ placement of the light bar during the SVV task appears to be similar but not identical to their perception of the earth-vertical, we can still draw meaningful conclusions because we were able to compare responses on multiple testing paradigms. Several of the paradigms, for example, varied canal rotational cues while maintaining similar gravito-inertial cues. Direct comparison of the SVV responses during these paradigms allows us to examine the dependence of tilt percepts on the interaction between canal and otolith inputs, even if the monkeys’ SVV responses do not correspond exactly with their perceived earth-vertical.

The monkeys were trained during roll tilts (where the orientation of the GIF is always aligned with the earth-vertical), but we postulated that during testing they would align the light bar close to their perceived direction of gravity even when it was dissociated from the earth-vertical (12 o’clock position) by inertial cues. Our results demonstrate clearly that when the head remained upright and the GIF
rotated in the roll plane, SVV responses shifted towards alignment with the GIF, away from the earth-vertical orientation (Figs. 6-8).

In summary, the monkeys were trained to align the light bar parallel to the earth-vertical, the training rule most likely introduced some (presumably small) discrepancies between the SVV responses and the perceived earth-vertical, and the animals were able to generalize the training rule to align the light bar close to the perceived direction of gravity even when it tilted away from the earth-vertical orientation. Our results, which are discussed in detail below, demonstrate a large number of features that have been described previously in human subjects. The large number of similarities observed between species would be highly improbable if the monkeys’ SVV responses did not capture percepts of head orientation that are reasonable close to those obtained in human subjects who are given explicit verbal directions to align a light bar with the perceived vertical.

b) SVV as a measure of perceived head orientation: It is evident from human studies that different psychophysical tests such as the SVV, subjective postural vertical, and somatosensory bar, result in different estimates of roll tilt in normal subjects and patients with vestibular disorders (Wade and Curthoys 1997; Mast 2000; Merfeld et al 2001; Jarchow and Mast 1999). We employed the SVV task because it was the method that could be taught most readily to rhesus monkeys and because the preponderance of the human tilt psychophysical literature utilizes this approach. While SVV responses in humans (and presumably monkeys) diverge from the true earth-vertical for large head tilts, these perceptual errors are relatively small for the limited range of tilt angles we employed (Van Beuzekom and Van Gisbergen 2000).

The possible effect of torsional eye position on the perceived spatial orientation of a visual line remains uncertain (reviewed in Mast 2000). While most studies indicate that ocular torsion only minimally influences SVV measurements (see for example Haustein and Mittelstaedt 1990, Haustein
1992), there is evidence that the SVV could be offset by a magnitude close the amount of torsion (Wade and Curthoys 1997). We cannot directly address this possibility in our study, as we did not measure torsional eye position or make other psychophysical measures that were independent of vision. Given the small amplitude of ocular counter-rolling produced by roll tilt, IA translation, and centrifugation (Angelaki 1998; Wearne et al 1999; Suzuki et al 1997), however, it is unlikely that the SVV responses we recorded in rhesus monkeys were substantially altered by the influence of ocular torsion.

2) **SVV responses during static tilt of the head or the GIF:**

   a) **Roll tilt of the head:** When the head was statically tilted in the roll plane, the monkeys aligned the light-bar close to the earth-vertical (Fig. 1, top panel), indicating a nearly veridical perception of the head tilt angle. Small orientation-dependent inaccuracies were observed in both animals (Fig. 1, bottom panel), however, with a slight overestimation of smaller tilt angles (20 deg or less) and possibly an underestimation of larger angles. These findings are qualitatively similar to the orientation-dependence of SVV responses described in humans (A and E effects, Guedry 1974, Van Beuzekom and Van Gisbergen 2000). The relatively small perceptual errors observed in the two monkeys may relate to their extensive training, as they were taught to rotate the light bar within +/- 4 deg of the true earth-vertical.

