

## VII. POSTERS

### MODULATION OF THE CALORIC NYSTAGMUS IN RESPONSE TO DIFFERENT SEMICIRCULAR CANAL ORIENTATIONS

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We studied the modulation of the caloric nystagmus in response to different head orientations during warm continuous caloric stimulation of the right ear in 7 subjects. The plane of the lateral semicircular canal was rotated through 270 deg in pitch, in 7 sequential 45 deg steps at one minute interval. It was also rotated in roll through 360 deg in 8 sequential 45 deg steps. The caloric nystagmus was analysed in three dimensions and the magnitude of each semicircular canal's contribution to the overall caloric response was determined in non-orthogonal, contravariant canal plane coordinates. The results showed a sinusoidal modulation of the horizontal and torsional components of the nystagmus. When the right lateral canal was stimulated in the maximum excitatory position, the eye rotation axis (ERA) aligned with the on-direction of the right lateral canal. Conversely, when the right lateral canal was stimulated in the maximum inhibitory position, the ERA aligned with the on-direction of the left lateral canal. These ERAs during excitation and inhibition were mirror images of each other and were not diametrically opposed, showing the "push-pull" arrangement of the lateral semicircular canal in three dimensions. When the lateral canal plane was reoriented from excitatory or inhibitory position into earth horizontal position, the nystagmus did not subside, but instead the ERA of the nystagmus deviated towards the on-direction of the contralateral canal which was suggestive of an adaptive response. The lateral canal response magnitude in the maximum excitatory position was more than twice the response generated in the inhibitory position.

### POSITION DEPENDENT LINEAR NYSTAGMUS IN THE DARK IN NORMALS

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Horizontal and vertical components of spontaneous nystagmus in the dark were assessed in 9 healthy subjects without history of neuro-otological disease, strabismus, latent or congenital nystagmus with a monocular 2D video-oculography system (SMI). Five different head in space positions were used: sitting upright, lying face up, down, right and left, the head on trunk position being kept the same in each position. 7 subjects had a horizontal and 8 a vertical nystagmus component in at least one of the positions tested. The slow phase velocities (SPV) were low: vertical n=31, mean=1.26 /s  $\pm$ 0.83; horizontal n=25, mean=0.85 /s  $\pm$ 0.34). The

magnitude and direction of the SPV were modulated by the different head positions in space. The horizontal component was influenced more by changes in the roll plane whereas the vertical component predominantly by changes in the pitch plane.

Conclusion: Most normal subjects have an oblique, vertical or horizontal nystagmus of low velocity in the dark modulated by head position in space, presumably under otolith influence.

## THE KEY CONFLICT IN MOTION SICKNESS

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Motion sickness is generally supposed to correlate with all kinds of (intersensory) conflicts. We postulate, however, that the key role is played by only a conflict between two estimates of gravity (verticals), one generated by the senses, the other by an internal model. The determination of these estimates can be modelled by a low pass filter acting on otolith afferents.

Because our expectation, as modelled by the internal model, only derives its input from the senses in the case of passively endured motion, the expected vertical will always lag that of the senses. Motion sickness severity is therefore frequency dependent, with an optimum (or pessimum) predicted by the time constant of the otolith filtering. For vertical motions (sea-sickness) the model has quantitatively been validated.

## HORIZONTAL OR VERTICAL OPTOKINETIC STIMULATION ACTIVATES VISUAL MOTION-SENSITIVE, OCULAR MOTOR, AND VESTIBULAR CORTEX AREAS WITH RIGHT HEMISPHERIC DOMINANCE: A FMRI STUDY

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The differential effects of optokinetic stimulation with and without fixation suppression were analyzed in an functional MRI (fMRI) study in ten right-handed healthy subjects. Horizontal or vertical optokinetic stimulation activated the same multiple visual, ocular motor, and vestibular cortical and subcortical areas independent of the stimulus direction. Several new aspects were discovered: All activated areas representing cortical (occipitotemporal cortex, parietal eye field, frontal eye field, prefrontal cortex, supplementary eye field) and subcortical (caudate nucleus, putamen, globus pallidus) ocular motor structures were activated under both experimental conditions, but the activation was significantly stronger with optokinetic nystagmus (OKN) than with fixation of a stationary target during optokinetic stimulation. The anterior and posterior parts of the insula (human homologue of the parieto-insular vestibular cortex) were activated during OKN but not during fixation of a stationary target. The only relatively increased activity

during fixation suppression was seen in the superior frontal gyrus (supplementary eye field) and the anterior cingulate gyrus. A significant right hemispheric dominance was found under both conditions in the ocular motor centers; this was most prominent in the occipitotemporal cortex, but did not occur in the primary visual cortex and in subcortical ocular motor structures (putamen, globus pallidus). There is evidence that activation of the vestibular cortex by optokinetic stimulation is related to ocular motor function rather than self-motion perception.

#### DIRECTION SENSITIVITY OF STRETCH REFLEXES AND BALANCE CORRECTIONS FOR NORMAL SUBJECTS IN THE ROLL AND PITCH PLANES

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In order to prevent a fall, the CNS must rapidly initiate and accurately modulate appropriate balance corrections based on a convergence of sensory information. A large body of evidence has been collected to describe the parameters associated with automatic balance corrections to perturbations in the pitch plane. However, perturbations to equilibrium can be expected from multiple directions. Previous studies have demonstrated that muscle response amplitudes vary with respect to direction and indicate that the direction of perturbation is a significant factor in the organization of a balance response. The purpose of the present study was to separate the contributions of stretch reflex and automatic balance correcting responses and thereby increase the understanding of postural control mechanisms through an examination of the muscular and biomechanical responses to rotational perturbations in pitch and roll combinations. More specifically, automatic postural responses were analyzed with the intent to identify possible origins of directionally specific triggering information and examine how sensory information is used to modulate triggered postural responses with respect to direction.

Seven male and 7 female healthy adults (mean age=22.71+/-2.40 yrs) were required to stand on a dual axis rotating platform capable of delivering rotational perturbations with constant amplitude (7.5 deg) and velocity (50 deg/s) through multiple directions in the pitch and roll planes. Each subject was randomly presented with 44 support surface rotations through 16 different directions separated by 22.5 deg under eyes open and eyes closed conditions. Bilateral muscle activity from tibialis anterior, soleus, quadriceps and paraspinals were collected, averaged across direction, and areas calculated relative to balance-related time intervals. Trunk angular velocity and ankle torque data was averaged for pitch and roll directions over intervals corresponding to significant biomechanical events. Muscle activity responses through all stages of balance reactions were sensitive to the direction of the perturbation. Stretch reflex (40-100, 80-120 ms) and automatic balance correcting responses (120-220 ms) in the same muscle were sensitive to distinctly different directions. Whereas the maximum balance correcting activity

in lower leg muscles was oriented approximately 180 deg from maximum stretch responses, stretch reflexes in paraspinal muscles were tuned 90 deg to automatic balance corrections and 180 degrees to unloading responses in the same muscle. Stretch reflexes in paraspinal muscles were observed at 50 ms, as early as those of soleus muscles, in contrast to tibialis anterior and quadriceps stretch reflexes observed at 80 ms. Unloading reflexes in released paraspinal muscles were also observed at 30 ms for perturbations which caused backward pitching of the trunk. Trunk roll velocities (30 ms) were observed prior to pitch velocities (50 ms) for all perturbation directions. When considered together, early stretch and unloading of paraspinals and roll velocities of the trunk bring into question previous hypotheses of an ankle based trigger for postural reactions, and implicate stretch, force and joint related proprioceptive receptors at the level of the trunk as possible candidates for a directionally sensitive triggering mechanism. Accelerometer recordings from the head identified vertical linear accelerations for pitch movements and angular roll accelerations during roll perturbations with latencies as early as 15 ms. Thus, it appears that balance corrections in postural leg and trunk muscles may receive strong, receptor dependent and directionally sensitive amplitude modulating input from vestibulo-spinal signals. These findings collaborate with previous work which has demonstrated directional sensitivity of vestibulocollic reflexes, vestibular afferents and neurons particularly in the roll plane.

