Do humans show velocity-storage in the vertical rVOR?

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Abstract

To investigate the contribution of the vestibular velocity-storage mechanism (VSM) to the vertical rotational vestibulo-ocular reflex (rVOR) we recorded eye movements evoked by off-vertical axis rotation (OVAR) using whole-body constant-velocity pitch rotations about an earth-horizontal, interaural axis in four healthy human subjects. Subjects were tumbled forward, and backward, at 60 deg/s for over 1 min using a 3D turntable. Slow-phase velocity (SPV) responses were similar to the horizontal responses elicited by OVAR along the body longitudinal axis, ('barbecue' rotation), with exponentially decaying amplitudes and a residual, otolith-driven sinusoidal response with a bias. The time constants of the vertical SPV ranged from 6 to 9 s. These values are closer to those that reflect the dynamic properties of vestibular afferents than the typical 20 s produced by the VSM in the horizontal plane, confirming the relatively smaller contribution of the VSM to these vertical responses. Our preliminary results also agree with the idea that the VSM velocity response aligns with the direction of gravity. The horizontal and torsional eye velocity traces were also sinusoidally modulated by the change in gravity, but showed no exponential decay.
Do humans show velocity-storage in the vertical rVOR?

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Abstract

To investigate the contribution of the vestibular velocity-storage mechanism (VSM) to the vertical rotational vestibulo-ocular reflex (rVOR) we recorded eye movements evoked by off-vertical axis rotation (OVAR) using whole-body constant-velocity pitch rotations about an earth-horizontal, interaural axis in four healthy human subjects. Subjects were tumbled forward, and backward, at 60 deg/s for over one minute using a 3D turntable. Slow-phase velocity (SPV) responses were similar to the horizontal responses elicited by OVAR along the body longitudinal axis, (‘barbecue’ rotation), with exponentially decaying amplitudes and a residual, otolith-driven sinusoidal response with a bias. The time constants of the vertical SPV ranged from 6 to 9 seconds. These values are closer to those that reflect the dynamic properties of vestibular afferents than the typical 20 s produced by the VSM in the horizontal plane, confirming the relatively smaller contribution of the VSM to these vertical responses. Our preliminary results also agree with the idea that the VSM velocity response aligns with the direction of gravity. The horizontal and torsional eye velocity traces were also sinusoidally modulated by the change in gravity, but showed no exponential decay.

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Introduction

The horizontal rotational vestibular ocular reflex (rVOR) has been investigated extensively, but the vertical rVOR much less so, especially for human subjects. The existence of a velocity-storage mechanism (VSM), which prolongs the time constant of the horizontal rVOR, is unclear for the vertical rVOR. Here we investigated this issue further by recording eye movements in normal subjects to constant-velocity rotation around the pitch axis.
1. Materials and Methods

1.1 Vestibular stimulation

Using dual scleral search coils we recorded the three-dimensional eye movements of four healthy subjects monocularly while they were rotated forward and backward about the earth-horizontal interaural axis (pitch rotations) at 60 deg/s in total darkness for over one minute. The experiments were performed using a motor-driven turntable (prototype built by Acutronic, Switzerland). The turntable was accelerated at 10 deg/s², reaching the constant-velocity in 6 s. Details of the coil calibration procedure can be found elsewhere (Marti et al., 2005).

1.2 Data analysis

Saccades were interactively removed from the velocity signal, which was linearly interpolated over the intervals corresponding to the removed saccades. The resulting vertical slow-phase velocity (SPV) showed an exponentially decaying amplitude and a residual, otolith-driven, sinusoidal response with a bias. A fit of the sinusoid was estimated from the later part of the response, over 60 s from motion onset, when the rVOR response had presumably vanished even if the overall rVOR time constant is 20 s. The following sinusoidal function was used to fit the otolith response data