   b) **Roll tilt of the GIF:** Sustained 30 deg tilts of the GIF during parabolic variable-radius and fixed-radius centrifugation resulted in a shift in PT towards alignment with the GIF, but the perceived tilt indicated by the SVV responses systematically underestimated the extent of GIF tilt (by an average of 21%, Figs. 7,8). In contrast, the PT responses during static 30 deg roll tilts of the head were larger, underestimating the head tilt angle by only 3.5% on average (Fig. 1). The reasons for this discrepancy are uncertain. The centrifugation paradigms were associated with either a yaw rotational cue that gradually decayed (fixed-radius) or an absence of canal rotational cues (variable-radius). It is possible that the presence of orthogonal canal cues or the absence of coplanar cues affected the maximum PT that
developed during the 120 s of GIF tilt, but this seems unlikely since the effect of the canal cues would presumably dissipate during the sustained period of centrifugation. Similarly, the small difference in the magnitude of the GIF during roll tilt (1 g) and centrifugation (1.16 g) appears unlikely to influence the perceived tilt in a significant manner. It is possible that residual visual information may have contributed to the differences in PT observed in the tilt and centrifugation paradigms. While we attempted to minimize visual orientation cues (see Methods), a small amount of light was produced by the LCD panel that displayed the SVV light bar. Since the visual display and surrounding draping remained upright during all experiments, any residual visual information indicating the direction of gravity could have reduced the amplitude of the SVV shift away from the earth-vertical during centrifugation. Other non-vestibular, non-visual sensory cues, such as tactile information from the chair, could also have affected the monkeys’ responses during centrifugation.

Both animals showed a substantial decay in PT (mean 48%) during the sustained GIF tilt produced by parabolic variable-radius centrifugation, followed by reversal in PT (mean 39%) when the centrifugal force was removed. Qualitatively similar observations have been made in human subjects tested with variable-radius protocols (Seidman et al 1998). While the decline in PT could reflect habituation or adaptation, the reversal (after-effect) indicates that a central or peripheral adaptive process must have contributed to the response decay observed during centrifugation.

3) SVV responses during dynamic tilt of the head or the GIF:

a) Evidence for canal-otolith interactions: The canal-otolith interaction model of GIF resolution (Merfeld and Zupan 2003; Merfeld et al 1993) proposes that a central synthesis of canal and otolith cues contributes to the brain’s estimate of head orientation. This model predicts, therefore, that percepts of head orientation should be affected by changes in canal-mediated rotational cues when gravito-inertial cues remain invariant. To investigate this hypothesis, we utilized three motion paradigms that shifted
the GIF in the roll plane in a similar manner but provided different canal cues. Specifically, the slow roll tilt paradigm rotated the GIF by 30 deg over 10 s at a constant velocity and was associated with coplanar roll canal cues; the parabolic variable-radius and fixed-radius centrifugation paradigms rotated the GIF by 30 deg over 10 s in an approximately parabolic manner with either no canal cues (variable-radius) or with orthogonal yaw canal cues (fixed-radius).

Similar to prior reports in human subjects (Merfeld et al 2001; Stockwell and Guedry 1970; Seidman et al 1998), we found that the canal cues had a substantial effect on the dynamics of tilt perception. During roll tilt, the SVV responses aligned with gravity without any appreciable delay, and the accuracy of the PT was the same if the head was moving or stationary. The congruent canal and otolith information during roll tilt appeared to facilitate the central processing that allowed the brain to rapidly and accurately estimate the underlying motion pattern (Stockwell and Guedry 1970). In contrast, parabolic variable-radius centrifugation shifted PT responses towards alignment with the GIF more slowly, and it therefore appears that the absence of a congruent canal cue slowed the neural processing that identified the motion pattern as a roll tilt of the head. Finally, fixed-radius centrifugation shifted SVV responses towards the GIF most slowly, and it is likely that the large orthogonal yaw rotational cue inhibited the development of the roll tilt percept, possibly because a sensory conflict developed when the GIF was tilted in the presence of a yaw rotational cue while the head was upright (Graybiel and Brown 1951; Merfeld et al 2001). Taken together, these results provide convincing evidence that a central interaction between canal and otolith cues (Curthoys 1996) contributes to neural estimates of head orientation in rhesus monkeys.

b) Evidence for frequency-segregation: While these results are consistent with predictions made by the canal-otolith interaction model of GIF resolution (e.g. Merfeld and Zupan 2002; Merfeld et al 1993), they do not exclude contributions from the frequency-segregation model, which proposes that lower
frequency shifts in GIF orientation are interpreted by the brain as gravitational in origin and higher
certainty, in particular, appear to support contributions from frequency-segregation. Similar
to prior reports in human subjects (Merfeld et al 2005; Glasauer 1995; Zupan and Merfeld 2005),
ilusions of roll tilt were greatest at the lowest frequency and became smaller as the frequency of
translation increased. While these findings suggest that high and low-pass filters may disambiguate the
shifts in GIF produced by head translation (Paige and Tomko 1991; Merfeld et al 2005), the frequency-
independence of the phase is not consistent with a simple filtering mechanism (Glausauer 1995).