## THE OTOLITH-OCULAR RESPONSE TO LOW FREQUENCY LINEAR ACCELERATION

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During constant velocity rotation about the earth-vertical axis, eccentric displacement of the head can be used to generate adequate stimulation of the otolith organs. In general this is exploited to generate bilateral stimuli with radii ranging between 50cm and 10m. More recently, studies have been performed with a variable radius rotatory chair, which permits a controlled modulation of the centripetal or radial acceleration, to achieve linear acceleratory frequencies much lower than with a conventional linear sled.

In the present study, frequency response and threshold testing was performed using sinusoidal modulation of the chair radius. For threshold estimation, the radial acceleration level was adjusted by modifying angular rate. Three-dimensional eye movements were recorded with binocular video oculography, to yield a discretely sampled measure (25/s, resolution  $< 0.1^\circ$ ) of the horizontal, vertical and torsional eye position in Fick co-ordinates. To facilitate torsional measurement, high-contrast artificial tincture landmarks were applied to the limbus. This guarantees a near ideal contrast profile for the polar correlation algorithm employed.

The gain and phase relationships of the OOR show a lowpass characteristic over the measured range of 0.03 - 1.0 Hz. This may be compared to the neurophysiologi-

cal recordings from the otolith afferent, which show a near flat response over the frequency range of DC to 2.0 Hz. This demonstrates that any lowpass filtering of otolith afferents, e.g. as required by recent models for the discrimination of tilt and translation, occurs at the level of the vestibular nuclei.

The subjective threshold for the perception of lateral acceleration has been estimated to be of the order of  $0.06 \text{ m/s}^2$ . The preliminary findings demonstrate a detectable OOR at acceleration levels of  $0.03 \text{ m/s}^2$ .

### MILD BRAIN INJURY CAN DISTURB THE INTERACTION OF THE VESTIBULAR SUBSYSTEMS AND CHANGE EVOKED OTOACOUSTIC ACTIVITY IN HUMANS

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Mild brain injury and acceleration/deceleration trauma are soft-tissue lesions of the cervical column which are frequently accompanied by brain-stem compression.

Fifty-two of those patients who suffered from such an accident (3 months - 2.8 years) complained of dizziness, blurred vision and hyperacusis. Caloric testing showed a hyperactivity in 85% with unilateral predominance, dynamic posturography evidenced distinct patterns of below-average sensory testing (vestibulo-ocular, vestibular) and Dix-Hallpike was positive in about 35% of the patients.

Blurred vision was hardly to verify since ERG was normal, but visual acuity and fields were reduced in the few patients with these subjective complaints (22%). Most interestingly, 96% of the patients showed a lack or statistical significant reduction of transiently evoked otoacoustic emissions at 2 and 4 kHz while having a normal pure-tone threshold without hearing loss.

Suppression of otoacoustic emissions was - in contrast to the normal-hearing controls - impossible in the patient population. These findings suggest that patients after mild brain injury with/without acceleration/deceleration mechanism might be characterized by a disturbed interaction of the vestibular subsystems at the level of the brain-stem since the crossing olivo-cochlear fibres which control otoacoustic emissions were shown to be desynchronized.

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### THE EFFECT OF OTOLITH AND SEMICIRCULAR CANAL CONVERGENCE ON THE VOR DURING ECCENTRIC ROTATION

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Convergence of otolith and semicircular canal afferences causes gain enhancement of the vestibulo-ocular reflex (VOR) during eccentric sinusoidal rotation-(ESR)

if the nose of the subject is facing outwards. Ambiguous results for experiments performed in subjects with the nose facing inwards prompted us to systematically examine the VOR gain modulation with the subject facing inwards especially for near targets.

In the present study eye movements during ESR (nose in/out, amplitudes 5 - 40, frequencies 0.25 - 1.43 Hz) at 6 eccentricities (0 - 50 cm) were recorded in the rhesus monkey using search coil technique in the light, in the dark and with earth stationary LED targets (distance between eyes and targets 12 - 180 cm).

Between VOR gain enhancement and eccentricity a robust linear relationship was found in the dark proving equal strength of VOR gain enhancement and decrement. Unexpectedly, slope of gain modulation depended on stimulation frequency with 0.4/m at 0.25 Hz and 1.2/m at 1.3 Hz.

Also in the light at high frequencies, when smooth pursuit mechanisms do not play a role, VOR gain modulation during ESR was always fully compensatory for retinal image slip. Both results in the dark and light indicate the essential role of otolith/canal convergence.

## INVOLUNTARY TORSIONAL HEAD OSCILLATIONS IN SEE-SAW NYSTAGMUS

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See-saw nystagmus (SSN) is characterized by alternating vertical skew deviation and conjugate torsional eye movements. The more common symptomatic acquired forms of SSN have to be distinguished from the congenital forms. Since the latter can evolve in adulthood, diagnostic criteria are required to separate the two forms due to their differential therapeutic consequences. Moreover, some forms of SSN are associated with involuntary head movements, the clinical significance of them is, however, unclear.

We report about a 37-year-old patient with an intermittent pendular SSN of congenital origin who developed this torsional/vertical nystagmus in adulthood. Clinically, the pendular torsional nystagmus was associated by torsional head oscillations. Three-dimensional search coil recording of both eyes and the head under head-free conditions revealed that torsional head movements were pendular and in phase with the torsional components of SSN, i.e. they did not compensate for the ocular torsion. This is the first scleral search coil study on pendular SSN and head movements. The in-phase-relation of torsional eye and head movements suggest a common generator and a congenital origin of this pendular SSN. The congenital origin is supported by normal high-resolution MRI of the brain stem and normal visually evoked potentials. In conclusion, head movement recordings might help to distinguish congenital and acquired forms of SSN.

## THE ROLE OF VESTIBULAR AND PROPRIOCEPTIVE VELOCITY INPUTS IN HUMAN POSTURAL CONTROL

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It was previously shown that the effect of galvanic vestibular stimulation on postural responses to platform translation increased with the velocity of platform motion (*J. Neurophysiol.*, **73**: 896-901, 1995). Similarly, during the dynamic part of voluntary bending the effect of vestibular stimuli was potentiated (*J. Physiol., Lond.*, **494**: 66P, 1996).

Two studies investigate the role of vestibular and proprioceptive velocity inputs in postural control: 1) Different velocities of backward body lean caused by vibration of the soleus muscles were paired with bipolar galvanic vestibular stimulation; 2) Forward velocity of body lean due to backward platform translation was applied in at 4 different times during galvanic vestibular stimulation.

During soleus muscle vibration or platform translation, vestibular stimulation with eyes closed and head turned caused forward or backward movements of body center of pressure (CoP). The vestibular effects peaked at 1.5-2 s following the vibration or platform translation. The effect of paired galvanic-vibration and galvanic-translation stimulation was larger than the summation of these stimulations alone.

The enhancement of galvanic stimulation was related to velocity of body lean induced by soleus muscle vibration. Galvanic vestibular stimulation during faster CoP displacements had larger effects than during slow body lean or quiet stance. The velocity of CoP responses to muscle vibration was correlated with the size of effect of galvanic vestibular stimulation. During platform translations, the enhancement of vestibular stimulation was significant when the platform motion started during the dynamic part of galvanic postural response and velocity profiles of CoP responses to galvanic current and to platform motion coincided.

These results show that velocity of induced body movements is related to the enhancement of vestibular stimulation on posture. The maximum effects of combining vestibular and proprioceptive inputs occurs when the responses are in the same directions and when timing of both sensory inputs produces simultaneous change in body velocity. Vestibulospinal information may be more important during the dynamic part of postural movements, especially for the correction of the latest or final part of postural responses aimed at finding a new equilibrium point of stance.

