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## *II. HIGH FUNCTIONS*

# OCULAR TILT, POSTURAL ASYMMETRY, VESTIBULO-OCULAR DISORDERS, AND PERCEPTUAL DEFICITS RELATED TO ASYMMETRIES IN VESTIBULAR ORGANS ORIENTATION.

D. ROUSIÉ[1], J.C. BAUDRILLARD[2], J.C. HACHE[1], P. PELLERIN[1], P. VAN TICHELEN[1] AND A. BERTHOZ[3]

*[1]Centre Hospitalo-Universitaire, Lille, France, [2]Centre Hospitalo-Universitaire, Lens, France, et [3]Laboratoire de Physiologie de la Perception et de l'Action, CNRS Collège de France, Paris, France*

This study was prompted by the observations of systematic complaints by patients suffering from facial asymmetries of postural anomalies, deviations of the eyes, deficits in the perception of the vertical and horizontal and also occasional reports of spatial disorientation during navigation in outdoors environments. A first population of 90 patients have been subjected to magnetic resonance ( MRI) imaging of the head using the method of reference developed by Baudrillard and Rousié (1995). Another population of 250 patients was subjected to a systematic identification of the clinical signs. Functional central and peripheral acuity was measured and vision was also explored with classical tests: synoptophore, slit lamp, retinal correspondence and finally measure of ocular tilt with a laser scanning opthalmoscope. Postural deficits have been assessed by several techniques: X rays of the rachis; Fukuda test, and measurement of the deviations of head, trunk and limb posture by video computerised technique (VICON) both during static posture and locomotion; and vertical deviation of the finger position with respect to the horizontal. Vestibuloocular function was tested by video-nystagmo-oculography. The MRI scanning has revealed in all subjects an asymmetry of the anterior base of the skull with asymmetries of the orbits and/or an asymmetry of the two posterior hemibases which contain the vestibular organs. The semicircular canals and otoliths had either positional or orientational asymmetries.

LSO test revealed an exo-cyclotorsion (2 to 9 degrees) in the left eye in 85% of cases. Visual acuity test have revealed a curvature astigmatism in 75% of cases in the same eye as the one exhibiting exo-cyclotorsion.

In 95% of cases the X ray examination has revealed the presence of a general scoliotic postural bias or of a true lumbar scoliosis associated with a head tilt in roll. The head is tilted to the opposite side to the lumbar convexity and reflects an ipsilateral mucular hypotonia. In 75% of cases the lumbar convexity is to the left and the head tilt is to the right in accordance with a right side mucular hypotonia. Fukuda test shows a deviation of the direction of the body during blind walking in place to the opposite side to the dominant head tilt. The test of the subjective horizontal with the finger pointing task has shown a downward bias of the position of the right finger ipsilateral to the head tilt. This bias is not due to a lowered shoulder but to a true deviation of the direction of pointing.

The measurement of the surface and of the centre of gravity projection indicated significant deviations.

Video-nystagmography during horizontal rotation in the dark has revealed more variability than the other tests. The head shaking tests was abnormal in 65% of the cases, and the postrotatory test indicated a right side functional deficit as in the other tests.

We tried to correct for the motor and perceptual biases by prisms placed on the two eyes. Two prisms of 2 dioptries (Press on from 3M) have been placed on both eyes on standard glasses. For example for a left eye torsion the edges of each prisms have been placed vertically towards the right. Significant improvements in all deficits was obtained following prismation thus providing a clinical method for compensating the vestibular asymmetries and argument for interpretations of the underlying mechanisms. These results will be discussed also in the frame of the theory proposed by Diamond and Markham concerning the origin of space sickness.