4) SVV responses during roll optokinetic stimulation:

Although the optokinetic stimulus we used was relatively small, filling only the central 30 deg of the
visual field, both monkeys developed substantial shifts in SVV responses when exposed to the OK
stimulation (mean magnitude of the shift was 12.4 deg for monkey H and 4.5 deg for monkey A). While
we did not measure torsional eye position, prior studies have shown only small torsional deviations of
the eyes during roll optokinetic stimulation (Zupan and Merfeld 2003; Ibbotson et al 2005). Therefore it
is unlikely that the shift in SVV responses resulted solely from changes in torsional eye position.
Furthermore, prior work in human subjects has demonstrated that the SVV shifts produced by OK
stimulation are not a visual illusion, since subjective postural and visual vertical responses were affected
similarly (Dichgans et al 1972). Although we could not perform these postural controls in our animals,
it is highly likely that roll OK stimulation induced an illusion of roll tilt in the rhesus monkeys. The tilt
illusion was consistent with the OK cues produced during true roll tilt, with perceived head orientation
shifting towards the right during CCW OK stimulation and towards the left during CW stimulation.
Since an illusion of roll tilt was produced by visually-mediated rotational cues without shifts in GIF
orientation, percepts of head orientation in monkeys, like humans (Dichgans et al. 1972; Dichgans et al.
1974; Zupan and Merfeld 2003) appear to depend at least in part on a central fusion of (visual) rotational cues and the otolith cues that sense the GIF.

The size of the SVV deviation depended on an interaction between the OK stimulation and static head orientation, as the deviations were larger when the head was tilted in the direction of the optokinetic stimulation. For example, monkey A viewed a CW OK stimulus and the shift in SVV responses towards the right (negative in Fig. 5) was larger when the head was statically tilted towards the right. The basis of this interaction in rhesus monkeys, which is the reverse of that described in human subjects (Dichgans et al 1974), is uncertain. Since the ocular counter-rolling associated with static head tilt in the direction of the OK stimulation should shift the torsional position of the eyes in the opposite direction (Suzuki et al 1998), counter-rolling would be expected to reduce, not augment any component of the SVV shift that results from torsional deviation of the eyes. A more likely explanation for these results is that the roll OK stimulation rendered the monkey’s estimate of the earth-vertical less reliable and they responded by orientating the light bar closer to their own longitudinal axis.

5) Comparing psychophysical and oculomotor responses in monkeys: Vestibular-mediated perceptual and oculomotor responses appear to utilize qualitatively similar mechanisms in rhesus monkeys. Roll tilts, for example, produce veridical shifts in perceived tilt as well as eye movements that are compensatory for roll (torsion), without a significant horizontal (translational VOR) response (Angelaki et al 1999). Sinusoidal variable-radius centrifugation elicits percepts of roll tilt that decline as the frequency increases, similar to the frequency-dependence of the torsional eye movement response during IA translation (Telford et al 1997), and both tilt perception and torsional eye movements have compensatory phases during low frequency translations (Angelaki 1998). Finally, fixed-radius centrifugation produces a gradual shift in both PT and in the rotational axis of the eye (Wearne et al
1999). These results suggest that both the perceptual and oculomotor correlates of roll tilt in rhesus monkeys depend, at least in part, on a central synthesis of rotational and gravito-inertial cues.

6) Conclusions and future directions: Our results suggest that tilt psychophysics in rhesus monkeys and humans are qualitatively similar. In both species, the perception of roll tilt, measured with a subjective visual vertical task, appears to depend on a synthesis of the otolith cues that sense gravity and linear acceleration, and the canal and visual cues that sense head rotation. We cannot make quantitative comparisons between rhesus and human psychophysical results, however, given the small number of monkeys studied, the inherent variability in SVV responses, and the differences in the motion paradigms employed in various studies. Future experiments that include a larger number of monkeys and motion paradigms that are identical to those used with human subjects would facilitate direct quantitative comparisons between human and non-human primates. The psychophysical approach we have developed also allows the use invasive experimental techniques such as vestibular stimulation (Lewis et al 2006) and ablation (Lewis et al 2007), and neural recordings to facilitate the study of spatial orientation in non-human primates.
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Disclosures

None.
References


Glasauer S. Linear acceleration perception: frequency dependence of the hilltop


**Graybiel A and Brown R.** The delay in visual reorientation following exposure to a change in direction of resultant force on a human centrifuge. *J Gen Psychol* 45:143-150, 1951.