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## HIGH-FREQUENCY DYNAMICS OF THE HORIZONTAL VOR FOLLOWING UNILATERAL LABYRINTHECTOMY IN THE SQUIRREL MONKEY

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We studied the horizontal VOR evoked by sinusoidal head rotations (2 - 20 Hz) and steps of head acceleration (3000 o/s<sup>2</sup> to 150 /s peak velocity) given in darkness in 2 squirrel monkeys following unilateral labyrinthectomy with removal of Scarpa's ganglion. Animals were maintained in darkness for 4 days after labyrinthectomy. Spontaneous nystagmus was noted to decrease postoperatively from an initial level of about 20 °/s (slow phases directed ipsilesionally) to 10 °/s. Following return to light, however, the nystagmus worsened to immediately postoperative levels for about a day and then recovered an equal amount. Ga measured from the step acceleration during this period was  $0.66 \pm .14$  contralesionally and  $0.53 \pm .10$  ipsilesionally while animals were in darkness. During the first day after returning to light, Ga for contralesional rotations improved to  $1.01 \pm .11$  but only increased to  $.67 \pm .12$  ipsilesionally.

Responses to sinusoidal rotations showed a diminished gain immediately after labyrinthectomy ( $.61 \pm .04$ ) that improved with time after the lesion ( $.78 \pm .05$ , at 21 days). A phase lag measuring  $13.7 \pm 1.1$  at 20 Hz immediately postoperatively grew to  $-32.6 \pm 1.5$  at 21 days after the lesion.

The findings indicate that asymmetries similar to those identified initially after unilateral canal plugging are also present after labyrinthectomy. A major difference between the effects of the two lesions is the prominent phase lag, which may represent a fixed time delay, noted at higher frequencies following labyrinthectomy but not after canal plugging. Restoration of tonic activity in the vestibular nuclei on the lesioned side as well as recalibration of gain may involve the addition of signals that are time-delayed and/or low-pass filtered relative to direct pathways. These signals, which are due to retinal slip after return of the animal to light, are used for VOR recalibration and are responsible for a temporary increase in spontaneous nystagmus and gain.

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## ORIENTATION AND MOTION INFORMATION FROM THE VESTIBULAR SYSTEM

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As subjects move on the ground, the continuous integration of their own position with respect to the starting point allows them to return at any time during motion to this point; this is the integration over space (path integration), advocated by Mittelstaedt. But the same behaviour is also possible if the velocity signals delivered by the vestibular system during motion are time-integrated with respect to the



starting point. We had done specific experiments on “return to the starting point”, and were surprised to find only a difference in the variability of the responses, depending upon whether subjects had seen or not a visual starting point before to be moved. Now we wonder which information is really used by the subjects, and in order to try to answer this question we compare different experiments, which were performed in different laboratories, with different equipments and different subjects, but could give a new insight on orientation from selfmotion, when compared.

Subjects were submitted to pure rotations in the dark, of various amplitudes, and had to perform different responses, driving themselves on a rotating chair with a joystick. Both motion magnitude and duration were analyzed. We computed the regression line between the passively imposed and the self-driven rotations, for each subject. We divided the constant (intercept) through the total stimulus range: maximum - minimum stimulus (angle or duration), so that spatial and temporal relative intercepts can be compared.

A) During a return task, we had found that motion duration is also memorized and reproduced.

B) During a reproduction task, in which motion does not change direction, we found that performance was better than in return (A). As for the duration, the slope was similar to that of return, and the intercept much smaller.

C) In a new series of experiments, we compared return, reproduction, and completion (subjects had to pursue the imposed rotation until a complete turn of 360 is accomplished). All tasks were applied with constant duration (CD).

Surprisingly, return and reproduction in CD was better than with variable duration (VD), even though in VD stimulus duration was correlated with the amplitude (A,B).

The slope for completion was right between that of return and reproduction, and the intercept was close to that of return. Indeed, subjects could not replicate stimulus motion for completion, but had to rely mostly on their memory of the starting point, also capital in return.

In the return task, subjects could use the memory of both the motion and the starting point, but it seems that this was too much choice among too many information channels, since return responses were the worst. Similarly, the subjects could use both amplitude and duration in VD (A,B), but spatial responses in CD (with no information from duration) were mostly better than in VD.

This reduction of the “degrees of freedom” suggests that subjects rather use a simple reproduction of the imposed motion, being apparently not able to link it to the external world, i.e. to combine vestibular motion information with visual static information. The vestibular system gives information about motion, not orientation, and the starting point should probably be internally deliberately identified, in order to play a role in orientation.

## VESTIBULAR TURNING SENSATION: A COMPARISON OF THE PERCEPTIONS OF ANGULAR VELOCITY AND DISPLACEMENT IN SITTING POSITION AND DURING UPRIGHT STANCE

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**Introduction:** Naturally behaving humans move and orient themselves in space mostly in upright position. However, most studies of the horizontal canal contribution to the perception of self-rotation and to orientation only have considered subjects seated on a chair. Furthermore, many of these studies proceed from the assumption that perceived angular displacement and perceived angular velocity are equivalent measures, one being the time integral of the other. We here report on experiments comparing vestibular perception of angular velocity and displacement in upright and seated position. These experiments are a first step toward a quantitative study of the relative contributions of vestibular, motor and somatosensory signals to orientation during active motion.

**Methods:** Stimuli consisted of trains of sinusoidal oscillations of various frequencies (0.028 - 0.45 Hz), peak to peak amplitudes (11.25 - 180°), and peak velocities (4°/s - 64°/s). A session consisted of a pseudorandom sequence of 24 such trains and lasted 35 min. Each fourth train in a session was a standard stimulus (0.11 Hz, 16°/s, 45°). While either seated (S) on a Bárány chair or standing in orthostatic (O) position on a platform, subjects (Ss; N=12) verbally estimated either peak angular velocity (V) or peak to peak angular displacement (D) in relation to the standard stimulus (Stevens' method of magnitude estimation); the V standard stimulus was assigned a modulus of 10, the D modulus was 45°. The resulting 4 tasks (VS, VO, DS, and DO) were performed during 4 consecutive sessions (order of presentation: 2 x 2 design), and the experiment was repeated in different order on a second day.

**Results:** Considering stimuli of fixed frequency ( $f=0.11$  Hz) and varying amplitude, V-estimates saturated with increasing amplitude and were best described by a log function. VO-estimates (upright) were significantly smaller than VS-estimates (seated); fits to the VO-data yielded estimates of  $23.1 \pm 2.2^\circ$  for stimuli of 64°/s (correct estimate: 40) as compared to  $27.7 \pm 3.1^\circ$  with VS ( $p<0.005$ ). Subjects delivering large V estimates in one condition (O or S) were likely to do so also in the other condition (coefficient of correlation, 0.8). D-estimates did not saturate (linear function) and did not differ between upright and seated, and they were highly veridical: Linear fits yielded  $189 \pm 8.6^\circ$  (S) and  $185.1 \pm 10.4^\circ$  (O) for stimuli of 180°.

Variability of D-estimates (~ 5%) was roughly half that of V-estimates (~10%); these values apply to both the intraindividual and interindividual variabilities, and to both the seated and upright positions.

With amplitude fixed at 45° and frequency varying, Ss' D-estimates were slightly larger than those reconstructed from their V-estimates, but otherwise exhibited the same dependence on frequency.

In a control experiment (8 different Ss) we asked whether the use of the  $^{\circ}$ -scale for D-estimates (modulus  $45^{\circ}$  !), because it can easily be linked to the body scheme, might explain the linearity of the D-estimates as opposed to the log-law for V-estimates. Therefore, the modulus for D- estimates was changed to '10'. However, D-estimates were again approximately linear functions of stimulus amplitude, whereas V-estimates saturated. The control experiment also confirmed that VO-estimates are smaller than VS-estimates.

Conclusion: Results on displacement perception obtained in sitting position also are valid for situations involving upright stance. The cognitive representations of angular velocity and displacement are based on different principles. Velocity estimates are subject to the limitations of psychophysical scaling which cannot linearly reproduce large variations of a perceptual signal. The conscious perception of velocity may also depend on the number of contributing sensory channels, a possibility that might explain why velocity perception is slightly larger in seated than in upright position (stimulation of skin receptors). Angular displacement, on the other hand, appears to be represented on a cognitive map (conceivably using a circular place code) that basically preserves the linear relation between the percept and the stimulus. Hence, displacement perception does not exactly equal the time integral of reported velocity.