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## CHARACTERISATION OF SYSTEMATIC AND RANDOM ERRORS IN ROLL-TILT ESTIMATES OBTAINED WITH THREE DIFFERENT PARADIGMS

J.A.M. VAN GISBERGEN AND A.D. VAN BEUZEKOM
*Medical Physics and Biophysics, University of Nijmegen, Nijmegen, The Netherlands*

Roll-tilted subjects make considerable systematic errors in estimating the subjective visual vertical (SVV) but seem rather better informed about their body orientation in space. If that is the case, errors in the SVV task do not simply reflect imperfect body-orientation signals but may incorporate tilt-dependent properties of the spatial-vision system that is used as the indicator in the SVV task. Such factors may include the effects of uncompensated eye torsion and the proposed effect of the idiotronic vector in the theory developed by Mittelstaedt (*Naturwissenschaften*, **70**: 272-281, 1983). In order to get more insight into the question of what causes the large systematic errors in the perception of verticality it is of interest to explore the use of alternative paradigms.

In the present experiments, we have used the oculomotor system as a nonvisual alternative indicator of internal tilt-related signals. To assess the subjective oculomotor vertical and horizontal (SOV and SOH, respectively), subjects were asked to make appropriately aligned voluntary eye movements. In other experiments, the SVV was measured using the luminous- line method. Subjects were also asked to verbally report their estimated body orientation, using a clock scale. These measures were obtained in complete darkness for 36 tilt angles covering the entire range of 360 deg, each trial starting from the upright position.

A principal-component analysis of the SVV responses from all five subjects revealed that the errors from each individual could be described as a combination of a scaled tilt-dependent basis function (the first principal function), common for all subjects, and a tilt-dependent random noise term. The weight of the basis function varied considerably among subjects but the amount of residual noise was

quite constant. The shape of the SVV basis function, which represents the tilt-dependent pattern of systematic errors, showed a very clear A-effect but virtually no E-effect. The same analysis applied to the oculomotor-pointing data showed similar patterns. Remarkably, while the SOH basis function closely resembled the shape of the SW function, the SOV function was different in showing a clear E-effect, along with an A-effect (cf. Pettorossi et al., *Exp. Brain Res.*, 1998, in press). Finally, analysis of the body-orientation perceptual data demonstrated relatively smaller errors with a weak A-effect. Judged from the perspective of the idiotropic vector theory, developed on the basis of SVV experiments, our data indicate that this mechanism is equally expressed in oculomotor gravity pointing. The finding that the systematic errors of our subjects could be described, in first approximation, as scaled versions of an invariant function deserves further attention. From the idiotropic theory, one rather expects the shape of the systematic-error function to depend on its magnitude: Clear E-effects are predicted in the subjects with the smallest A-effect but none in individuals with a large A-effect. Such a linkage of A- and E-effects is not what we saw: irrespective of whether the A-effect was large or small, the E-effect was notably absent in our SVV data. In our oculomotor data, the E-effect was only visible in the subjective vertical task. Since the E-effect was absent in the subjective visual vertical (as well as in the subjective oculomotor horizontal data), we propose that its occurrence in the oculomotor vertical task may represent a peculiarity of the oculomotor pointer which requires further investigation.

## RECIPROCAL INHIBITORY VISUAL-VESTIBULAR INTERACTION: VISUAL MOTION STIMULATION DEACTIVATES THE PARIETO-INSULAR VESTIBULAR CORTEX

T. BRANDT[1], P. BARTENSTEIN[2], A. JANEK[2] AND M. DIETERICH[1]

*[1]Department of Neurology, Ludwig-Maximilians-University, Klinikum Grosshadern, Münich, Germany, and [2]Department of Nuclear Medicine, Technical University, Münich, Germany*

The vestibular system - a sensor of head accelerations - cannot detect self-motion at constant velocity and thus requires supplementary visual information. The perception of self-motion during constant velocity is completely dependent on visually induced vection (linearvection; circularvection, CV). CV is induced by large-field visual motion stimulation during which the subject perceives the actually moving surroundings as being stable, while he is being moved. To determine the unknown cortical visual-vestibular interaction during CV, we conducted a PET activation study on CV in 10 human volunteers (Brain, 1998). The PET images of activated cortical areas during motion stimulation without CV were compared to those with CV. Hitherto, CV was explained neurophysiologically by visual-vestibular convergence with activation of the vestibular nuclei, thalamic subnuclei, and the vestibular cortex. If CV were mediated by the vestibular cortex, one would expect that an adequate visual motion stimulation would activate both the visual and the vestibular cortex. Contrary to this expectation, it was shown for the first time that