Figure legends:

**Fig 1:** SVV responses during static roll tilt for the two monkeys. Top panels: perceived tilt (PT) plotted against the actual head tilt (HT) for one experimental session, where $PT = HT + SVV$ error. Positive values indicate tilts towards the right-ear-down orientation. The lines represent perfectly veridical responses ($PT = HT$). Bottom panels: SVV error plotted against head tilt for all eight static roll tilt experimental sessions in each animal. The mean +/- one SEM are illustrated, and the bias for each animal (+0.73 deg for monkey H, +0.1 deg for monkey A) has been subtracted from the SVV error values. In these and subsequent plots of SVV error versus head tilt angle, positive SVV errors associated with positive (rightward) head tilts indicate overestimation of tilt angle, as do negative SVV errors associated with negative (leftward) head tilts. The insert shows the sign orientation for head tilt (HT), subjective visual vertical (SVV), and gravito-inertial force (GIF) orientation. Head tilts towards the right-ear-down orientation are positive, GIF shifts towards the right ear (as would occur with a rightward head tilt) are positive, and SVV deviations towards the left are positive.

**Fig 2:** Examples of SVV responses during slow roll tilts (30 deg over 10 sec) for each monkey. The top panels plot PT responses (squares) and HT angle (line) versus time, while the bottom panels plot PT responses versus HT angle. The PT closely approximated the HT angle, both while the head was stationary and moving. The lines in the bottom panels indicate perfectly veridical responses ($PT = HT$).

**Fig 3:** SVV error plotted against head tilt during the slow 30 deg roll tilts. Each plot shows the data obtained from fifteen tilt cycles. Large diamonds are the mean errors while head was statically positioned at right and left 30 deg and upright orientations +/- one SEM. Small circles are the individual responses while the head was in motion between these static positions. Linear regressions for the static (solid lines) and dynamic (dashed lines) responses are also illustrated.
**Fig 4:** Examples of SVV responses during rapid roll tilts between the upright position and left or right 10, 20, and 30 deg. The top panels plot PT and HT angle versus time, while the bottom panels plot PT versus HT (lines are PT = HT).

**Fig 5:** Mean SVV error (diamonds) +/- one SEM for all optokinetic trials (seven CCW trials for monkey H, six CW trials for monkey A) compared to the mean SVV error in the same head orientations without the optokinetic stimulus (squares). Linear regressions of the two data sets (OK present, OK absent) are also illustrated for each animal. For monkey H, the OK stimulus rotated counter-clockwise and induced an illusion of tilt towards the right (leftward = positive SVV errors); for monkey A, the OK stimulus rotated clockwise and induced a leftward illusion of tilt (rightward = negative SVV errors).

**Fig 6:** Example of SVV responses during sinusoidal variable-radius centrifugation for monkey A at 0.01 Hz, counter-clockwise chair rotation. In the left panel, the solid line shows the sinusoidal modulation in GIF angle and crosses show individual PT responses. The right panel shows the cycles in the trial superimposed, with the solid line representing the GIF angle and the dashed line showing a sinusoidal fit to the PT responses.

**Fig 7:** Averaged SVV responses during parabolic variable-radius centrifugation for clockwise chair rotations, facing and back-to-motion. Plotted are the mean PT (solid lines) +/- one SEM (shaded regions) for 4-8 combined centrifugation trials, and the GIF angle. Motion paradigms are illustrated by the inserts.