## CORTICAL AREAS ACTIVATED BY PURSUIT EYE MOVEMENTS: A FMRI STUDY

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Gradient-echo, echo-planar imaging (EPI) was used to investigate BOLD contrast effects in occipital, parietal and prefrontal cortex evoked during smooth pursuit eye movements. Our aim was to differentiate between the sensory and motor components of the pursuit response. Imaging was performed with a 1.5 T whole body Siemens Magnetom. Ten 4-mm planes, positioned oblique to the axial plane, were imaged every 3 sec using a T2\*-weighted sequence (TR=1.76 ms, TE=84 ms, =90 FOV 256x256 mm<sup>2</sup>, 128x128 voxels). The visual stimuli were created on a VSG graphics board and shown in back-projection with an LCD-projector corrected for gamma. Eye movements were recorded using infrared light reflection technique with a newly designed fiber optic device. Smooth pursuit was measured for sinusoidal movements of a red dot superimposed on a dark background, on a light background, and on a random noise background. Each baseline epoch (32 sec; blank field, same mean luminance, fixation cross only) was followed by an epoch of oculomotor activity, and this rest-stimulation sequence was repeated three times for each paradigm. The resulting images were first corrected for residual head motion, and then cross-correlation was performed. As control conditions, subjects fixated a stationary dot without a background or with a stationary/ moving background. A further comparison was made between smooth pursuit and saccadic eye

movements. The results indicate that pursuit is accompanied by a pronounced activation in the V5/V5a motion complex. This activation is significantly greater during active pursuit compared to fixation with background motion. Significant voxel clusters were also evident in prefrontal BA 6 (frontal eye fields) bilaterally during pursuit, but not during fixation with background motion.

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## POSTURAL CONTROL NEAR THE LIMIT OF STABILITY AT VARIOUS SENSORY CONDITIONS IN PATIENTS SUFFERING FROM VERTIGO OR BALANCE DISORDERS

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A new measuring system was developed to evaluate the postural system near the limit of stability where subjects are forced to perform optimally to prevent a fall. This approach resulted in a good reproducibility and allowed evaluation of the impact of the visual, vestibular and proprioceptive input to the postural control system using various perturbation techniques like sway referencing the supporting platform, sway referencing the visual surround, closing the eyes, vibration of the Achilles tendons and by chilling the foot soles. In the present study, this new technique was applied in patients suffering from long lasting persistent vertigo (whiplash syndrome, Meniere's disease, acute or gradual peripheral function loss) with various abnormalities detected by standard vestibular examination and a clinical statolith function test (ocular counter rolling upon lateroflexion). Similar to the results obtained in healthy subjects, posture control in these patients - on average - was maximally affected by closure of the eyes and by vibration of the Achilles tendons. The other perturbation techniques applied were less effective. The combination of vibration and a sway referencing platform was the most effective technique used to disturb the proprioceptive input. No consistent typical pattern found by the new posturography test was observed that could classify the patients with respect to the history or outcome of the standard vestibular examination: the individual data indicate that the contribution of the sensory inputs toward postural control varies considerably between patients and clearly limits the clinical relevance of this type of dynamic posturography. Postural control near the limit of stability was significantly decreased in the majority of chronic Whiplash patients with vertigo or balance disorders, as well as patients suffering from Meniere's disease or known with a central compensated peripheral vestibular function loss. More than ninety three percent of the patients could be classified with use of the postural control test, specially when the responses on the sway referenced surround, the eyes closed condition with and without the sway referenced platform were taken into account. However, based upon their postural control no discrimination could be made between the four different patient groups.

### THREE-DIMENSIONAL FAST SPIN ECHO T2 WEIGHTED MR IMAGES OF THE CEREBELLOPONTINE ANGLE AND INNER EAR

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**Rationale:** In patients with dizziness and hearing disorders it is essential to rule out the possibility of an intracranial affection, typically a cerebellopontine angle process. This is clinically often done using audiology, otoneurology and by interpreting the time course of the symptoms. However, in many cases we must resort to imaging of the temporal bone and the cerebello-brainstem area. We present a technique by which a three-dimensional (3D) high resolution MR image can be an alternative in this respect.

**Material and methods:** A series of 152 patients were investigated from September 1996 to November 1997 in our lab. The use of 3D Fast Spin Echo (FSE) T2 weighted images can in many cases eliminate the need of gadolinium contrast administration, offering a cheaper and quicker investigation procedure. Special algorithms allow presentation of data in a 3D form. Slice thickness can be reduced to approximately 0.7 mm.

**Results:** In subjects free of tumor in the cerebellopontine angle the 7th and 8th nerves could be followed accurately from the internal auditory meatus to the brainstem. The found tumors could be outlined with reasonable accuracy even without gadolinium contrast. The inner ear had high signal, like liquor. Patency of the cochlea could be estimated accurately.

**Conclusion:** 3D FSE T2 weighted images are useful in evaluation of the cerebellopontine angle in cases of tumor suspicion. Most often the use of gadolinium can be avoided, except in cases of nerve inflammation. Gadolinium is also necessary for differentiation of pathology within the inner ear. This method is an attractive alternative for of imaging of patients with hearing disorders and dizziness.

### SYNAPTIC INNERVATION IN THE EARLY POSTNATAL MOUSE UTRICULAR MACULA

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As part of an ongoing study on early postnatal development of the mouse utricle, we have been re-examining the question of early synaptic innervation. We chose to examine the developmental stages of PD0 (day of birth), PD4, PD7, PD10 and PD28, in order to correlate these data with our morphological studies on the transition from supporting cells to hair cells, and with subsequent type I and type II hair cell development (Rusch et al, 1998). We are also interested in these early stages as a means to establish baseline data for future spaceflights involving developing mammals.

Multiple samples were taken from each of the 5 postnatal stages. Dissector

counts of synaptic ribbons were made as described previously in a study of the chinchilla crista ampullaris (Lysakowski and Goldberg, 1997). Results revealed that synaptic innervation in both types of hair cells proceeds at an orderly rate. Our results differ from a previous study of synaptic innervation in cats in which the numbers of synaptic ribbons in type I hair cells decreased 93% from birth to adulthood (Favre and Sans, 1979).

The average number of ribbons per hair cell is initially high, 41.7 ribbons per hair cell at PD0, decreases during the immediate perinatal period to 10.3 (PD4), and then increases with each postnatal day to 13.2 (PD10) to 22.4 (PD28). Immature hair cells had many fewer synaptic ribbons than mature hair cells at each developmental stage. There was also some tendency for type II hair cells to have more synaptic ribbons than type I hair cells, especially later in development. Comparing our results to the previous study by Favre and Sans, the differences may perhaps be explained either by a species difference, or by our use of serial sections, or by our use of the disector method compared to their use of a ratio method of counting.

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## PERCEPTION AND NYSTAGMUS DURING ACTIVE AND PASSIVE ROTATION

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Subjects estimated subjective velocity after acceleration to a constant rotation of 30-50 deg/sec in five experimental paradigms. Subjects were blindfolded (except in paradigm E) and earphoned with pink noise. They stood or walked on a disk at radii of  $r=0.15$  to 1.6m while gripping a radial bar that

A rotated with the disk,

B rotated while the disk was room-fixed,

C was room-fixed while the disk rotated backwards,

D was freely mobile about the axis while the disk rotated backwards,

E as in C, but with a distant optical fixation point. In paradigm A and B the horizontal VOR was measured simultaneously.

Extant experiments similar to A, B and C by W. Bles, F. Guedry, I. P. Howard, D. Solomon and B. Cohen were extended by systematically varying the angular and linear parameters. Moreover in A and B the time course of perceived rotation and the VOR was simultaneously recorded.

Main results:

1. The subjective velocity decreases with time in the paradigms A, D and E whereas it increases in the paradigms B and C.

