

#### **IV. VESTIBULO-SPINAL FUNCTIONS**

##### **VESTIBULOSPINAL MECHANISMS IN THE SQUIRREL MONKEY**

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This presentation is dedicated to the important and lasting contributions to our understanding of vestibulospinal anatomy and physiology made by our honorees, Ottavio Pompeiano and Victor Wilson. We restrict our attention here to the morphology of individual, second-order vestibulospinal neurons belonging to both the lateral (LVST) and medial vestibulospinal (MVST) tracts in the brain stem and cervical spinal segments in the squirrel monkey. Using intra-somatic and intra-axonal recording techniques, vestibulospinal neurons were identified by their short latency response to electrical stimulation of the VIIIth nerve in the anaesthetized animal; electric pulses applied to wires inserted i) in the rostral MLF between the IVth and IIIrd nuclei identified vestibulo-ocular collic (VOC) neurons and ii) in the ventral horn at lower thoracic levels identified the lumbosacral-projecting cells. After identification, the cells were labelled using biocytin. Within each group of vestibulospinal cells, the termination patterns on average share similar features, but there are interesting variations. For example, VOC cells have the greatest number of collaterals to brain stem nuclei, primarily precerebellar, and to the ventral horn. MVST cells target the upper, middle or lower cervical segments, or distribute collateral input along the entire cervical cord from C1 to C8. LVST cells travel a varied course to their targets in the ventral horn. Those traveling in the lateral funiculus issue medially directed collaterals, and those in the ventral funiculus issue dorsally directed ones. The anterior-posterior terminal field of a collateral of a LVST axon can cover an entire segment. Vestibulospinal cells can course in and out and back in to particular tracks, changing their termination pattern as they do so. For example, a cell entering the spinal cord in the ventromedial funiculus can provide collateral input to the upper cervical segments characteristic of MVST cells, then course through the spinal gray to the ventral funiculus and issue dorsally directed collaterals, including input to lamina IX, over several segments before returning to the ventromedial funiculus and issuing laterally-directed collaterals to the axon terminus in the lower cervical segments. Similarly, axons entering the cervical cord in the lateral funiculus can course through the spinal gray and assume a course in the ventromedial funiculus. LVST cells antidromically identified to reach the lumbar cord can be characterized as a straight channel, issuing collaterals neither in the brainstem nor the cervical segments. LVST and MVST cells studied in the same preparation can have overlapping terminal fields in the ventral horn. Targets of vestibulospinal axons, such as spinal accessory, splenius and semispinalis motoneurons, long proprio spinal cells, and central cervical nucleus cells have been identified and individually labelled. We will briefly discuss the morphological properties of the vestibulospinal neu-

rons with the firing behavior of antidromically-identified, second-order MVST and LVST cells in the alert monkey, that suggest the importance of both distributing specific labyrinth information to particular target sites and providing a general excitation to the entire cervical spinal cord.

## DO GRAVICEPTORS CONTROL THE BODY ORIENTATION AND/OR THE CENTER OF MASS POSITION?

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The gravity vector is a permanent constraint which influences the building of the body posture. It is primarily monitored by the otoliths, but also by a series of so called body graviceptors, the evidence of which being indirect. Among these body graviceptors, some are located around the kidney, whereas others are distributed along the body segments.

The question which will be analyzed here is the contribution of the graviceptors to the erect posture. Two alternative interpretations of the control of erect posture may be proposed. According to the one, the body axis or trunk axis is aligned with the vertical axis. Erect posture is then mainly determined by the body orientation with respect to space. According to the other, the variable controlled is the position of the center of mass with respect to the support base. Erect posture is then determined by the distribution of the body segment masses.

The question of the variable controlled during erect posture is still unsolved under normogravity condition, due to the presence of balance constraints. Investigations in microgravity with the feet fixed to the floor, offers the possibility to compare the trunk axis orientation and the positioning of the center of mass in absence of equilibrium constraints. It was shown that two parallel controls are present during erect posture, one for trunk orientation, the other for the positioning of the center of mass. There is a trend in microgravity for a forward inclination of the trunk and for a backward shift of the center of mass, indicating together with other experimental evidences that graviceptors play a role in both trunk orientation and center of mass positioning. In this presentation, the time course of the effect of gravity on body segments orientation and on body center of mass positioning will be discussed. The regulation of the center of mass position with respect to the support base during leg or trunk movement will also be compared in normogravity, and in microgravity where the equilibrium constraints are absent.