visual motion stimulation with CV not only bilaterally activates a medial parieto-occipital visual area separate from MT/MST, but simultaneously deactivates the parieto-insular vestibular cortex. There was a positive correlation between the perceived intensity of CV and relative rCBF changes in parietal and occipital areas. These findings support a new functional interpretation: reciprocal inhibitory visual-vestibular interaction as a multisensory mechanism for self-motion perception. Inhibitory visual-vestibular interaction might protect visual perception of self-motion from potential vestibular mismatches caused by involuntary head accelerations during locomotion and would allow the dominant sensorial weight during self-motion perception to shift from one sensory modality to the other.

## PERCEPTION OF ANGULAR VELOCITY IN NORMAL SUBJECTS AND PATIENTS WITH EXCESSIVE OR REDUCED EYE MOVEMENTS

A.M. BRONSTEIN, L. CASSIDY, E. GRUNFELD, T. OKADA AND J. SHALLO-HOFFMANN

*MRC Human Movement and Balance Unit, National Hospital for Neurology and Neurosurgery, Queen Square, London, UK*

A technique is described to assess vestibular sensation. The two main goals of the study were 1) to compare the perception of angular velocity with the eye velocity output of the vestibulo-ocular reflex and 2) to study vestibular sensation in patients with congenital nystagmus (CN; 'excessive eye movements') and severe ocular myasthenia gravis (MG; 'reduced eye movements'). Subjects indicated their perceived angular velocity by turning the wheel of a tachogenerator. The vestibular stimuli used consisted of sudden deceleration from rotation at a constant horizontal velocity of 90 deg/s ('stopping' responses) in the dark. Eye movements were recorded with electro-oculography (E.G.). In normal subjects the perceived angular velocity decayed from the moment of deceleration with an exponential waveform. The mean duration of sensation was 32 s with a time constant of decay of 16 s. Eye movement velocity decayed with a similar exponential trajectory (duration 38 s, time constant 16 s). Both perceptual and eye velocity responses were slightly but significantly reduced by repeated rotations and by prolonged optokinetic stimulation (habituation). CN and MG patients showed vestibular sensation time constants reduced by approximately 50 and 40% respectively. The following conclusions can be drawn. I) The similarity of the eye velocity and perceptual responses suggests that these two systems receive a similarly processed vestibular signal; II) the time constant of the responses indicate that this vestibular signal probably originates in the same brainstem, 'velocity storage' integrator; III) The technique described is useful for clinical assessment of vestibular function, particularly in patients with ocular motility disorders; IV) Habituation of vestibular sensation can be induced by vestibular and optokinetic stimulation; IV) Patients with CN and MG have abnormal vestibular processing; this is probably due to changes in the velocity storage brought about by the persistent retinal image slippage present in these patients.

## GALVANIC STIMULATION AT MASTOID LEVEL ACTIVATES CORTICAL VESTIBULAR, AUDITORY, AND NOCICEPTIVE AREAS (A FMRI STUDY)

M. DIETERICH, S.F. BUCHER, M. WIESMANN[1], A. WEISS, R. ZINK, T.A. YOUSRY[1] AND T. BRANDT

*Departments of Neurology and Neuroradiology[1], Ludwig-Maximilians-University, Münich, Germany*

Experimental vestibular stimulation is obtained by using caloric irrigation or galvanic stimulation at mastoid level. Caloric irrigation involves only semicircular canal function, while galvanic stimulation involves semicircular canal and otolith function. Anodal stimulation of the mastoid at low current intensities of 1-3 mA elicits ipsiversive tonic ocular torsion of up to 5.4°, and a tilt of the peripheral visual field of 1-9°, without additional nystagmus. These ocular motor and perceptual effects reflect otolith stimulation.