2. Angular velocity and excentricity have different influences in the five paradigms.

3. The dynamics of the VOR in paradigms A and B do not reflect those of perception.

## OBJECT LOCALIZATION IN SPACE AND RELATIVE TO THE OWN BODY DURING NECK PROPRIOCEPTIVE AND VESTIBULAR STIMULATION IS NORMAL IN PATIENTS WITH IDIOPATHIC TORTICOLLIS

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It has been postulated that abnormalities in sensory afferent inflow are responsible for dystonic symptoms, for example abnormal vestibular and neck proprioceptive inputs in spasmodic torticollis (ST). It is known that normal subject use vestibular and neck proprioceptive signals when judging the location of a visual object in space. If these signals were asymmetric in patients with ST, one would expect these patients to have abnormal spatial perception. We tested this idea by measuring patients' ability to reproduce the location of a light spot in space (I, "space task") before and after a passive horizontal rotations of the head and/or trunk. In addition we test how accurately the patients can set the spot into the head (II) and trunk (III) mid-sagittal planes before and after these stimuli. During the tests a light spot was stepped 10° either to the right or left side and subjects were asked to restore the instructed location of it (I-III) by means of a joystick. Rotations of head in space and trunk relative to the head of 16° amplitude, showing a "raised-cosine" velocity profile, were applied in darkness for vestibular and neck stimulation, respectively (VEST, NECK). In addition a combination of these two stimuli was applied (head rotation on stationary trunk; VEST+NECK). Three different stimulus durations were used (10, 5 and 1.25s), with the corresponding peak velocities amounting to 2, 4 and 14°/s. Thirteen ST patients (44.3 ± 10.3 yrs) were compared with fifteen age-matched controls.

The magnitudes of the patients' estimates were not statistically different from those of normal subjects for all experimental tasks (I, II and III) and all stimulus conditions (VEST, NECK and VEST+NECK) and durations. In particular, the veridical estimates of object localization with respect to the trunk mid-sagittal plane after NECK stimulation suggest that the neck input may be normal in ST patients or, alternatively, that asymmetries of the sensory inflow are compensated for at central levels. The same conclusion holds for the horizontal canal input (inferred by the veridical estimates of the patients in the "space task" after VEST) as well as for vestibular-neck interaction.

Our findings vote against the assumption that asymmetries in afferent vestibular or neck inflow are responsible for the asymmetry of motor output in ST.

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## OPTOKINETIC AFTERNYSTAGMUS RE-ORIENTATION BY GRAVITY: EFFECT OF LONG LASTING OPTOKINETIC STIMULATION IN THE RABBIT

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Prolonged binocular optokinetic stimulation (OKS) in the rabbit induces a high velocity negative optokinetic afternystagmus (OKAN II) that persists for several hours. We have taken advantage of this uniform nystagmus to study how changes in static head orientation in the pitch plane might influence the orientation of the slow phase of the nystagmus. Following horizontal OKS, the rotation axis of the OKAN II remained aligned with the gravity vector by as much as 80 up and 35 down of head pitch angle. This indicates that OKAN II is coded in gravity-centered rather than in head-centered coordinates. Moreover, the reorientation was accompanied by slow phase eye velocity abatement, related to the head pitch angle.

Thereafter, we analyzed the orientation of the nystagmus plane following different conditioning procedure, in which head and/or the OKS were pitched in upward and downward directions. We found that OKAN II did not remain in the horizontal plane nor in the plane of the stimulus rehead coordinates, but it aligned its rotation axis with that of the OKS re-space. As after short lasting OKS, the eye responses align toward the horizon, we suggest that long lasting OKS induces a change in the internal space coordinates building a new reference according to the orientation of optokinetic stimulus. The nystagmus slow phase eye velocity was also affected by the head position during the conditioning procedure, because the velocity maximal value was observed at the same head pitch position as that held during the conditioning. This suggests that nystagmus velocity attenuation is directly dependent on the mismatch between the space centered plane, and that of the head centered optokinetic pathway activated during the OKS.

## INTERACTION OF VESTIBULAR, SOMATOSENSORY AND VISUAL SIGNALS FOR POSTURAL CONTROL - A CONCEPTUAL MODEL

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Our poster considers the question to what extent the sensory mechanisms which are involved in human postural control are shaped or determined by biomechanical and physical constraints. The interactions between the relevant sensory signals cannot be easily inferred from observation of postural reactions, because they are obscured by several 'complications' (biomechanics, multibody dynamics, multimodal feedback control, cognition etc.). Insights into the sensory mechanisms can be obtained by psychophysical investigations. Previous studies of human selfmotion perception from our laboratory have led to a model of vestibular-somatosensory



interaction, the basic aspects of which are applicable to postural control. In the model two major steps are performed: (i) Vestibular information arising in the head is used to evaluate the kinematic state of the body support by means of a proprioceptive coordinate transformation ('down-channeling'; with the proprioceptive signals centrally receiving the non-ideal vestibular transfer characteristics), and (ii) movements of a given body part (e.g. of the trunk) are perceived relative to the support by means of an up-going coordinate transformation using almost ideal proprioceptive signals ('up-channeling'). Together the two steps allow self-motion perception in space. It involves vestibular input when the support is perceived as moving and is based primarily on proprioceptive input (up-channeling alone) when the support is stationary. We asked how this model relates to the postural control of a multi-segment body under gravitational conditions.

We hold that postural control has to account for the fact (a) that gravity (and body inertia in general) evokes ground reaction forces that are measured by the somatosensory system, (b) that the body site where the reaction forces have impact may change from moment to moment (e.g. during walking it may shift from one leg to the other), (c) that it is advantageous to induce changes in the reaction forces, which we create in response to external disturbances, close to the site of the reaction forces, and (d) that in view of the hierarchy of segmental movements, which is dictated by gravity (a lower segment represents the platform for the upper ones) is best accounted for by controlling posture in a bottom-up way.

These aspects are reflected in our postural control model by two steps. (A) 'Local' body-on-support control. The body is controlled in relation to its support by linking, in bottom-up direction, the proprioceptive feedback loops for the inter-segmental joints, thereby adjusting or maintaining a given inter-segmental and body-to-support geometry. This mechanism takes into account the available limits of support (involving deep sensors that measure 'load') and copes with external forces like push or pull on the body, for instance. (B) 'Global' body-in-space control. The kinematic state of a given body segment in space is controlled by using the vestibular signal and transforming it to the segment with the help of proprioceptive input. However, the transformation is not direct, but via the body site of support (i.e., first 'downwards' and then 'up', via A), so that the state of the lower segments is taken into accounting. The global control signal is fed into the local loops in the form of a set point signal (compare equilibrium point hypothesis).

We hold that these mechanism developed through experience of inertial and gravitational reaction forces. The linkages that are established between the body and the support allow to incorporate both into a notion (Gestalt) of ourselves in the environment. The fact that the model allows for local control of intersegmental angles, but in addition uses a global reference system as a common linkage across the whole body makes the system very robust with respect to local disturbances and makes it highly flexible with respect to variations of the behavioral conditions, on one hand, and it reduces the computational complexity of the system as a whole,

on the other hand. Visual input may well be incorporated into the model, but by no means can substitute the inertial (vestibular) sensor in this condition.

The model predicts that the same mechanisms that are used for the control of body in space can also be used for an object that is linked to the body. Imagine that you are on a swaying ship and the waiter tries to bring you a glass of beer. Our prediction is that you will remain thirsty if his vestibular system is not well functioning.

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## VISUAL-VESTIBULAR INTERACTION FOR SELF-MOTION PERCEPTION IN NORMALS AND IN PATIENTS WITH LOSS OF VESTIBULAR FUNCTIONS

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It is still an enigma how normal subjects make use of visual information for self-motion perception, thereby successfully minimizing the danger of visual self-motion illusions. The perception appears to be the result of a complex mechanism involving cognition and attention factors rather than a simple vestibular-visual interaction mechanism, because under laboratory conditions minor changes of the situation (instructions, previous stimuli, 3D property of the visual stimulus etc.) may change it and lead to visual self-motion illusions. In an attempt to elucidate some of the relevant factors involved, we presented normal subjects (Ns) with a number of different vestibular-visual stimulus combinations and compared the results to those of patients with loss of vestibular function (Ps). The experiments represent an extension of a previous study in which we used only one visual stimulus (visual scene), by now adding a visual object which served as fixation point.