**Fig 8:** Averaged SVV responses during fixed-radius centrifugation for counter-clockwise chair rotations, facing and back-to-motion. Plotted are the mean PT +/- one SEM for 4-10 combined centrifugation trials, and the GIF angle. Motion paradigms are illustrated by the insert.
Fig. 1:

**Monkey H**

- Perceived tilt (deg)
  - Head tilt (deg)
  - SVV error (deg)
  - SVV (+)
  - GIF (+)

**Monkey A**

- Perceived tilt (deg)
  - Head tilt (deg)
  - SVV error (deg)
Fig. 2: 

![Graphs showing head tilt and perceived tilt for Monkey H and Monkey A over time.](image-url)
Fig. 3:

![Graph showing SVV error (deg) vs Head tilt (deg) for Monkey H and Monkey A.](image-url)
Fig. 4:

Monkeys H and A show similar patterns of head tilt over time, with fluctuations in angle (deg) and perceived tilt (deg) relative to head tilt (deg).
Fig. 5:

Monkeys H and A showed a decrease in SVV error with an increase in head tilt. The plots show the SVV error (deg) against head tilt (deg) for both clockwise (CW) and counterclockwise (CCW) OK stimulation. The data points represent the SVV error under conditions with and without OK stimulation.

- Monkey H: CCW OK stimulation
  - OK Stim: ▲
  - No OK Stim: ■

- Monkey A: CW OK stimulation
  - OK Stim: ▲
  - No OK Stim: ■

The graphs indicate that the SVV error decreases as the head tilt increases, with a steeper decrease in SVV error under OK stimulation compared to no OK stimulation.
Fig. 6:
Fig. 7:

Monkey H

CW, back-to-motion

CW, facing motion

Monkey A

CW, back-to-motion

CW, facing motion
Fig. 8:

Monkey H
CCW, facing motion

Monkey A
CCW, facing motion

CCW, back-to-motion

CCW, back-to-motion
Table 1: Sinusoidal variable-radius centrifugation

<table>
<thead>
<tr>
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<th>Gain</th>
<th>Phase</th>
<th>Bias</th>
<th>n</th>
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</thead>
<tbody>
<tr>
<td>Monkey H</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.01 Hz</td>
<td>CW</td>
<td>0.82 +/- 0.01</td>
<td>5.00 +/- 0.95</td>
<td>2.90 +/- 0.47</td>
</tr>
<tr>
<td></td>
<td>CCW</td>
<td>0.80 +/- 0.06</td>
<td>1.46 +/- 1.85</td>
<td>2.53 +/- 0.61</td>
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<tr>
<td>0.05 Hz</td>
<td>CW</td>
<td>0.72 +/- 0.08</td>
<td>-7.46 +/- 2.49</td>
<td>3.99 +/- 0.73</td>
</tr>
<tr>
<td></td>
<td>CCW</td>
<td>0.68 +/- 0.08</td>
<td>-3.67 +/- 2.47</td>
<td>4.03 +/- 0.68</td>
</tr>
<tr>
<td>0.1 Hz</td>
<td>CW</td>
<td>0.64 +/- 0.06</td>
<td>0.23 +/- 3.58</td>
<td>2.36 +/- 0.85</td>
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<tr>
<td></td>
<td>CCW</td>
<td>0.61 +/- 0.04</td>
<td>1.83 +/- 3.13</td>
<td>5.22 +/- 0.57</td>
</tr>
<tr>
<td>Monkey A</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>0.01 Hz</td>
<td>CW</td>
<td>0.81 +/- 0.07</td>
<td>0.80 +/- 2.59</td>
<td>0.91 +/- 1.25</td>
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<td></td>
<td>CCW</td>
<td>0.77 +/- 0.05</td>
<td>0.00 +/- 1.32</td>
<td>0.43 +/- 1.58</td>
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<td>0.05 Hz</td>
<td>CW</td>
<td>0.70 +/- 0.05</td>
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<td>2.61 +/- 0.83</td>
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<tr>
<td></td>
<td>CCW</td>
<td>0.60 +/- 0.08</td>
<td>-4.50 +/- 8.06</td>
<td>0.42 +/- 0.45</td>
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</table>

Values are means +/- one standard error. n is the number of trials that were averaged. Gain, phase, and bias of the SVV responses were calculated as described in the methods; negative phase indicates a lag between the stimulation (tilt of the GIF) and the SVV response. Phases were corrected for the obligate 0.3 s delay associated with the timing criteria of the SVV task (see Methods). Phase and bias are in degrees.
Table 2: Parabolic variable-radius and fixed-radius centrifugation