Our interest in experimental activation of the vestibular cortex prompted the following investigation of cerebral activation with functional MRI during galvanic stimulation of the mastoid in six right-handed healthy volunteers. Since galvanic stimulation also elicits moderate pain, cutaneous stimulation at neck C4/C5 level served as a control to differentiate between brain activation patterns caused by pain and those mediating vestibular function. During mastoid stimulation bilateral vestibular activation occurred in the posterior insula - the human homologue of the monkey parieto-insular vestibular cortex (PIVC) - and the thalamic pulvinar. Furthermore, auditory activation was observed in the transverse temporal (Heschl's) gyrus without accompanying acoustic sensations. The cutaneous pain simultaneously elicited by galvanic stimulation caused bilateral activity of separate areas in the medial part of the insula and the anterior median thalamus. Thus, galvanic stimulation at the mastoid level activates three different sensory systems with distinct locations in the insula-thalamic region: the vestibular, auditory and nociceptive system.

## FUNCTIONAL MRI OF GALVANIC VESTIBULAR STIMULATION

E. LOBEL[1,3], J.F. KLEINE[2], A. LEROY-WILLIG[3], D. LE BIHAN[3], O.-J. GRUSSER[2] AND A. BERTHOZ[1]

*[1]Laboratoire de Physiologie de la Perception et de l'Action, Collège de France, Paris, France, [2]Department of Physiology, Freie Universität, Berlin, Germany, and [3]Service Hospitalier Frédéric Joliot, C.E.A., Orsay, France*

The cortical processing of vestibular information is not hierarchically organized as the processing of signals in the visual and auditory modalities. Anatomical and electrophysiological studies in the monkey revealed the existence of multiple interconnected areas, in which vestibular signals converge with visual and/or somatosensory inputs. Althongh recent functional imaging studies using caloric vestibular stimulation (CVS) suggest that vestibular signals in the human cerebral cortex may be similarly distributed, some areas which apparently form essential constituents of the monkey cortical vestibular system have not yet been identified in humans.

Galvanic vestibular stimulation (GVS) has been used for almost 200 years for the exploration of the vestibular system. By contrast with CVS, which mediates its effects mainly via the semicircular canals (SCC), GVS has been shown to act equally on SCC and otolith afferents. Since the magnitude and temporal evolution of the galvanic stimuli can be precisely controlled, GVS is ideally suited for the investigation of the vestibular cortex by means of functional imaging techniques.

We studied the brain areas activated by sinusoidal GVS using functional magnetic resonance imaging (fMRI). An adapted set-up including LC-filters tuned for resonance at the Larmor frequency protected the volunteers against burns throngh radiofrequency pickup by the stimulation electrodes. Control experiments ensured that potentially harmful effects or degradation of the functional images did not occur.

Six male, right-handed volunteers participated in the study. In all of them, GVS induced clear perceptions of body movement and moderate cutaneous sensations at the electrode sites. Comparison with anatomic data on the primate cortical vestibular system and with imaging studies using somatosensory stimulation indicated, that most activation foci could be related to the vestibular component of the stimulus.

Activation appeared in the region of the temporo-parietal junction, the central sulcus and the intraparietal sulcus. These areas may be analogous to areas PIVC, 3aV and 2v, respectively, in the monkey brain, which form the 'inner vestibular circle' (Guldin et al., *J. Comp. Neurol.*, **326**: 375-401, 1992) of the cortical vestibular system. Activation also occurred in premotor regions of the frontal lobe. Although undetected in previous imaging-studies using CVS, involvement of these areas could be predicted from anatomic data showing projections from the anterior ventral part of area 6 to the inner vestibular circle and the vestibular nuclei.

Using a simple paradigm we showed that GVS can be safely implemented in the fMRI environment. Manipulating stimulus waveforms and thus the GVS-induced subjective vestibular sensations in future imaging studies may yield further insights into the cortical processing of vestibular signals.

## VESTIBULAR CAPTURE OF SELF MOTION

L. HARRIS, M. JENKIN AND D. ZIKOVITZ
*Depts Psychology, Computer Science and Biology, York University, Canada*

When we move around the world there are a number of cues available that can potentially be used to update our knowledge of our position in space. Here we assess the relative contributions of visual and vestibular information to the perception of linear displacement.

