

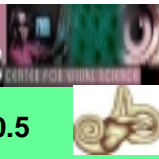


HUMAN LINEAR VESTIBULO-OCULAR REFLEX DURING NASO-OCCIPITAL MOTION (NO-LVOR)

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Introduction

The vestibular system is crucial for maintaining orientation in space. One of its outputs, the vestibulo-ocular reflex (VOR), generates compensatory eye rotations in response to angular and linear head motion in order to maintain binocular fixation on visual targets. The linear VOR during naso-occipital motion (NO-LVOR) is among the most fascinating vestibular reflexes because of its remarkable dependency on fixation characteristics and its implications for underlying neural structure and function. Previous work has focused on the NO-LVOR in monkeys. We quantified influences of stimulus frequency, viewing distance, gaze eccentricity and visual context on the human NO-LVOR.

Methods

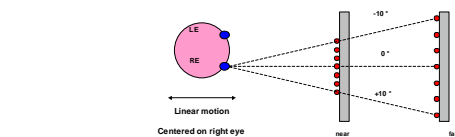
Subjects: Ten healthy adults (age range 18-45, 6 male and 4 female).

Eye Movement Recording: A binocular CCD (EI-Mar) infrared video-based eye tracker was used to record R and L horizontal and vertical eye position. Only horizontal responses were quantified (vertical was used to ensure fixation stability in darkness).

Motion Control: Linear motion was produced using a multi-axis servo-controlled sled/rotator. The NO-LVOR was quantified during sinusoidal linear oscillations of the subject with the head's NO axis aligned with the axis of linear sled motion.

Frequency Hz	Peak acceleration g	Peak acceleration cm/s^2	Peak velocity cm/s	Peak position cm
0.25	0.025	24.5	15.6	9.94
0.5	0.10	98.1	31.2	9.94
1.0	0.20	196.2	31.2	4.97
2.0	0.20	196.2	15.6	1.24

Visual targets were presented using earth-fixed (ef) or a head-fixed (hf) displays 25 or 50 cm away, comprised of 7 small LEDs over a horizontal range of $\pm 10^\circ$ centered on the right eye. For each target and stimulus frequency, data were collected with the LED on (ef & hf-LVOR) and after it was extinguished (ief & ihf-LVOR). Subjects were instructed to maintain "target" fixation in darkness, aided by a tone related to vergence angle.

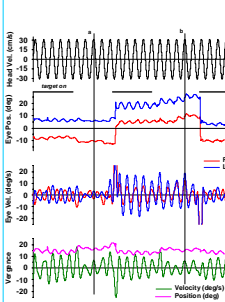


Data Analysis: Sled and all eye position signals were digitized at 100 Hz. Horizontal ocular records were then desaccaded and subjected to cycle-by-cycle harmonic analysis. Sensitivities (deg/cm) and phases (deg) were computed, and subdivided further into ef, hf, ief & ihf-LVOR responses, and for near and far targets. Results were then binned by gaze eccentricity or fixation distance. Our analysis of NO-LVOR responses were applied separately to each eye and to vergence angle (L-R horizontal eye position).

Results

Raw Horizontal Ocular Responses to NO Motion (1 Hz ef- and ief-LVOR)

Effect of Gaze Eccentricity

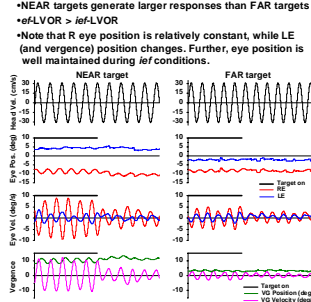


- R eye velocity in darkness shifts 180 deg. between references 'a' and 'b' (as gaze shifts from L to R), while the L eye does not (gaze is always to the R).
- L eye response increases with gaze eccentricity, reflected as a greater peak velocity at 'b' than at 'a'.
- Vergence response magnitude and phase remain similar at 'a' and 'b', as does vergence angle.
- All responses are greater with the target on (ef-LVOR) than with the target off (ief-LVOR).



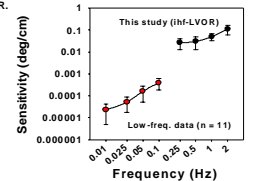
Graphical depiction of stimulus geometry used to generate data shown at left. Point "a" is -10° left of the midline of the right eye, while point "b" is -8° right.

Effect of Binocular Fixation Distance



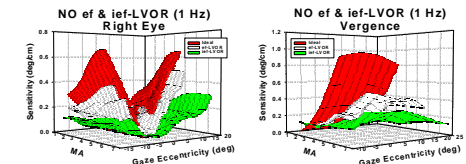
- NEAR targets generate larger responses than FAR targets
- ef-LVOR > ief-LVOR
- Note that R eye position is relatively constant, while LE (and vergence) position changes. Further, eye position is well maintained during ief conditions.

Broadband NO-LVOR sensitivity, including low-frequency responses to NO acceleration along with the current data, is plotted below, demonstrating the high-pass characteristics of this translational LVOR.