<table>
<thead>
<tr>
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<th>Time to 0.63 x peak (s)</th>
<th>Gain</th>
<th>PT decay (%)</th>
<th>After-effect (%)</th>
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<td>Monkey H</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>CW, back (+)</td>
<td>12.9 +/-0.9</td>
<td>0.94 +/-0.02</td>
<td>41.5 +/-4.1</td>
<td>27.7 +/-1.5</td>
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<td>CCW, face (+)</td>
<td>11.3 +/-1.1</td>
<td>0.90 +/-0.02</td>
<td>52.2 +/-4.5</td>
<td>23.3 +/-3.6</td>
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</tr>
<tr>
<td>CW, face (-)</td>
<td>12.0 +/-1.5</td>
<td>0.68 +/-0.03</td>
<td>35.3 +/-6.03</td>
<td>42.6 +/-6.6</td>
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<tr>
<td>CCW, back (-)</td>
<td>14.4 +/-2.1</td>
<td>0.74 +/-0.03</td>
<td>41.9 +/-1.8</td>
<td>36.5 +/-4.3</td>
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<tr>
<td>Monkey A</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CW, back (+)</td>
<td>14.4 +/-2.5</td>
<td>0.93 +/-0.03</td>
<td>51.6 +/-5.3</td>
<td>34.4 +/-4.8</td>
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<td>9.2 +/-0.6</td>
<td>0.90 +/-0.07</td>
<td>67.8 +/-4.4</td>
<td>37.8 +/-1.6</td>
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<tr>
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<td>11.7 +/-1.1</td>
<td>0.65 +/-0.01</td>
<td>32.3 +/-2.3</td>
<td>55.4 +/-3.1</td>
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<td>12.1 +/-1.1</td>
<td>0.69 +/-0.05</td>
<td>60.0 +/-2.9</td>
<td>52.2 +/-10.8</td>
<td>4</td>
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<tr>
<td><strong>Fixed-radius</strong></td>
<td></td>
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<tr>
<td>Monkey H</td>
<td></td>
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</tr>
<tr>
<td>CW, back (+)</td>
<td>46 +/-2.3</td>
<td>0.87 +/-0.03</td>
<td>0</td>
<td>1.1 +/-3.4</td>
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<tr>
<td>CCW, face (+)</td>
<td>33 +/-2.9</td>
<td>0.73 +/-0.03</td>
<td>0</td>
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<td>10</td>
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<tr>
<td>CW, face (-)</td>
<td>36 +/-4.3</td>
<td>0.71 +/-0.05</td>
<td>0</td>
<td>7.0 +/-5.1</td>
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<tr>
<td>CCW, back (-)</td>
<td>34 +/-3.9</td>
<td>0.76 +/-0.04</td>
<td>9.2 +/-6.5</td>
<td>3.9 +/-2.4</td>
<td>5</td>
</tr>
<tr>
<td>Monkey A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CW, back (+)</td>
<td>37.4 +/-2.5</td>
<td>0.79 +/-0.04</td>
<td>7.6 +/-2.8</td>
<td>2.5 +/-1.7</td>
<td>5</td>
</tr>
<tr>
<td>CCW, face (+)</td>
<td>42.7 +/-2.1</td>
<td>0.81 +/-0.04</td>
<td>11.1 +/-1.2</td>
<td>7.4 +/-2.4</td>
<td>4</td>
</tr>
<tr>
<td>CW, face (-)</td>
<td>38.8 +/-2.7</td>
<td>0.77 +/-0.15</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>CCW, back (-)</td>
<td>34.5 +/-3.0</td>
<td>0.76 +/-0.04</td>
<td>6.6 +/-5.9</td>
<td>5.3 +/-3.0</td>
<td>5</td>
</tr>
</tbody>
</table>
Values are means +/- one standard error. Time to 0.63 x peak is the time in seconds required for the SVV response to reach 0.63 of its maximum value, measured from the onset of the centrifugal force application (t = 15 s). Gain is the peak SVV deviation divided by the peak tilt of the GIF (30 deg). PT decay is defined as the magnitude of the decline in perceived tilt (maximum PT – minimum PT) during sustained centrifugal force, expressed as a percentage of the maximum PT. After-effect is the magnitude of the reversal in PT that occurred after the centrifugal force was removed, expressed as a percentage of the maximum PT. Centrifugation trials that rotate the GIF towards the right ear are indicated by plus (+) signs and trials that rotate it towards the left ear by minus (-) signs (see Fig. 1 insert).