Physical motion and visual motion were dissociated both in amplitude and direction by moving subjects passively on a cart while presenting visual motion throngh a carefully-calibrated virtual reality system. The cart was moved at constant acceleration (0.07-0.7m/s/s). Subjects wore a virtual reality helmet (field of

view: 84°x 65°) in which motion along a corridor (2m x 2.5m x 50m) was simulated. The walls of the corridor were textured with dynamically-varying features to limit the subject's ability to track fixed points. Motion could be either (i) vestibular only (dark), (ii) visual motion only (arranged to match vestibular only), (iii) both motions in the same direction and of the same amplitude, (iv) both motions in the same direction but of different amplitudes and (v) both motions of the same amplitude but in different directions. Subjects indicated when they felt they had gone throngh a given distance. Target distances were presented beforehand either by providing a virtual, visual target or by physically moving the person through the target distance.

When subjects were physically moved in the dark, they accurately estimated when they had passed throngh a distance previously presented by physical motion. When they were presented with visual movement alone, they accurately estimated when they reached the position of a previously-presented visual target. However, when estimating when they had physically moved to a previously-presented visual target, subjects grossly overestimated their self motion, feeling that they had reached the target much too early. Surprisingly, this overestimation persisted when both physical and visual cues were presented . The presence of simultaneous visual motion had little effect on the perceived amplitude of self motion which seemed to be determined almost exclusively by the amplitude of the physical motion.

When visual and physical motion were in different directions, the *amplitude* of the perceived motion depended on the vector of the physical motion in the direction of the visual motion. The perceived *direction* of self motion followed the visual cue.

We conclude from these experiments that the amplitude of physical motion provided by nonvisual systems, especially the vestibular system, captures the visual system in determining the amplitude but not the direction of self motion.

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## PARIETAL RECEPTIVE FIELD SHIFTS EVOKED BY SLOW EYE AND HEAD MOVEMENTS

M.E. GOLDBERG, A.Z. ZIVOTOFSKY AND K.D. POWELL
*Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health, Bethesda, MD 20892, USA*

Neurons in the lateral intraparietal area (LIP) have visual receptive fields related to a specific area of the retina when studied in a fixation task. However, immediately before a saccade the receptive fields often shift, so that a stimulus that appears briefly outside the classic receptive field will excite a neuron when a saccade brings the spatial location of the now-vanished stimulus into the fixation receptive field (Duhamel et al., 1992). In these experiments we extended this observation to slow gaze shifts evoked by smooth pursuit and the suppression of the vestibuloocular reflex.

Monkeys were trained to perform memory-guided saccades, smooth pursuit, and

to suppress their vestibuloocular reflex by fixating a spot that moved with them during whole body rotation. On some trials they had to make a saccade to a stimulus that flashed before the epoch of pursuit or rotation. Neurons were studied using these tasks. When a stimulus flashed outside the receptive field and the slow gaze shift brought the spatial location of the now-vanished stimulus into the receptive field, LIP neurons often responded as if the stimulus were still there. This activity did not depend upon the monkey's making a saccade to the stimulus. Althongh most of the neurons responded in association with both VOR suppression and smooth pursuit, some responded to either one or the other, suggesting that the cortical signals for smooth pursuit and VOR suppression are not identical.

Humans viewing a dot moving horizontally across a vertically moving flow field perceive the dot to be moving diagonally, with the vertical component of perceived motion opposite the flow field. When they pursue the stimulus, their eye movements are accurate, although they perceive that their pursuit trajectory is also diagonal. However, when they make saccades to targets flashed at the beginning of the pursuit trajectory, their saccades are inaccurate, as if the subjects compensate for the perceived eye movement instead of the actual eye movement (Zivotofsky et al., 1996).

Monkeys make similar inaccurate saccades to targets flashed before an epoch of smooth pursuit orthogonal to a flow field. Neurons recorded in LIP reflect this perceptual distortion: when the sum of pursuit and perceptual distortion moved the spatial location of the vanished stimulus into the receptive field, the neurons responded. This occured even if the same pursuit trajectory without the flow field failed to move the spatial location of the stimulus into the receptive field, in which case the cells did not discharge. These results suggest that LIP neurons use vestibular, oculomotor, and perceptual signals to determine the spatial location of visual stimuli.

