Otolith–Canal Interaction During Pitch While Rotating

T. HASLWANTER,[a] R, JAEGER, AND M. FETTER

Department of Neurology, University Hospital Tübingen, Hoppe-Seyler-Str. 3, D-72076, Tübingen, Germany

INTRODUCTION

Natural movements of the head in space consist of combined rotations and translations, even during such simple tasks as walking around a corner. Investigations of the respective contributions of the vestibular sensors involved, the otoliths and the semicircular canals, rely on paradigms that allow the simultaneous stimulation of both sensory systems. While most paradigms only induce a static or temporary stimulus to the otoliths or the canals, pitch while rotating (PWR) leads to a continuous stimulation of both systems. It is well known that in monkeys such a stimulation pattern leads to eye movements that are compensatory to the continuous rotation of the body in space.[1,2] But to date no experiments have been conducted to investigate human responses to such complex canal–otoliths stimulation. We have therefore recorded 3-dimensional eye movements in human subjects who actively oscillated their head in the pitch plane during a continuous rotation about an earth-vertical axis.

METHODS

Subjects were seated on a turntable and were firmly secured to the chair. At the beginning of the experiment the head was oriented such that Reid's line was oriented about 10 deg nose up. Three-dimensional eye movements were recorded with the dual search coil technique, and were sampled at 100 Hz. We tested 11 healthy subjects (age 24 ± 2.4a) during active head pitching while rotating about an earth-vertical axis. Before the beginning of the PWR experiments the pitching movement of the head was practiced at 1/3 Hz and 2/3 Hz, with an amplitude of ± 20 deg, while the subject was looking straight ahead at an earth-fixed target. The head movement was restricted by a helmet, which was mounted such that the subject could move the head around a horizontal axis located about 2 cm behind and above the intervestibular line. The speed of the sinusoidal movement was indicated by a metronome. Then the sphere was closed, all lights were turned off, and the subject was accelerated in complete darkness to a constant velocity of 100 deg/s. After 2 min of constant-velocity rotation the subject was instructed to pitch the head sinusoidally and keep on looking straight ahead. No visual target was presented. During this head pitching the metronome was adjusted to 1/3 Hz, and the clicks of the metronome were

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[a] To whom correspondence may be addressed. Phone: +41-1-255-5550; fax: +41-1-255-4507; e-mail: haslwant@neurol.unizh.ch

transmitted to the subject through an intercom system. After 40 s of head pitching the subject kept the head stationary for 1 min while the turntable continued to rotate at 100 deg/s. Then the head pitching was repeated for 40 s with a frequency of 2/3 Hz. After 2 more minutes of constant velocity rotation with the head stationary the subject was decelerated. When the postrotatory nystagmus had died down the whole experiment was repeated in the opposite direction.

From the recorded data the 3-dimensional angular eye velocity was calculated,[3] and the fast phases of the nystagmus were removed.[4] The data analysis was restricted to the horizontal and torsional velocity offsets, as well as the corresponding modulation amplitudes. These were determined by fitting the function

$$\text{eye\_vel} = \text{offset} + \text{amplitude} * \sin(2\pi\nu t+\Delta\phi)$$

to a hand-selected data interval of the eye velocity traces (ν is the frequency of the head pitching). For each subject the values for rotations to the right and the left were averaged such that the offset values correspond to a rotation to the left. The amplitudes of the active, approximately sinusoidal vertical head movements were highly variable, and the execution of the paradigm also showed substantial intersubject variability: while 8 of the 10 subjects kept the eyes approximately stable in space (modulation 1–7 deg), two subjects made eye-in-space movements that were larger than the head movements. Thus the vertical data traces were not analyzed, and no phase relationships were determined for the horizontal and torsional data.

RESULTS

A set of experimental data is shown in FIGURE 1. Over all subjects, the head pitching had an amplitude of 13 deg ± 3 deg. While there was no offset in the torsional component, the horizontal eye velocities showed for both frequencies of head pitching a small but significant offset (1.7 ± 1.3 deg/s at 1/3 Hz, and 1.0 ± 1.1 deg/s at 2/3 Hz). The offset was directed such that it was opposite to the sustained movement of the body in space.

The eye-velocity modulation had the same frequency as the head pitching. Its amplitude increased for the torsional component significantly with the frequency (from 7.9 ± 2.3 deg/s at 1/3 Hz, to 10.8 ± 4.5 deg/s at 2/3 Hz), but stayed approximately constant for the horizontal component (from 4.3 ± 1.6 deg/s to 4.4 ± 2.1 deg/s). There was a significant correlation between the amplitude of the head movements and the magnitude of the torsional eye-velocity modulation ($r = 0.78$).

MODELS

To better understand the task faced by the central nervous system in determining the movement in space from the dynamic canal and otoliths signals, we simulated the stimulation of the canals during PWR. Computational details of the calculation, which consider the mechanical properties of the canals, have been described elsewhere.[5]

FIGURE 2 indicates the complexity of the task: simply changing the frequency of the head pitching in FIGURE 2 by a factor of 10 changes not only the relative magnitude of the stimulation of the canals but also dramatically affects their phase relationships.