\[ y = A \cdot \sin (2\pi ft + \phi) + c \]  \hspace{1cm} \text{Eq. 1}

where \( A \) is the amplitude, \( f \) the frequency, \( \phi \) the phase, and \( c \) the offset. The frequency \( (f) \) was kept constant at 0.16 Hz (corresponding to a chair angular velocity of 60 deg/s), while the amplitude \( (A) \), the phase \( (\phi) \), and the offset \( (c) \) were iteratively optimized using a nonlinear least-squares algorithm. Once these parameters had been determined, the sinusoidal function was computed for the duration of the whole response, as shown in Figure 1 panels B-C, and was then subtracted from the slow-phase velocity data. Finally, the amplitude and the time constant of the rVOR response was estimated by fitting the resulting data with the following exponential function

\[ y = A \cdot \ e^{-t/\tau} \]  \hspace{1cm} \text{Eq. 2}

where \( A \) is the amplitude and \( \tau \) the time constant of the rVOR response.
Figure 1: a) Calibrated vertical eye velocity trace before removal of saccades. b) Solid line: Trace after saccades removal. Dashed line: sinusoidal fit. c) Detail of the sinusoidal fit.

Figure 2: Representative examples of processed responses to a) backward rotation, $\tau = 7.97$ s; b) forward rotation, $\tau = 6.10$ s. Solid line: processed SPV. Dashed Line: Exponential fit.
2. Results

Our subjects showed an intense vertical nystagmus (Figure 1A) with a SPV amplitude that decayed exponentially to a pure otolith-driven sinusoid with a bias. The inter-subject variability of the responses was considerable, as reflected by the standard deviation of the mean of pooled values. One subject showed a markedly larger amplitude of the exponential decay, the sinusoidal modulation and the bias compared to the others, yet the rVOR time constant did not differ from that of the other subjects. Mean values and standard deviations of the data without including that subject are therefore presented within brackets.

The gain of the response prior to subtraction of the otolith-driven sinusoid, estimated as the ratio of eye velocity to chair velocity between seconds two and three of the response (i.e. during the acceleration phase) was 0.34±0.08 (SD) [0.31±0.07]. The sinusoidal response had mean amplitude of 6.19±2.90 [4.72±2.20] deg/s, corresponding to a gain of 0.1±0.05 [0.08±0.04]. The mean of the absolute values of the bias was 5.22±6.67 [3.19±2.95] deg/s and it always introduced a velocity offset that was in the direction compensatory for head rotation. Two examples of the processed data showing the exponentially decaying SPV and the corresponding fit are shown in Figure 2 (A: backward rotation; B: forward rotation). The mean value of the rVOR time constant over the four subjects was 7.39±1.22 [7.07±1.25] s and its gain was 0.25±0.14 [0.18±0.03]. The time constants were similar for the backward (7.32±1.32 s) and forward (7.46±1.40 s) rotations. Horizontal and torsional eye velocity traces showed a small sinusoidal modulation, but no exponential decay of the response at the onset of constant velocity chair rotation.

3. Discussion

To assess the contribution of the velocity-storage mechanism to the pitch rVOR, we have studied the eye movements of four healthy subjects evoked by constant-velocity pitch rotations at 60 deg/s, in total darkness.
The gain of the pitch rVOR computed from the exponential decay of vertical eye velocity was only about 0.25, which is lower than the typical 0.5 measured for horizontal rVOR evoked by yaw rotations (Barr et al., 1976). Since our data showed no appreciable SPV plateau, we considered a single rVOR time constant corresponding to the original model suggested by Robinson (Robinson, 1977). The mean value of the rVOR time constant was 7.39±1.22 s. These values are lower than the classically considered 20 s, while similar to those reported for vestibular afferents both in monkeys and humans. Considering that recent studies have suggested shorter time constants for both the vestibular afferents (between 3.4 and 4 s) and the rVOR response (between 8 and 10 s) in humans (Gizzi and Harper, 2003; Dai et al., 1999), our findings confirm the relatively small contribution of the VSM to vertical responses. The horizontal and torsional eye velocity traces were also modulated sinusoidally by the change in gravity, but showed no exponential decay after the onset of chair rotation, thus no VSM contribution. These results agree with the hypothesis that the VSM velocity response is minimal (or absent) when the axis of rotation is not aligned with the gravity acceleration vector (Raphan et al., 1979). The absence of a VSM contribution to torsional and horizontal traces does not conflict with the cross-coupling hypothesis (Raphan and Cohen, 1988) since the direction of gravity with respect to the head continuously changed with our stimulus.

References