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## VISUAL-VESTIBULAR INTERACTION IN PRIMATE PARIETAL CORTEX

W. GRAF, F. BREMMER, F. KLAM, S. BEN HAMED
AND J.-R. DUHAMEL
*Lab. Physiologie de la Perception et de l'Action, CNRS - Collège de France, 75231 Paris Cedex 05, France*

Self-motion detection is the end product of multisensory interactions involving visual, vestibular, somatosensory and other cues. Since the parietal cortex is thought to play an important role in motion analysis, we quantified neuronal responses in the ventral-intraparietal area (VIP) during visual and vestibular stimulation.

Single cell responses were recorded extracellularly in two awake and head-fixed macaque monkeys (Macaca mulatta and Macaca fascicularis) who were trained to perform a fixation task. Visual stimuli and the fixation target were back-projected onto a translucent tangential screen. Vestibular stimuli were delivered by vertical axis (horizontal) rotation of a turntable either in total darkness or in light. An LED,

fastened to the turn-table, was used to test a given neuron's response under VOR suppression conditions.

About 40% of all recorded neurons (n=110) had vestibular sensitivity. Visual receptive fields were large, often covering more than an entire hemifield. Vestibular responses were in phase with head velocity and could signal position . Most cells carried two or more head rotation parameters, while a few coded only a single signal dimension, either velocity or acceleration. Associated optokinetic responses were always direction selective. However, preferred directions for vestibular and optokinetic activation were always non-complementary. i.e., the preferred direction of a visual stimulus was in the same direction as the vestibular on-direction, althongh the visual world typically moves on the retina in the opposite direction to a given head movement. In essence, this response pattern is geared to generate a sensory conflict situation.

Visual and vestibular on-directions were either to ipsilateral (with reference to the recording site), or to contralateral. Sensitivity to vestibular stimulation conld be high or low. In the former case, visual-vestibular interaction resulted in a decrease of the response gain reflecting the conflict nature of the two stimuli. In the majority of cases, however, vestibular sensitivity was low, but the conflicting visual input actually resulted in an amplification of the overall response. The investigated neurons also carried somatosensory signals, typically following stimulation of the surface of the face, that were also co-directional, i.e., non-complementary, with reference to the vestibular on-direction.

While all our neurons recorded in area VIP had non-complementary visual and vestibular on-directions, similar response characteristics in other cortical regions are not found uniformely. Our own recordings in area 2v revealed only the classical visual-vestibular interaction pattern with optokinetic on-directions opposite to the vestibular on-direction. Other authors, however, also reported non-complementary responses in area 2v, in the parieto-insular vestibular cortex (PIVC), and in thalamic nuclei. The only other region with exclusively non-complementary visual-vestibular reactions (in vertical planes) is area 7a.

The non-complementary visual-vestibular response characteristics could be interpreted as indicating overcompensation of an eye or head movement response, as detecting constant spatial coordinates, or as signalling head rotation during linear forward motion while fixating a target in near-personal space. A final answer to these questions has to come from recordings in head-free animals.

## CORTICAL AND CEREBELLAR CONTROL OF SEQUENCES OF MEMORY-GUIDED SACCADES: THE ROLE OF EFFERENCE COPY

W. HEIDE[1], F. BINKOFSKI[2], M.F. NITSCHKE[1], R.J. SEITZ[2], S. POSSE[3], D. KÖMPF[1] AND H.-J. FREUND[2]

*Depts. of Neurology, [1]Med. University, D-23538 Lübeck, Germany, [2]Univ. of Dusseldorf, Germany, and [3]Institute of Medicine, Research Center Jülich, Germany*