## NEW TECHNIQUES IN THE ANALYSIS OF POSTURE

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In this study we present new methods for improved data analysis of simultaneous multiple measurements of kinematics and stabilizing forces (and possibly



other variables) related to physiology of human postural dynamics. From experimental multivariate data we derive linear dynamic models of relationship among data. In evaluation, we focus on predictive accuracy, statistical inference properties and low model complexity. Another requirement is that the resultant multivariate model should be compatible with modeling by first principles. One promising approach is multivariable linear dynamic models estimated according to principles of subspace model identification - i.e. a recent trend in time-series analysis.

Each subject in a group of normal subjects ( $n=10$ ) was tested with eyes open and eyes closed with simultaneous but uncorrelated vestibular and proprioceptive stimuli in order to investigate contributions of individual sensory feedback loops. Kinematics and forces/moments were measured in three spatial dimensions. Statistical analysis was made by means of multi-input multi-output identification of a transfer function from stimuli to stabilizing forces of the feet and the resulting body position, the transfer function being compatible with a biomechanical model formulated as a stabilized segmented inverted pendulum subject to feedback of body sway and position. Models are supported by statistical validation tests (analysis of variance, Kolmogorov-Smirnov distribution test, residual autocorrelation, stimulus-residual covariance at  $p<0.05$ ) for all subjects tested. Predictive accuracy as measured by the predictive error-to-signal variance ratio for eyes closed conditions (mean 10.1%; variation range 2.8-20.8%) eyes open conditions (mean 6.7%; variation range 3.6-16.8%) represents a significant improvement of posturographic modeling.

Each individual model estimated is effective in predicting a healthy subject's response to new stimuli and to describe the interacting effects of stimuli on body kinetics. The proposed methodology responds to current needs for data analysis of multi-stimulus multi-response experiments.

## VESTIBULAR INFLUENCES ON HUMAN POSTURAL CONTROL IN COMBINATIONS OF PITCH AND ROLL PLANES

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Uni-directional rotations or translations of the support surface in the pitch plane represent the most conventional method employed by researchers to examine the influence of peripheral vestibular deficits on postural control. Significant reductions in amplitude of automatic balance corrections (120-220 ms) were observed in tibialis anterior, soleus and quadriceps muscles (Allum et al. JVR 4:1994) followed by excessive stabilizing reactions, particularly in paraspinal muscles. The timing and pattern of muscle responses to pitch perturbations were unaffected by bilateral vestibular loss. The purpose of the present study was to tax the postural control system of normal and bilateral vestibular loss patients in other directions with perturbations in multiple planes of pitch and roll combinations to verify and broaden the scope of understanding surrounding the role of the vestibular system

in initiating and modulating automatic postural responses in relation to the direction of the perturbation. 14 normal (20-35 yrs) and 5 bilateral loss subjects (32-46 yrs, no response to bithermal caloric irrigation and abnormally weak response to rotating chair  $80 \text{ deg/sec}^2$  accelerations) volunteered for the study. Each subject was randomly presented with 44 support surface rotations ( $50 \text{ deg/s}$ ,  $7.5 \text{ deg}$ ) through 8 different directions separated by  $45 \text{ deg}$  under eyes open and eyes closed conditions. Muscle activity from tibialis anterior, soleus, quadriceps and paraspinals were collected bilaterally, 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. Stretch reflex (40-100, 80-120 ms) and automatic balance correcting responses (120-220 ms) demonstrated a different muscle specific sensitivity to the direction of the perturbation. The direction of maximum activity in lower leg muscles was aligned just off-axis of the pitch plane, with maximum balance correcting activity oriented approximately  $180 \text{ deg}$  from maximum stretch responses. Maximum activity in paraspinal muscles were tuned to the  $45 \text{ deg}$  directions, with maximum balance correcting and stretch reflexes oriented at  $90 \text{ deg}$  to one another. No significant differences in amplitude modulation were observed for stretch related responses between vestibular-loss and normal subjects. A marked reduction in automatic balance correcting response amplitudes of tibialis and soleus muscles coincided with vestibular loss for all perturbation directions. Decreased balance correcting responses in vestibular-loss patients were accompanied by significantly lower A-P and M-L ankle torques between 160- 260 ms followed by significantly larger responses between 280-380 ms. Vestibular loss was also characterized by early increased magnitude of trunk pitch velocities and decreased trunk roll velocities with an extended delay to stabilization of trunk movement, particularly in the roll directions. Therefore, vestibular loss appears to have a profound influence upon muscular and biomechanical responses to unexpected perturbations in multiple directions. Accelerometer recordings from the head describe large linear-vertical and angular roll accelerations in response to pitch and roll movements of the platform respectively with latencies as early as 30 ms. We assume that with vestibular loss an inability to centrally integrate early head linear and angular acceleration information underlies changes observed in muscle response amplitudes and trunk instability. Maximum activity directions for postural muscles and directions of reaction torque vectors were not significantly different between normal and vestibular populations suggesting a non-vestibular origin for a directionally sensitive trigger of postural reactions. Instead, the distinct variation in amplitude of lower leg and trunk muscles between normal and vestibular patients suggests a modulatory role of vestibular organs for postural control.