We also tested to what extent a model of canal–otolith interaction, which was based on ideas from Merfeld,[6] and which we developed to predict three-dimensional eye movements during OVAR, would be able to reproduce the observed eye velocities. This model reproduced the main features seen in the recorded data: modulations in all three velocity

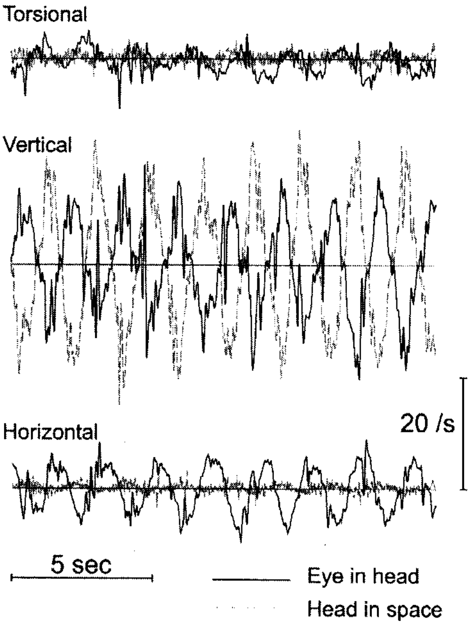

FIGURE 1. Torsional, vertical, and horizontal eye- and head-velocity components during pitch while rotating (PWR). The rotational velocity was 100 deg/s, and the pitching was executed with 2/3 Hz. The *thick solid lines* indicate the velocity of the eye-in-the-head, and the *thin dashed lines* the velocity of the head with respect to the rotating turntable.

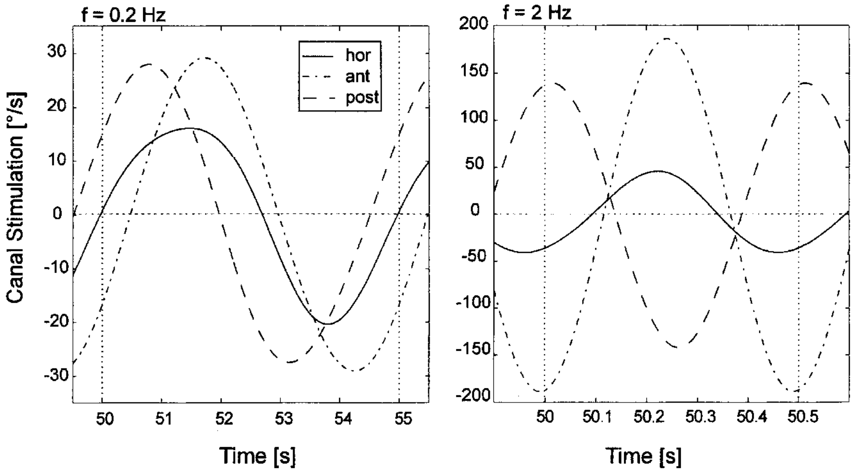

FIGURE 2. Stimulation of the horizontal, anterior, and posterior canal on the right side, during PWR with 0.2 Hz (**left**) and 2 Hz (**right**). The data correspond to a rotation about an earth-vertical axis with 100 deg/s, and a sinusoidal oscillation of the head in the pitch plane by ± 20 deg. In the zero position the head was oriented such that Reid's line was 10 deg nose up with respect to the earth vertical. These positions are marked by the *dotted vertical lines*. The units indicate the velocity "sensed" by each canal during this movement.

components, but no clear offset. When tested with the parameters that simulate the behavior of rhesus monkeys during OVAR, the model also correctly reproduced a compensatory horizontal velocity offset, as found in the experiments.

DISCUSSION

In this study, the first ever of PWR in humans, we found a horizontal velocity offset that is compensatory for the movement in space, but that is—unlike in monkeys[1]—extremely small. This confirms earlier findings in our laboratory, indicating drastically reduced otolith–canal interaction in humans compared to monkeys.[7] A surprising finding has been the increase in modulation of the torsional velocity component with increasing pitch-frequency. The models do not show this increase. They show, however, that any explanation of the origin of the compensatory eye-movement response in monkeys must consider the mechanical properties of the semicircular canals, since they lead to a frequency-dependent phase shift of the stimulation patterns in the canals.

In our experiment the subjects started with the head in a comfortable upright position, which resulted in a nose-up tilt of the lateral semicircular canals by about 30 deg. As a result the frequency of the modulation of the horizontal and torsional velocity was the same as the frequency of the head pitching. In contrast, in experiments with monkeys the head is usually initially oriented such that the lateral canals are parallel to the earth-horizontal axis. In that case, the frequency of the modulation of the horizontal eye-velocity is twice the frequency of the head pitching.[2]

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