If sequences of memory-guided saccades are performed in darkness, such as during the double-step task, the brain has to use extraretinal information about

previous eye displacement (efference copy) in order to achieve spatial accuracy for the subsequent saccade. Lesion studies in stroke patients have demonstrated the critical role of the parietal eye field (PEF) for this spatial computation, whereas the frontal eye field (FEF) and the supplementary eye field (SEF), located in the supplementary motor area, control rather the initiation and the timing of these sequences. To delineate the whole network of cortical and cerebellar area involved in these functions, we performed functional magnetic resonance imaging (fMRI) in 6 healthy right-handed adults, using echoplanar sequences (TR=3 s, TE=66 ms, a=90°, voxel size 3x3x4 mm), alternating between activation and control conditions (each lasting 24s). After realignment, spatial normalization and smoothing, individual and group analysis was performed using SPM96b ($P<0.01$). We applied a triple-step stimulus consisting of 3 successively flashed laser targets that had to be memorized and fixated in darkness after a delay of 500 ms. To isolate the contribution of relevant subfunctions of triple-step saccades, we used various control conditions including fixation, visually-guided saccades, single memory-guided saccades, and a spatial working memory task (SWM), where a target had to be acquired by a saccade only when its location was identical to one of the 3 triple-step targets presented 2.5 s earlier. Triple-step saccades as well as the SWM task activated the FEF, the premotor cortex (PMC), the SEF, the anterior cingulate (AC) gyrus, the cerebellar posterior vermis, the cerebellar hemispheres, and 3 centers around the medial and posterior portion of intraparietal sulcus, the probable location of the human PEF. Comparison of the activation patterns in the different task-control conditions permitted the following conclusions: The FEF is important for the initiation of any type of voluntary saccades, the SEF for the triggering of saccadic sequences, the AC probably for sustained attention, the parietal centers and the PMC for spatially-directed attention and spatial coding prior to an intended saccade. The prefrontal cortex is more involved in spatial working memory than in the generation of saccades. In the cerebellum, the posterior vermis is the predominant structure for the control of all types of saccadic eye movements. In addition, triple-step saccades and the SWM task activate the cerebellar hemispheres, consistent with previous studies demonstrating cerebellar hemispheric activation in other cognitive tasks. However, neither parietal nor cerebellar activation was particularly related to the spatial programming of triple-step saccades. Thus it was not possible to delineate a specific correlate of saccade-related efference copy by functional brain imaging.

## VESTIBULAR - PODOKINETIC INTERACTIONS IN THE LOCOMOTOR CONTROL OF SPATIAL ORIENTATION

G. MELVILL JONES, H.L.GALIANA[1], W.A. FLETCHER, W.D. WEBER, AND E.W. BLOCK

*Dept. of Clinical Neurosciences, University of Calgary, Alberta, and [1]Dept. of Biomedical Engineering, McGill University, Québec, Canada*

Previous work investigated the dynamic characteristics of a "Podokinetic" system involved in the control of locomotor trajectory through reference of body

orientation to the space-stable stance foot. The findings are compatible with the corresponding psychophysical observations of Mergner et al. (e.g. *J. Vest. Res.*, 1993). The present study investigates somatic motor responses in the stepping subject during post rotational vestibular stimulation.

Normal, blindfolded, subjects were first exposed to a passively induced post-rotational vestibular stimulus of 45 deg/sec, achieved by stopping a rotating platform after slow sub-threshold acceleration. While still blindfolded they were then immediately required to attempt stepping-in-place (i.e., without turning relative to space) on the centre of the now stationary platform. With no sensation of rotation, they first turned themselves rapidly (~30 deg/sec) in the same direction as the previous turntable rotation and then, after about 30 sec smoothly reversed direction at a slower angular velocity which, after first increasing, gradually decayed over the next few minutes. The pattern of response was robust, being repeatable both within and between subjects.

This complex pattern of vestibulo-spinal response is reminescent of the more familiar post and post-post rotational VOR. But whereas the oculomotor output of the VOR is an open ended response, the rotational podokinetic response necessarily feeds back directly into the peripheral vestibular sansory system, thus closing a tight, mechanically coupled, loop between the vestibular and podokinetic systems. To investigate putative response characteristics of this closed loop system we attemped its simulation with a simple model. A time constant of 15 sec was ascribed to the familiar first order lead characterisctic of the vestibular system. Based on a previous study of adaptation in the podokinetic system (Weber et al., 1998), this latter was modeled by a first order lag characteristic of time constant 300 sec. Using these transfer functions, simulation of the closed loop response to a 'post-rotational stimulus' of 45 deg/sec yielded a temporal pattern of 'body rotation' closely analogous to that obtained from the above experimental paradigm. Possibly such a combination of experimental and simulation procedures offers a novel approach to clinical testing of the vestibulo-spinal system.