Subjects sat on a rotation chair which allowed horizontal whole-body rotation. They were surrounded by a cylindrical screen ( $r=1$  m, vertical axis) onto which a black and white random-patch pattern (visual scene) was projected. In addition, a small spot of red light (0.5 deg) was projected onto the screen at eye level, which subjects fixated or tracked with their eyes. These two visual stimuli could be rotated as well, independently of each other and of the chair. We applied vestibular stimuli (VEST, body rotation; in a 'VEST only' condition spot and visual scene were kept head-stationary), retinal stimuli (RET, visual scene rotated relative to spot; in 'RET only' spot and body were stationary), visuo-oculomotor stimuli (OM, rotation of spot; in 'OM only' spot and scene were rotated about stationary body), and various combinations of these stimuli. Stimuli had sinusoidal waveforms and covered a frequency range of 0.025 to 0.4 Hz, the peak amplitude normally amounted to 8. Gain and phase values of self-motion perception were extracted from subjects' self-motion indications with the help of a pointer (unseen).

'VEST only'. Ns' self-motion perception showed a similar gain and phase behavior over frequency as in the dark, with a gain attenuation and slight phase advance at low frequency. Ps felt stationary up to 0.2 Hz and perceived some self-motion at 0.4 Hz ( $G < 1$ , large scatter), also similar as in the dark.

'RET only'. Ns felt stationary and perceived the scene as moving over the whole frequency range tested. Only when they, on instruction, no longer fixated the spot and were 'staring through' the visual stimuli, circular vection (CV) was evoked. Ps, in contrast, always experienced 'full' CV. Also Ns experienced full CV over the frequency range tested when they, prior to the self-motion estimation, performed a visual task (estimation of object motion in space; in the 'RET only' condition there was a cogent object motion illusion, called Dunker's induced motion).

'OM only'. During spot and scene rotation with the eyes pursuing the spot, Ns had no CV. Ps, in contrast, had full CV.

The results of the stimulus combinations ('VEST+RET', 'VEST-RET', 'OM+RET', 'OM-RET', 'VEST+OM', and 'VEST-OM'; plus signs indicating in-phase combinations, minus signs counter-phase combinations) can be summarized as follows. Ps extracted from retinal and visuo-oculomotor inputs a notion of visual scene motion relative to the own body and always interpreted the scene as stationary in space; on this they based their self-motion perception. Also Ns extracted a notion of scene motion relative to the body, but evaluated its motion in space with the help of the vestibular signal.

The present results confirm our previous findings on vestibular-visual interaction, which were obtained with only the scene as visual stimulus and with the subjects, on instruction, staring through it. Basic aspects of the results can be described by a model which is similar to the previous one (containing both a vestibular-visual fusion and a conflict mechanism that suppresses visual contributions), which we extended such that it includes a second visual stimulus (fixation spot).

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## ADAPTATION TO VESTIBULAR LOSS: CONTROL OF HEAD AND TRUNK DURING POSTURAL PERTURBATIONS

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The role of information from the vestibular and other sensory systems in automatic postural responses to balance perturbations is incompletely understood and may change depending on the requirements of the particular balance task. Normal subjects with intact vestibular systems maintain balance on short or compliant support surfaces using hip strategy, and also combine hip strategy with ankle

strategy to maintain balance in response to fast rearward support-surface translations. However, some previous studies have found that patients with profound bilateral vestibular loss are unable to control posture when standing on short support surfaces and that they also show abnormalities in the control of the head and trunk. This suggests that normal vestibular function is necessary for normal automatic postural responses in tasks requiring hip strategy, which requires good control of trunk position.

To test this hypothesis, patients with profound bilateral vestibular loss and age-matched controls underwent 20-cm rearward support surface translations with velocities ranging from 5-35 cm/s. Velocities were presented in random order, and eyes were closed to eliminate the effect of vision. Muscle activations and body kinematics were recorded and shank, thigh, and trunk segment angles were calculated. Joint torques at the ankle, knee, and hip were also calculated.

At higher velocities (30 cm/s) all subjects added early abdominal activations, suggesting the addition of hip strategy at these velocities. Fast translation velocities (30 cm/s) also induced a subject-independent, triphasic pattern of early hip torque (first 400 ms) in control subjects consistent with the addition of hip strategy to the response. Patients who lost vestibular function as adults responded with similar early hip torques. However, some differences in trunk and head control were noted between normal control subjects and patients with vestibular loss. Both trunk velocity and head velocity increased linearly with platform velocity for control subjects. However, while peak head velocities are similar for patients and normals, peak trunk velocities are lower for patients, especially at high platform velocities.

Contrary to our hypothesis, we conclude that vestibular function is not necessary to trigger a hip strategy. We postulate, therefore, that the balance deficit associated with the use of hip strategy previously reported in vestibular patients may be due to the nature of the tasks studied in those experiments. Each of the previously used tasks alters at least one of the following task characteristics: the dynamics (e.g., shortened and compliant surfaces render ankle torque less effective), the state of the body (e.g., tandem and unipedal stance), biomechanical limits of stability (e.g., shortened support surfaces, unipedal stance, and tandem stance decrease the area of the effective base-of-support), or the availability of lower leg sensory input (e.g., ischemia). Many of these tasks also modify the pattern of somatosensory information coming from the support surface. The rules governing the sensorimotor process of postural strategy selection may require modification in order to deal with the constraints imposed in these postural tasks. The results of this study suggest that the interaction of information from vestibular system and from the somatosensory system in the CNS may play a critical role in that modification process. Further, the finding that vestibular patients have lower trunk velocities than normals, but similar head velocities, suggests that patients may adapt to vestibular loss by limiting trunk movement to enhance the control of head position during postural responses.

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### 3D OCULAR ROTATIONS IN PATIENTS WITH FOURTH NERVE PALSY: EFFECT OF THE BIELSCHOWSKY HEAD-TILT TEST ON PRIMARY POSITION

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The Bielschowsky head-tilt maneuver is a sensitive test to detect an oblique extra-ocular muscle weakness. In patients with fourth nerve palsy, tilting the head to the side of the paretic eye results in an extorsional-upward deviation of the affected eye. We asked whether this torsional-vertical divergence is accompanied by an additional change of primary eye position. (Primary eye position = position from which any other eye position in Listing's plane can be reached by a rotation with no torsional component).

In patients with 4th nerve palsy, we recorded three-dimensional positions of both eyes with dual search coils. So far, 6 patients (right eye: 4; left eye: 2; all data are mirrored to the right side) participated in this study. Here we report on data that we collected when the affected eye was fixing stationary targets on a tangent screen (distance 1.24 m) with the unaffected eye covered. Head position, as controlled with a bite bar, was either upright, 30° right-ear-, or 30° left-ear-down.

The difference of ocular counterroll between the right-ear- and left-ear-down head positions were small ( $-1.4 \pm 2.0^\circ$ ). The horizontal component of primary position changed in an unsystematic way. The vertical component of primary position, however, showed a close relation to roll head position: When the head was tilted from upright to the side of the affected eye, primary position moved upward by  $8.3 \pm 5.7^\circ$  (t-test:  $p = 0.016$ ). With the head tilted to the other side, primary position moved downward by  $8.3 \pm 3.2^\circ$  ( $p < 0.01$ ).

These preliminary data suggest that, during the Bielschowsky head-tilt test, primary position of the eye with fourth nerve palsy moves up when the head is rolled toward the pathological eye, even with this eye viewing identical Hess screen targets. This finding reflects the fact that the extorsional gradient of the affected eye, as it moves from ad- to abduction, is more pronounced with the head tilted to the ipsilateral side.

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### MAPPING THE OCULOMOTOR SYSTEM: THE POWER OF TRANSNEURONAL TRACING

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Retrograde transneuronal tracing with rabies virus allows specific labeling of synaptically connected neurons (Ugolini, 1995, J. Comp. Neurol. 356:457). This

method was applied to the oculomotor system to test the hypothesis of a modular organization of eye movement circuits. In guinea pigs, rabies virus (CVS strain; 1:1) was injected into one medial rectus (MR) muscle. This muscle was chosen because of its special innervation pattern (ascending tract of Deiters, abducens internuclear pathway). The CNS distribution of the virus was studied immunohistochemically at sequential 12 hr intervals from 2 to 6.5 days post-inoculation (p.i.). Specificity of uptake was demonstrated by double immunofluorescence for rabies and choline acetyl-transferase (CAT; a motoneuron marker) in sections of the oculomotor, trochlear and abducens nuclei.