## VESTIBULOSPINAL CONTROL IN PATIENTS WITH SOMATOSENSORY LOSS

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We tested the hypothesis that somatosensory loss can result in an increase of vestibulospinal sensitivity. Previous studies showed that responses to galvanic vestibular stimulation is increased during surface perturbations or voluntary movements, suggesting that sensitivity to vestibulospinal information for posture is higher when the surface is perceived to be unstable.

We tested this hypothesis in a series of experiments involving both control subjects and subjects with loss of somatosensory information due to diabetic peripheral neuropathy. Bipolar galvanic vestibular stimulation was applied to subjects who were standing on a force sensing platform, either on a fixed surface or on foam. Also, the galvanic stimulus was applied either during quiet stance or during a backward platform translation. The intensity of the galvanic stimulus was varied from .25 to 1 mA. The amplitude of the whole body CoP displacement in response to the galvanic stimulus was plotted as a function of stimulus intensity, and the slope of the resulting curve was determined for each individual. Higher slopes indicate a greater increase in postural sway for a given increase in galvanic current, and were interpreted as indicating greater sensitivity to vestibulospinal information. We also tested sensitivity to galvanic stimulation in a unique subject with total body somatosensory loss.

Higher sensitivity to vestibulospinal information (i.e., increased slopes) were found whenever the pattern of somatosensory information from the support surface was altered. First, patients with somatosensory loss in the feet due to diabetes showed higher slopes than normals when tested on a fixed support surface. Control subjects and patients with somatosensory loss standing on foam also showed increased galvanic response gains compared to stance on a fixed surface. Administering the galvanic stimulus to subjects standing on a moving support surface (i.e., during responses to backward platform translations) also increased galvanic sensitivity in controls and patients with somatosensory loss. The severity of the somatosensory loss in the feet as assessed by both nerve conduction velocities and clinical sensory testing correlated with the amount of the increased sensitivity to galvanic vestibular stimulation.

Responses to galvanic stimulation in the patient with total body somatosensory loss were quite different from either those of normal subjects or patients with somatosensory loss due to diabetic neuropathy, in which the sensory loss is confined to the feet. Whereas both normal subjects and patients with diabetic neuropathy sway to the side of the anode, the patient with total body somatosensory loss swayed to the side of the cathode. This patient had very poor balance, and she required 10% of her body weight to be supported by a harness during testing. Control subjects who were also tested with 10% of their body weight supported also responded to galvanic stimulation differently; they showed very little body

sway in response to the galvanic stimulation, but reported strong illusions of surface tilts toward the side of the cathode.

These results show that responses to a galvanic vestibular stimulus changes depending on the presence and the pattern of somatosensory information. Decreased somatosensory information, due either to neurological disorders or changes in the characteristics of the support surface produces higher vestibulospinal sensitivity. Also the results of the patient with total body somatosensory loss suggest normal somatosensory information is required for accurate interpretation of vestibular signals regarding body motion.

## ATTEMPTS TO QUANTIFY CONTINUOUS ADAPTATION IN HUMAN POSTURAL CONTROL

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Adaptation to various and changing demands and constraints are probable of utmost importance for the human postural control in every day life. It may even be hypothesised that decreased ability to adapt or delay of the process may result in severe postural problems.