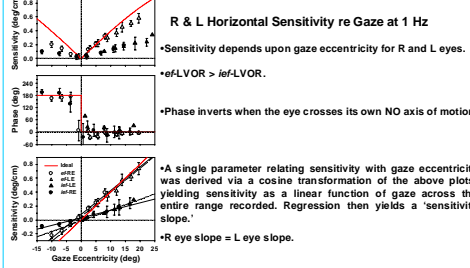


Conclusions

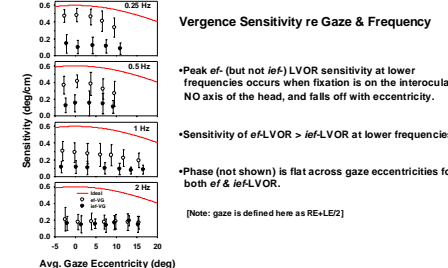
- LVOR responses to NO linear acceleration are robust across a range of frequencies typical of natural motion.
- R and L ocular responses are systematically modulated in amplitude by gaze eccentricity and fixation distance, while phase inverts (each eye) when position crosses its NO axis of motion, as expected on geometrical grounds.
- The NO-LVOR is under-compensatory except when vergence is small (fixation distance is far).
- Visual influences (real or imagined) modify response sensitivities, but the effects follow low-pass dynamics, unlike the high-pass dynamics of the NO-LVOR itself.
- A graphic depiction of NO-LVOR sensitivity, incorporating gaze eccentricity and viewing distance, is shown below:



Response Properties as a Function of Gaze Eccentricity (near targets)



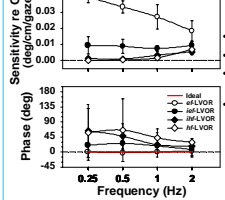
- Sensitivity depends upon gaze eccentricity for R and L eyes.
- ef-LVOR > ief-LVOR.
- Phase inverts when the eye crosses its own NO axis of motion.
- A single parameter relating sensitivity with gaze eccentricity was derived via a cosine transformation of the above plots, yielding sensitivity as a linear function of gaze across the entire range recorded. Regression then yields a 'sensitivity slope.'
- R eye slope = L eye slope.



- Peak ef- (but not ief-) LVOR sensitivity at lower frequencies occurs when fixation is on the interocular NO axis of the head, and falls off with eccentricity.
- Sensitivity of ef-LVOR > ief-LVOR at lower frequencies.
- Phase (not shown) is flat across gaze eccentricities for both ef & ief-LVOR.

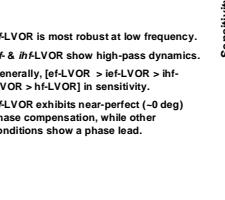
NO-LVOR Frequency Response (0.25 - 2 Hz)

R Eye Response



- ef-LVOR is most robust at low frequency.
- hf & ihf-LVOR show high-pass dynamics.
- Generally, [ef-LVOR > ief-LVOR > ihf-LVOR > hf-LVOR] in sensitivity.
- ef-LVOR exhibits near-perfect (-0 deg) phase compensation, while other conditions show a phase lead.

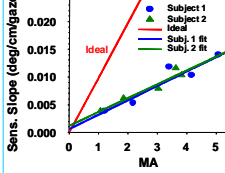
Vergence Response



- Vergence response properties qualitatively resemble those for the R Eye (note different units).

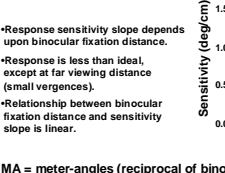
Influence of Binocular Fixation Distance on Response Sensitivity at 2 Hz

R Eye Response (ief-LVOR)



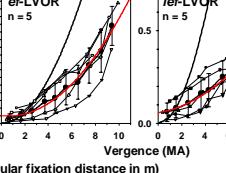
- Response sensitivity slope depends upon binocular fixation distance.
- Response is less than ideal, except at far viewing distance (small vergences).
- Relationship between binocular fixation distance and sensitivity slope is linear.

ef-LVOR



- Vergence response depends upon binocular fixation distance.
- Vergence response is below ideal during near fixation.
- The relationship between binocular fixation distance and vergence sensitivity is not linear (the fit here is a 2nd order polynomial).

ief-LVOR



- Vergence response depends upon binocular fixation distance.
- Vergence response is below ideal during near fixation.
- The relationship between binocular fixation distance and vergence sensitivity is not linear (the fit here is a 2nd order polynomial).

Abstract

We quantified the response properties of the human NO-LVOR as a function of stimulus frequency, binocular fixation distance (vergence angle) and gaze eccentricity, as well as its interactions with real & imagined visual targets. Ten normal subjects (age 18-46) were occluded sinusoidally (0.25-2 Hz, 0.025-0.2 g peak) on a linear sled with the head's NO axis aligned with the axis of motion. Eye movements were recorded binocularly by digital video-oculography. Targets were presented using an earth-fixed (ef) or head-fixed (hf) array of LEDs over a horizontal range of $\pm 10^\circ$, centered on the NO axis of the right eye and positioned at 25 & 50 cm distance. For each target and stimulus frequency, data were collected with the LED on (ef or hf) and off (ief or ihf) while subjects attempted to maintain target fixation in darkness. Another experiment used an ef (and left) target between the eyes at 10 distances from 0.1 to 1 m during 2 Hz oscillation. Response sensitivities (cm) and phases ($^\circ$) were computed and binned by gaze eccentricity and fixation distance. Sensitivity is -0° at 0° gaze, and rises with increasing eccentricity, yielding a 'V' pattern. Phase, however, is -0° during R gaze and -180° during L gaze in accord with kinematic requirements to maintain fixation. The slope of the 'V' is modulated by reciprocal fixation distance (m^{-1}). The two eyes behave incongruently, commensurate with their separation in the head, moving oppositely whenever fixation is between the eyes. This vergence VOR response is modulated as a progressive function of ambient vergence state, but not systematically by overall gaze angle within the range studied. Real targets increase [ef] or decrease [ihf] response sensitivity to near ideal at low frequency, but progressively less so as frequency rises. Imagined targets (ief & ihf) influence the NO-LVOR similarly, but less than real ones. Overall, the human NO-LVOR is a robust reflex compensating for NO head translations. L operates with high-pass dynamics that are complemented by vision (low-pass) and modulated in a geometrically appropriate fashion.

References

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