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## 2D NAVIGATION AND EYE MOVEMENTS

I. ISRAËL AND I. SIEGLER
*LPPA, CNRS - Collège de France, Paris*

We recently found that during 2D passive displacements in darkness, along circular or trapezoid trajectories, there was no correlation between concurrent manual tracking and retrospective pointing (Ivanenko et al., *Exp. Brain Res.*, **117**: 419-427, 1997). This suggests the existence of two different processes involved in 2D displacement perception and estimate, since eventhough it is known that retrospective and concurrent estimates usually yield different values, these values are correlated.

We then wondered whether using eye movements would bring some new insight on self-motion perception, as it has been shown that head (gaze) does anticipate

on circular locomotion (Grasso et al., *NeuroReport*, **7**: 1170-1174, 1996). One preliminary data collоction (Israël et al., *Exp. Brain Res.*, **112**: 411-419, 1996) showed that VOR suppression has no effect on 1D self-motion perception, which indeed suggests that the VOR could well bp used as self-motion perception estimator. More recent data on 1D rotations further told that there was no correlation between concurrent VOR gain and retrospective angle estimate with a pointer (Ivanenko et al., *Neurosci. Lett.*, **241**: 167-170, 1998), and no correlation between concurrent VOR gain and retrospective angle estimateJwith whole-body pointing (Israël and Siegler, in press).

So far, all data do actually coincide on this lack of correlation between concurrent and retrospective passive self-motion magnitude estimate, be it 1D or 2D self-motion, and manual or oculomotor estimate. However, we had found in former experiments, with former metEods, a high correlation between the so-called goal-directed VOR amplitude gain and retrospective Vestibular Memory-Contingent-Saccades (Israël et al., *Exp. Brain Res.*, **96**: 335-346, 1993), for 1D rotations. But with this former method, we simply omitted all dynamic components from the VOR, computing the overall cumulated eye movements (slow phases and saccades in the same direction) amplitude (and not velocity). Therefore, the lack of correlation between concurrent and retrospective estimates is most probably due to the velocity (dynamic) components.

Finally, we believe that measuring eye movements during 2D navigation will bring new insight on self-motion perception, provided the analysis is not restricted to the static amplitude. Convincing data on vestibular nystagmus beating field during active/passive transport will be presented.

## PATH INTEGRATION

H. MITTELSTAEDT
*Max-Planck-Institut für Verhaltensphysiologie, Seewiesen, Germany*

Arthropods as well as mammals are able to return straight home after a random search excursion under conditions that are designed to exclude all external cues. This capability must then be based on the integration and storage of the animal's own movements. In 1973, in order to come to grips with results of Peter Görner, Marie-Luise Mittelstaedt, myself and our colleagues, we have defined spatial information that can only be gained by means of the agent's active or passive movement as *idiothetic* information. By exclusion, *allothetic* is information yielded by external cues, that is, cues whose orientation can change independently of the animal's movement.

Idiothetic information could be gained in two basically different ways: l) from sense organs like the semicircular canals and the otolithic or truncal graviceptors, hence termed *inertial idiothesis*, or 2) from those proprioceptors or efference copies whose signals are normally correlated with, and hence allow inferences about, the agent's course with respect to ground, air, or water, hence termed *substratal idiothesis*.

Gained idiothetically and/or allothetically, the rotatory components of the movement must be integrated over the translatory displacement along the path in order to obtain the coordinates of the agent's location with respect to his starting point. Hence we have named this performance *Wegintegration* or *path integration*, respectively

After presenting extant and new results that demonstrate the role of the vestibular system in path integration of rodents and humans, two principal ways are introduced of how this performance can be achieved. The structural and causal properties of the two models are compared with the well-know functional properties of the hippocampal head direction and place cells.

Whereas representations of beeline distance and beeline direction, as demanded by an interative polar model, are not found in the hippocampus, a continuous Cartesian model appears to be in basic agreement with the neurophysiological data.