To quantify the postural adjustments over time, normal subjects were investigated during perturbation of stance with two high intensity vibrators applying Pseudo-random stimulation toward the calf or the paraspinal neck muscles, eyes open vs. eyes closed. The responses were measured with posturography. The stimulus-response adjustments over time i.e. adaptation, were found to be almost identical for all test conditions, though the amplitude of the responses were smaller during eyes open conditions. To determine the response adjustments and thus the dynamics of postural control, a system identification methodology incorporating both step response and dynamic feedback components was developed. This methodology can be used to quantify both short-term stimulus response and postural adaptive adjustments when evaluating postural control performance.

The methods were then developed to determine the dynamic changes of postural control during the initial exposure of large perturbations of stance. The new methods use a system identification approach, which distinguishes between feedback control, adaptation of postural responses and adaptation to stimulus. This approach makes it possible to quantify motion dynamics and complexity, stimulus impact and adjustments of postural control. Hopefully, quantification of the different adaptive responses could be useful for diagnostic purposes, in evaluating treatment efficacy and patient progress in rehabilitation programs.

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## EVIDENCE FOR A SUPRA-MODAL VESTIBULO-SOMATOSENSORY CONTROL OF POSTURE

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There is general agreement that human control of upright posture normally is based on vestibular, somatosensory and visual cues. These sensory signals interact in the CNS in a complex way which still is not well understood to date. Evidence from psychophysical studies suggest that normal subjects stabilize their bodies in two steps. One step is to stabilize the body relative to the support, using almost ideal proprioceptive input ('up-channeling'). The second step comes into play when the support is moving in space; then, in addition, the kinematic state of the support is taken into account. This is achieved by using signals from the inertial sensors in the head (the vestibular system) and performing a coordinate transformation (in abstract terms) of them to the haptically perceived support, using proprioceptive signals which centrally are given the vestibular transfer characteristics ('down-channeling'). This concept allows to make a simple prediction for patients with loss of vestibular function as compared to normal controls: In a condition in which visual cues are not available or deliver unreliable input, one should be able to disclose that normals use both the down- and up-channeling, while patients only use the up-channeling. We searched for evidence of this concept and studied postural control in seven normal subjects and three vestibular loss patients.

Subjects stood on a motion platform that was tilted in the sagittal plane with an axis through the platform. Transient platform tilts with a dominant frequency of 0.2 Hz were applied in forward or backward direction, reaching an excursion of 1, 2, 4 and 8°, followed by a return to the primary (earth-horizontal) position. Visual cues were either absent (homogenous blue screen) or unreliable (a potentially moving artificial visual room generated with the help of a 3D projection system). In the latter conditions both normal subjects and patients showed only a small, but consistent modulation of their postural responses, which helped us to differentiate between active and passive responses. We recorded the 6 DoF upper trunk and hip positions (in some conditions also of the head) and the center of pressure (COP) position together with platform and visual room angles, and we derived in addition velocity values of these data.

Normal subjects had no difficulty in maintaining balance up to 8° tilt. They did so by zeroing body and COP velocity, thereby preventing large body and COP excursions in space. This active response occurred rapidly, i.e. shortly after an initial passive response which reflects body inertia as well as elastic and viscous forces. In addition, normal subjects tended to keep the upper trunk upright on the hip. Noticeably, there were instances with a clear active response, although the head almost remained stationary in space (head movement below vestibular threshold). We assume that normal subjects controlled posture in these instances with the help of a supra-modal signal of support motion in space derived from a combination of vestibular and proprioceptive signals, in line with our concept (see above).

Patients were able to maintain equilibrium with the 1, 2 and 4° tilt (with 8° they tended to fall). Following the initial passive response, they actively kept the body-to-platform angle approximately constant during the tilt, which led to body excursions close to the limits of stability (with 8° tilt it exceeded this limit). Only when coming close to the limits they developed a slow lean back towards the primary position. Thus it appears that patients stabilize their bodies primarily relative to the support, in line with our concept. We conclude furthermore that gravito-inertial somatosensory inputs appear to play some role for keeping the body within the stability limits, but their role is very limited, due obviously to low precision and poor dynamics.