Transneuronal transfer was time-dependent. Initially, labeling involved only MR motoneurons 2 days p.i. (first-order) in the ipsilateral oculomotor nucleus. At 2.5 days p.i., the onset of transfer visualized abducens internuclear neurons contralaterally, and other cell groups of the horizontal system that project directly to medial rectus motoneurons, i.e. ipsilateral prepositus hypoglossi neurons, ipsilateral medial vestibular nucleus neurons of the ascending tract of Deiters, bilaterally distributed interneurons (CAT-negative) in the oculomotor and trochlear nuclei and the supra oculomotor region and neurons associated with saccade generation in the nucleus reticularis cuneiformis. At 3 days p.i., additional labeling involved consistently many neurons in the contralateral medial vestibular nucleus, caudal parts of the ipsilateral medial vestibular nucleus, the superior vestibular nucleus (mainly ipsilaterally), the paramedian pontine reticular formation, paramedian tract neurons and also some neurons in contralateral Y group and in the interstitial nucleus of Cajal. Inconsistent labeling of a few neurons in the latter cell groups occurred already in some cases at 2.5 days p.i.. From 3.5 days p.i. onwards, transfer to higher-order neurons occurred in the descending vestibular nucleus, Scarpa's ganglion, the ipsilateral cerebellar flocculus (FL) and deep cerebellar nuclei, and several other cortical and subcortical cell groups. Additional labeling appeared at longer survival times.

Purkinje cells (PCs) were labeled at 3.5 days p.i. in the ipsilateral FL in a single band that ran diagonally from caudomedial to rostromedial in an intermediate position. This band corresponds to the so-called "horizontal zone". In some cases, labeling continued laterally across the posterolateral fissure into the ventral paraflocculus. At longer survival times (between 3.5 and 4 days p.i.), the initial band became slightly broader and additional separate bands of labeled PCs appeared rostromedially and caudolaterally in the FL. At these times, an intermediately positioned band also appeared in the contralateral FL that mirrored the one initially labeled in the ipsilateral FL. The time difference in the appearance between the initial band in the ipsilateral and contralateral FL reflects a similar time difference in labeling in ipsilateral versus contralateral magnocellular medial vestibular nucleus neurons. A few hours later, additional bands developed in the contralateral FL as observed earlier in the ipsilateral FL. After 4 days, the areas adjacent to the "horizontal zone" in both FL became gradually filled with labeled PCs, but even at 6.5 days p.i. some parts of the FL remained unlabelled. This increase suggests an involvement of PCs belonging to "vertical zones" in horizontal eye movement

circuits via neurons in the vestibular nuclei or the deep cerebellar nuclei and possible the Y group.

These first results suggest a modular organization at the level of basic neuronal circuits involved in spatial coordination of eye movements, but also indicate a much more complex network for the control of horizontal eye movements than anticipated earlier, that involve multiple diverging and converging connectivities.

## IDENTIFICATION OF SENSORY INFORMATION IN HUMAN BALANCE CONTROL

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It is known from human balance experiments that altered or ambiguous sensory input conditions affect balance. However, existing models of human balance control do not focus on the problem of neural time delays and how all the different sensory information humans utilise in maintaining balance is integrated.

A human balance control model is developed, which includes the different sensory systems as well as neural time delays. In the model, the difference between the expected sensory output (efferent copy) and the actual sensory output is weighted to drive the estimate of body orientation to the actual body orientation. The weighting of this difference (sensory conflict) depends on the precision of the sensors and the environmental conditions. In the model a regulator uses the estimate of body orientation to maintain erect standing. By linearizing the human balance control model, a closed form expression for the variance of the segment angles can be obtained. This expression is a function of the; (1) modelled body and sensor dynamics; (2) neural time delay of 100 s; (3) variances of second and third derivatives of horizontal platform movements and of the second derivative of platform rotations; (4) unknown weights in the objective function of the controller; (5) unknown variance's of the noise afflicting the sensory output of the modelled sensory systems ( $V=E\{v^T v\}$ ). The precision of the sensors was quantified by the variances of sensor noise. These unknown model variances of sensor noise were found by a optimization method, which minimised the differences between model predictions and experimental results.

Platform perturbation experiments were done to quantify the precision of the different sensory systems by matching model predictions with experimental results. Six male subjects (age  $31 \pm 5$  yrs, body mass  $86.5 \pm 9.8$  kg, body height  $1.83 \pm 0.05$  m, leg length  $0.92 \pm 0.14$  m) participated in this study. The subjects were instructed to stand as still as possible on a 6 DOF movable platform (a hexapod) for 200 s. each trial. The study consisted of eight trials with four different random platform movements in the sagittal plane with eyes open and blindfolded. Platform rotations and translations were generated by band-pass filtering a random signal with a second order Butterworth filter and limited to 3.5 degrees and 6 cm respec-

tively. With eyes open the subjects had to look at a structured visual scene, generated by a 3D virtual environment program. Headphones were worn to exclude auditory clues from the platform. During the execution of the task, the movement patterns and the ground-reaction forces were recorded with a sample frequency of 100 Hz. Landmark co-ordinates were recorded with the aid of a motion analyser (Optotrack) and bandpass filtered with a second order Butterworth filter (.05-3 Hz). These co-ordinates were used to calculate the angles of the legs, trunk and head in the sagittal plane. For each time series of segment angles, the variance was calculated. Second and third derivatives of horizontal platform movements and second derivatives of platform rotations were computed numerically. The variance of the time series of these derivatives was also calculated.

One set of variances of the sensor noise, for which model predictions matched all experimental results, was not found. Different sets of variances of sensor noise were found for which the model predictions matched the results of the experiments with the same visual conditions and frequency content of the platform movement. The noise to signal ratios for the muscle spindles are 3-7% and for vision 11-14%. For the vestibular organs unambiguous noise to signal ratios could not be found. To find the noise to signal ratios of the vestibular organs and their thresholds the method of identifying sensory information has to be modified. During optimisation, the noise to signal ratios and the vestibular thresholds should be kept constant for the different experimental conditions, instead of the variance of sensor noise.

## OTOLITH PROJECTIONS IN THE HUMAN CORTEX

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We used evoked potentials to map the cortical projections of the otolithic vestibular inputs. We tested the hypothesis that, in humans, several cortical areas process saccular informations to update numerous variables such as egomotion sensation, subjective vertical and direction of heading required to control gaze and posture. Monaural clicks (100 sec duration) were delivered randomly in awake subjects at a mean 2Hz frequency, either in the left or in the right ear, to stimulate the saccule. The activated cortical areas were studied by using two different methods: the evoked potentials method and the positron emission tomography (PET).

In the evoked potentials method, voltage and current source density maps were obtained by spline interpolations of the scalp potentials of 31 electrode positions. The dipole sources were calculated using the Besa program. The clicks were delivered either at 100dB to stimulate the saccule and the cochlear cells, or at a lower intensity (60 dB) to only activate the acoustic system. Our results suggest that otolithical afferents input at short latencies the frontal lobe, the temporoparietal area, the supplementary eye field and the parietal posterior area.



Using PET, we also measured changes in regional cerebral perfusion (rCBF) induced by the saccular and acoustic stimulations. Different stimuli were used: 60dB clicks, 100 dB clicks, and of 60 and 100 dB whistles of 100msec duration. These two last stimuli stimulated the cochlear cells, but were unable to activate the saccule. Statistical analysis of the condition-specific mean rCBF brain images was performed on a voxel by voxel basis using statistical parametric mapping (SPM; Friston et al., *J. Cereb. Blood Flow Metab.*, **11**: 699-699, 1991). Our results reveal that saccular stimulations activate the supplementary eye fields, the precuneus and the ipsilateral fronto-insular gyrus.