Biomechanically, there is a clear asymmetry of the limits of stability in favor of the forward as compared to the backward tilt direction, due to the asymmetry of the foot (forefoot longer than heel). This fact was reflected in the data of both normal subjects and patients, in that the active responses which opposed the backward tilt came earlier and were more pronounced than those occurring with the forward tilt. We assume that this response asymmetry mainly reflects a learned behavior.

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#### FUNCTIONAL SYNERGIES OF NECK MUSCLES IMPLEMENTED BY SINGLE VESTIBULOCOLLIC AND RETICULOSPINAL NEURONS

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It has been tacitly assumed that each classical motor tract consists of private lines connecting a cell of origin to a single muscle, as a single motoneuron innervates a single muscle. This notion is no longer tenable, since intraaxonal staining has revealed that virtually all single long descending motor tract axons have multiple axon collaterals at different spinal segments and innervate multiple motor nuclei. These axons include axons in the cortico-, rubro-, vestibulo- and reticulospinal tracts. A given motor control signal may be economically distributed by way of a single neuron with divergent branches to multiple target sites that participate in coordination of muscles to produce a purposeful movement. The above findings further suggest that single motor tract axons with multiple spinal collaterals may play a part for selection of appropriate combinations of muscles (functional synergies).

In the present study we compared the innervation patterns of single vestibulospinal (VS) and reticulospinal (RS) axons over neck muscles, and discussed whether both systems may use the same functional synergies of neck muscles for control of head movements. Single VS and RS axons were intraaxonally stained with HRP after electrophysiological identification, and their axonal trajectories were reconstructed on serial sections. In the same preparations, motoneurons of different neck muscles were retrogradely labeled, and muscle groups innervated by single VS or



RS axons were investigated. Single VS axons receiving input from a particular semicircular canal had a homogeneous pattern of innervation of neck muscles, and there were three patterns of innervation, in which a group of neck muscles innervated by single VS axons was specific to their semicircular canal input. The innervation patterns of single RS axons were very similar to those of single VS axons. The present data provide the evidence of hard-wired neuronal implementation of functional synergies of neck muscles by single VS and RS neurons. In a redundant control system with many degrees of freedom like the neck system, where many muscles function at multiple joints to produce a particular head movement, this kind of multiple innervation of muscles by single motor tract axons may help decrease degrees of freedom in the system.

#### CONTRIBUTION OF THE CEREBELLAR ANTERIOR VERMIS TO THE GAIN AND SPATIOTEMPORAL PROPERTIES OF THE VESTIBULOSPINAL REFLEX: A BEHAVIORAL AND CELLULAR ANALYSIS

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Experiments were performed in decerebrate cats to investigate the role that the cerebellar cortex exerts on both amplitude and spatiotemporal properties of the vestibulospinal reflex (VSR).

In a first group of experiments, the multiunit EMG activity of the medial head of the forelimb extensor triceps brachii (TB) was recorded during wobble of the whole animal at 0.156 Hz, 10°, leading to stimulation of labyrinth receptors. With this procedure the direction of animal tilt was moved at a constant velocity over the 360° of the horizontal plane, both in a clockwise and counterclockwise direction. The sinusoidal modulation of the EMG activity during animal's wobble allowed to determine the muscle response vector, whose orientation corresponded to the direction of head displacement giving rise to the maximal EMG activity (preferred direction). In all the experiments the response vector of the TB was closely aligned with the transverse axis, pointing to the side-down direction. Unilateral inactivation of the cerebellar anterior vermis, following microinjection in one or two folia of lobule V of the GABA-A agonist muscimol (0.5 µl at 8 µg/µl saline), consistently and reversibly reduced in 20-40 min the amplitude of the EMG modulation of the ipsilateral TB to 46-80% of the control value, while only a small shift (~20°) of the direction of the response vector occurred, either nosewards or tailwards.

In a second group of experiments, the activity of 173 Purkinje (P)-cells located in the same corticocerebellar region was recorded during wobble stimulation. Most of the responsive units (117/143) were characterized by preferred directions which covered the whole extent of the horizontal plane. Moreover, all the possible response directions were found among units located within small areas of the explored corticocerebellar region.

The results obtained indicate that the P-cells of the cerebellar anterior vermis, which usually fired out of phase with respect to the vestibulospinal neurons (Denoth et al., *Pflügers Arch.*, **381**: 87-98, 1979), contribute positively to the amplitude of the VSRs. On the other hand, the observation that all the directions of animal displacement were represented within this neuronal population, explains why vermal inactivation greatly reduces the amplitude of the VSRs without producing prominent changes in their directional specificity.

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### CHARACTERISTICS OF HEAD MOVEMENTS IN MONKEYS AFTER BILATERAL SEMICIRCULAR CANAL PLUGGING

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Acute loss of semicircular canal sensory information leads to plane-specific instabilities in head and body posture that attenuates in a few days. We have measured spontaneous head movements in three macaque monkeys before and on day 1, 5, 7, 9, 32 and 105 after semicircular canal plugging. One animal had the right anterior and left posterior canals plugged (RALP), the other two animals were plugged in all vertical canals. Head position in space was recorded with nine head-mounted, pulsed LEDs (OPTOTRAK 3020). Translational and rotational head velocity was expressed in space-fixed and head-fixed coordinates, in order to compare the spatial characteristics of head movement instabilities with the orientation of the canals.

Using principal component analysis, we found predominantly horizontal head rotations along a (space- and head-) vertical axis in the intact animal. Plugging of the canals in the RALP plane led to increased head velocities (both translational and rotational) in the direction of that plane. Plugging of all vertical canals resulted in a backward head tilt of about 15° that gradually decreased. The predominant head rotation axis remained space-vertical. Corresponding head velocity amplitudes were increased in one, but unchanged in the other of the two all-vertical-canalplugged animals. Head velocity direction and amplitudes returned to pre-operative controls by post-op day 9 in the RALP animal and by post-op day 32 in the animals with all vertical canals plugged.

These findings indicate that canal-specific loss of angular head movement information leads to head instability in the direction of the lost canals. The faster normalization of instability in the RALP animal suggests that the remaining canals participate in the compensation for the lost canals.

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## EFFECTS OF WALKING VELOCITY ON VERTICAL HEAD AND BODY MOVEMENTS DURING LOCOMOTION

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Walking induces head oscillations that elicit ocular stabilization movements relative to the surround. We examined the relationship between vertical head translation, pitch rotation of the head, and pitch trunk rotation as a function of gait velocity. The aim was to determine the mechanisms for maintenance of head orientation while walking at different velocities. Subjects (26-44 years old) walked on a linear treadmill at velocities of 0.6 to 2.2 m/s. The head was modeled as a rigid body, and its rotation and translation were determined in space coordinates using a video-based motion analysis system. For walking velocities within 1.2 -1.8 m/s, which was an optimal walking range, amplitudes of head vertical translation and pitch rotation increased linearly with walking velocity and were highly coherent. The dominant frequency of head vertical translation was linearly related to gait velocity, and varied in a narrow frequency band between 1.8-2.2 Hz. To maintain this range, subjects tended to increase their stride length rather than step frequency to walk faster. Outside the optimal walking range, frequency of head translation rose to 2.5 Hz in conjunction with stepping frequency, but coherence between head pitch and vertical translation deteriorated. While vertical translation of the head had a spectral composition which was closely linked to stepping frequency over all walking velocities and the waveforms were highly coherent, head pitch was no longer related to vertical head translation at low walking velocities (below 1.0 m/s). Rather, it was more closely linked to trunk rotation. The coordination between the head and trunk stabilized head angular position in space within a few degrees. During moderate to fast walking, head rotation in space increased and compensated for increased vertical translation. The results suggest that there are two mechanisms that maintain head orientation and its pointing direction relatively invariant over a wide range of walking speeds. For slow walking, the trunk rotation is dominant and the head rotation relative to the trunk compensates for the trunk to maintain the appropriate pointing direction of the head in space. As walking velocity increases, trunk rotation remains approximately invariant, but a significant head translation develops. This induces head rotation in space, which maintains the head pointing direction in space approximately invariant. From consideration of the frequency characteristics of the compensatory head pitch rotation, we infer that it is produced by the linear vestibulo-collic reflex (IVCR).

## NON - LINEARITY AND ADAPTATION IN THE HEAD-NECK SYSTEM

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Previous studies indicated that reflexes controlling head stabilization could

contribute nonlinearities to human head-neck system at small input amplitudes. To uncover these potential nonlinearities, we have used pseudo-random stimulus waveforms that produced trunk acceleration amplitudes ranging over 20-200 deg/sec<sup>2</sup> root-mean-square (RMS). Each waveform consisted of four sine components scaled to have the same acceleration. These stimuli collectively covered a 0.2-10.0 Hz frequency range. Subjects were rotated about the vertical axis in a servo-controlled chair and performed mental arithmetic in the dark. Head and trunk motions were recorded using angular velocity sensors.