#### FUNCTIONAL MRI OF THE VESTIBULAR CORTEX IN PATIENTS AFTER ACOUSTIC NEUROMA REMOVAL

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Three patients (after surgical removal of small acoustic neuroma by translabyrinthine approach) underwent f-MRI with the following protocole.

The vestibular stimulus was a 30 sec cold irrigation of each ear. Coplanar images were acquired before any stimulation and 30 sec after the end of the irrigation. The sequence was repeated two times for each side. Cortical areas (parieto-insular, temporal and cingolar cortex) as well as putamen and thalamus were activated after intact side stimulation. These results were compared with those obtained in normal subjects using the same methodology.

#### ARE VESTIBULAR-ONLY (VO) AND VESTIBULAR-PLUS-SACCADE (VPS) NEURONS THE NEURONAL SUBSTRATE FOR VELOCITY STORAGE?

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It has been postulated that the process of velocity storage in the vestibular system is produced by activity of VO and/or VPS neurons (Reisine and Raphan, 1992; Yokota et al. 1992; Wearne et al. 1996; Holstein et al. 1996). The purpose of this study was to determine whether these neurons have the quantitative characteristics to be the neural substrate for this process. VO and VPS neurons were recorded in rostral medial vestibular nucleus (MVN) and superior vestibular nucleus (SVN). Semicircular canal input was determined physiologically by sinusoidal rotation in different head orientations. Animals were given steps of constant angular velocity (30-180 °/s) and yaw axis OKN and OKAN (60 & 90 °/s) while upright and tilted. There were increases in firing rate related to the initial jump in eye velocity during vestibular stimulation in both types of neurons. Activity of VO neurons had no relationship to eye position or saccades. VPS neurons also were

unrelated to eye position, but paused during all or part of saccades. Activity in VPS neurons declined when animals became drowsy and returned when animals were alerted. In contrast, the activity of VO did not depend on the state of alertness. That is, firing of VO neurons was maintained despite loss of eye velocity due to drowsiness, an important characteristic of the storage integrator. Both VO and VPS neurons were activated by angular head rotation and by counter-movement of the visual surround that produced optokinetic nystagmus and after-nystagmus (OKN and OKAN). VO neurons were not activated during sinusoidal OKN above 0.05 Hz, but were significantly modulated at 0.02Hz, similar to characteristics of the storage mechanism. Regardless of canal input, activity of all neurons was linearly correlated to yaw eye velocity during OKAN and vestibular nystagmus ( $p < 0.05$ ), vertical canal-related units responding in a Type II manner. The dominant time constant of both VO and VPS units changed in proportion to changes in the dominant time constant of yaw eye velocity, i.e., to the velocity storage integrator time constant, during head tilts. In some vertical canal-related units, activity was related to vertical or roll crosscoupled eye velocities in tilted positions. The coefficient of linear regression relating vertical/roll eye velocity sensitivity to changes in firing rate of vertical canal-related neurons remained constant during cross-coupling, independent of head tilt. When the velocity storage mechanism was inactivated by injection of baclofen (Cohen et al., 1987), a GABA agonist, the correlation between eye velocity and neuronal activity disappeared. These data provide strong support that VO neurons have appropriate qualitative and quantitative characteristics to be responsible for producing velocity storage. While VPS neurons are also closely associated with velocity storage, they are not likely to be responsible for its generation.

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## EFFECTS OF GALVANIC VESTIBULAR STIMULATION ON OTOLITHIC AND SEMICIRCULAR CANAL EYE MOVEMENTS

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The aim of this study was to determine the otolithic and semicircular canal contributions to eye movements during galvanic vestibular stimulation with increasing current strengths (1.0 to 7.0 mA). Eye movements were measured with a three-dimensional video-oculography technique (sampling frequency of 60 Hz) in 12 healthy volunteers (9 males, 4 females, mean age 30.8 years, range 23-46) during stimulation with a rectangular, unipolar binaural electric current applied to the subject's mastoid. Anodal stimulation of the right mastoid led to an ipsiversive tonic ocular torsion of up to 5.4, increasing in amplitude with increasing current strengths applied. This reflects otolith stimulation. In most subjects current strengths of 3 mA or more elicited a slight (horizontal-) torsional nystagmus (amplitude 1-2) that was superimposed on static torsion. This reflects horizontal and vertical semicircular canal stimulation. The lack of a vertical deviation and nystagmus can

be explained by the counterdirected vertical components of the anterior and posterior semicircular canal. A correlation was found between the amount of torsional eye movement and the applied current strength. Thus, galvanic vestibular stimulation at low current intensities (1-3 mA) preferably excites otolith responses which increase with increasing current intensity. With higher current intensity above 3 mA additional semicircular canal responses are elicited in the form of horizontal-rotatory nystagmus superimposed on static torsional deviations.

### HUMAN EYE MOVEMENT RESPONSES FOLLOWING POST-ROTATORY TILT ("DUMPING") INCLUDE AN INDUCED LINEAR VESTIBULO-OCULAR REFLEX

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We hypothesized that the horizontal eye movements evoked by a rapid tilt following a constant velocity rotation in yaw about an earth-vertical axis would include both an angular vestibulo-ocular reflex (VOR) component and a linear VOR component that depended upon the final orientation of the subject relative to gravity. This prediction is based on a model that hypothesizes that the total gravito-inertial force measured by the otoliths is resolved into components representing internal estimates of linear acceleration and gravity. Following the postrotatory tilt, the internal estimate of gravity is rotated away from the actual orientation of gravity by the post-rotatory semicircular canal response. The difference between a central estimate of gravity and the actual orientation of gravity as measured by the otolith organs corresponds to a central estimate of linear acceleration. When the subject is tilted to the nose up or nose down orientation, the primary component of this estimated linear acceleration is aligned with the interaural axis and produces a horizontal linear VOR. This primary linear VOR increases the magnitude of the total horizontal VOR (angular VOR plus linear VOR) when the subject is nose up and decreases the magnitude of the total horizontal VOR when the subject is nose down for both directions of rotation. When the subject is tilted with their right ear down or left ear down, the primary component of the estimated linear acceleration is aligned with the naso-occipital axis and induces no conjugate linear VOR when the subject is looking straight ahead. However, for a sufficiently large angular velocity of the upright rotation, the rotation of the internal estimate of gravity may be large enough to produce a non negligible secondary inter-aural estimate of the linear acceleration and thus a horizontal linear VOR. For clockwise rotations, this secondary linear VOR increases the magnitude of the horizontal VOR when the subject is left ear down and decreases the magnitude of the VOR when the subject is right ear down. For counterclockwise rotations, this secondary linear VOR decreases the magnitude of the horizontal VOR when the subject is left ear down and increases the magnitude of the VOR when the subject is right ear down.

To test these hypotheses, 4 human subjects were rotated in yaw about an earth-vertical axis (200 °/s CW or CCW velocity trapezoids, 150 s duration, 2 s

acceleration/deceleration times). Following the rotation, the subjects were quickly tilted (1.5 s duration) to a nose up, nose down, left ear down or right ear down orientation. Horizontal and vertical eye movements were measured binocularly using infrared video methods. A brisk post-rotatory horizontal VOR lasting 40-60 s was elicited. The primary linear VOR component was identified by subtracting the post-rotatory horizontal slow phase eye velocity during the nose-down condition from the nose-up condition for each direction of rotation (divided by 2). The secondary linear VOR component was identified by subtracting the post-rotatory horizontal slow phase eye velocity during the left ear down condition from the right ear down condition for each direction of rotation (divided by 2). These subtractions should be zero if no linear component was present. However all four subjects showed non-zero primary and secondary linear VOR components in the direction consistent with the predicted linear VOR responses. The primary linear VOR component reached an average peak velocity of about 15 °/s and decayed over a period of approximately 40 s with a small reversal. The secondary linear VOR component reached an average peak velocity of about 15 °/s and decayed over a period of approximately 20 s with no reversal. Since the secondary linear VOR component has approximately the same magnitude as the primary linear VOR component, this suggests that the central estimate of gravity is rotated significantly after a post-rotatory tilt following a 200 °/s rotation about an earth-vertical axis.

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