The vertical-axis components of head rotation responses did not have significant distortion and were fitted well by a 2nd-order transfer function with a damping ratio and other parameters. However, the damping ratio increased systematically with stimulus amplitude, indicating a "hidden" nonlinearity. Below is a simple model that explains these results.

The vestibulo-collic reflex (VCR) is represented by the vestibular feedback loop around a 2nd-order "plant", labeled Nonvestibular Dynamics. Plant dynamics are characterized by "open-loop" damping ratio (D) and natural frequency (W) parameters. Since D is on the order of 0.05, the plant is quite underdamped. Damping is increased by the rate feedback arm of the VCR, which consists of the differentiator (s), lead time constant (T) and threshold nonlinearity (Dead Zone). The arm represents a phase-advanced signal presumably originating in high-threshold, irregular canal afferents. The distortion contributed by the threshold is not reflected by the output since the plant acts as a low-pass filter. Thus for any fixed stimulus amplitude, the system appears linear, and the nonlinear feedback arm in the model can be replaced by a transfer function, (T's+1), where T' is an amplitude-dependent time constant.

We have been studying short-term adaptation of head-neck system to reduced plant damping induced by a 5-fold increase in the head moment of inertia. If closed-loop damping is determined by VCR rate feedback, larger stimuli should be more effective in eliciting adaptation. This hypothesis is supported by our data.

These findings indicate that dynamics and adaptation of the head-neck system is a function of stimulus amplitude. This is most likely due to internal nonlinearities. Supported by NSBRI, Clayton Foundation for Research and DC01913.

## HEAD STABILIZATION MECHANISMS ARE RESPONSIVE TO MORPHOLOGICAL CONSTRAINTS

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Past work on stabilization of the head has treated the neck as though it were a single joint between the trunk and head (Keshner and Peterson, 1996; Peng et al., 1996; Viviani and Berthoz, 1975). But the neck is actually a flexible, multisegmental spine, with multiple degrees of freedom for motion (Keshner et al., 1997). We have directly measured motion between the head and neck and the trunk and neck through videoanalysis (Pattin et al., 1997). Markers were placed on the head, neck,



and trunk of four seated subjects, and videoanalysis employed to determine the extent of motion about the two primary cenical axes (C1-Skull; C7 T1). We recorded dynamic head motions resulting from  $\pm 10^\circ$  position ramps ( $60^\circ/\text{s}$ ), with static holding periods between ramps, in the sagittal plane at the interaural axis. The trunk was fixed to the chair so that trunk motion reflected the input stimulus, and rotations occurred in the dark. Subjects performed mental arithmetic to minimize voluntary influences. Three repeatable response strategies emerged. Subjects exhibited angular rotation at both the upper and lower cenical spine, thereby producing a counter-rotation of the head to the trunk. Or, they locked either the upper or lower cenical spine so that the head appeared to move with the neck or the neck to move with the trunk, respectively. Consistency in the pattern of response across trials for each subject within a given ramp direction suggests that individual selection may determine the contributions of the two cervical axes to head motion.

Peng et al. (1996) claim that mechanical properties of soft tissue (inertia, stiffness and viscosity) dominate the control of horizontal head stabilization. When a 2nd order model was fit to head-free oscillation in the vertical plane (Li et al. 1997), the free vibration responses of the model were in good agreement with the observed head oscillation of most subjects, regardless of perturbation direction or initial body position in space, thus supporting the hypothesis of a response dominated by system mechanics. But, although the fit to the model was similar for both healthy and labyrinthine deficient subjects, healthy subjects also exhibited trials which were not well fit by the model. This would suggest that another control mechanism, presumably neurally generated (i.e., VCR, CCR, voluntary actions), was contributing to the response.

We used optimization methods to fit the mathematical model of Peng et al. (1996) to our experimental data in order to predict how neural control mechanisms were affected by changes in head-neck mechanics. To examine the relative influences of the mechanical and neural properties of the neck to head stabilization, the mathematical model has been fitted to data in which the mechanical properties of the system have been shifted either through active stiffness or increased inertia. Healthy human subjects were rotated in the horizontal plane in darkness while performing mental arithmetic to minimize voluntary influences. Head angular velocity responses were measured with both an unweighted and weighted head. For the weighted paradigm, head inertia was doubled using a 10 lb sandbag strapped to the subjects head

With increased inertia, our model predicts substantial changes in head movement from the unweighted paradigm. However, experimentally measured head movement changed relatively little in this situation, implying compensation by neural controllers to maintain constant head response dynamics. Optimal model fits accounted for 85-96% and 94-98% of the experimental response variances in the unweighted and weighted paradigms, respectively. In both paradigms, viscosity and CCR gain were best fit by 0. But stiffness and VCR gain increased significantly in the weighted as compared to the unweighted responses. Our results

suggest that healthy subjects have the ability to adjust neck stiffness and VCR gain to maintain constant head dynamics despite large changes in head mechanics, and that CCR and viscosity play an insignificant role in yaw head stabilization.

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### CEREBELLAR PATIENTS CAN MAKE ANTICIPATORY HAND AND EYE MOVEMENTS TO TRACK MOVING TARGETS, BUT THEIR VELOCITY CONTROL IS DEFICIENT

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The role of the cerebellum in the control and planning of voluntary movements has been investigated using an eye-hand tracking task. With the approval of the local ethics committee, we compared the performance of 5 cerebellar patients and 8 healthy control subjects. The patients had degenerative cerebellar lesions but had no extracerebellar pathology affecting the eyes or hand.

Subjects were seated in a darkened room with head fixed at the centre of a semicircular screen (radius 1.5 m), on to which a horizontally moving white target was projected via a motor-driven mirror. Eye position was measured using infra-red oculography. The subject's hand was placed in a low impedance manipulandum in a semi-pronated position. Wrist rotation about a vertical axis was measured by a potentiometer and the signal was used to drive a green cursor horizontally on the screen. Subjects were required to track the target with the cursor. Three stimuli were used; the first consisted of a continuously illuminated sinusoidal target moving sinusoidally at 5 discrete frequencies (range 0.20 Hz - 1.56 Hz). The second and third stimuli were intermittently illuminated ramps presented at regular intervals. Such stimuli have previously been shown to be an effective means of producing anticipatory eye movements prior to target onset. The target passed through the centre of the screen midway through each presentation period. Both the target and cursor were illuminated simultaneously for either 480ms (stimulus 2) or 240ms (stimulus 3). In stimulus 2 four target velocities (16 - 64 °/sec) were explored in separate sectors with an interpresentation interval of 1.51s. In stimulus 3 the target velocity was maintained at 40°/sec, but the inter-presentation interval varied from 0.96 - 3.73 s.

In the sinusoidal tracking task (stimulus 1) both groups showed the expected trends with increasing frequency, i.e. a decrease in gain and increase in phase lag for hand and eye displacement and for the smooth component of eye velocity. However, ANOVA revealed that the cerebellar group showed a significantly greater decrease in the gain of the response ( $p=0.006$ , eye and hand) and an increase in phase lag for the hand ( $p=0.045$ ) compared to the control subjects.

In the intermittent ramp tasks of stimulus 2, both control subjects and cerebellar patients were able to produce eye and hand movements prior to target onset. The magnitude of this anticipatory movement (V100) was assessed by measurement of the velocity 100ms after target onset, i.e. just prior to the influence of visual



feedback. In the controls V100 increased in proportion to target velocity and was thus truly predictive, but in the cerebellar patients, it was poorly scaled and significantly less than in the controls for both eye and hand ( $p < 0.001$ ).

Stimulus 3 allowed the timing of the anticipatory responses to be investigated for differing inter-presentation intervals (ISI). As ISI increased the time of movement onset prior to target onset also increased for both groups with the onset of the response showing greater variability for the longer intervals and in the Cerebellar group. A significant difference in the time of movement onset ( $p=0.001$ ) between the 2 groups was evident in response to the longer inter-stimulus intervals ( $>2s$ ), when the Cerebellar subjects often responded around or after target onset. The cerebellum has often been associated with the control of timing and this impairment in timing of anticipatory responses may be a reflection of this role. Thus, cerebellar patients could still make anticipatory movements, but could not scale them appropriately or time them correctly over long.