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RESEARCH NOTE

# Vestibular thresholds for yaw rotation about an earth-vertical axis as a function of frequency

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**Abstract** Perceptual direction detection thresholds for yaw rotation about an earth-vertical axis were measured at seven frequencies (0.05, 0.1, 0.2, 0.5, 1, 2, and 5 Hz) in seven subjects in the dark. Motion stimuli consisted of single cycles of sinusoidal acceleration and were generated by a motion platform. An adaptive two-alternative categorical forced-choice procedure was used. The subjects had to indicate by button presses whether they perceived yaw rotation to the left or to the right. Thresholds were measured using a 3-down, 1-up staircase paradigm. Mean yaw rotation velocity thresholds were 2.8 deg $s^{-1}$ for 0.05 Hz, 2.5 deg $s^{-1}$ for 0.1 Hz, 1.7 deg $s^{-1}$ for 0.2 Hz, 0.7 deg $s^{-1}$ for 0.5 Hz, 0.6 deg $s^{-1}$ for 1 Hz, 0.4 deg $s^{-1}$ for 2 Hz, and 0.6 deg $s^{-1}$ for 5 Hz. The results show that motion thresholds increase at 0.2 Hz and below and plateau at 0.5 Hz and above. Increasing velocity thresholds at lower frequencies qualitatively mimic the high-pass characteristics of the semicircular canals, since the increase at 0.2 Hz and below would be consistent with decreased gain/sensitivity observed in the VOR at lower frequencies. In fact, the measured dynamics are consistent with a high pass filter having a threshold plateau of 0.71 deg $s^{-1}$ and a cut-off frequency of 0.23 Hz, which corresponds to a time constant of approximately 0.70 s. These findings provide no evidence for an influence of velocity storage on perceptual yaw rotation thresholds.

**Keywords** Vestibular · Psychophysics · Semicircular canals · Sensory threshold · Human

## Introduction

Recent studies have shown that reflexes and perception evoked by the vestibular system can utilize qualitatively different mechanisms (Merfeld et al. 2005a, b). Because most studies of vestibular function focus on reflexive responses (e.g., posture, VOR), we know much less about the dynamics of vestibular perception than the dynamics of vestibulo-ocular reflexes. Therefore, in this study, we measured yaw rotation thresholds[1] as a function of frequency. Guedry (1974) and Clark (1967) previously reviewed the relevant vestibular threshold literature and reported that angular acceleration thresholds for healthy subjects ranged between 0.035 and 4 deg $s^{-2}$, which spans more than two orders of magnitude. Guedry (1974) suggested several reasons for these huge differences: (1) the use of different threshold criteria, (2) the use of long-duration stimuli that allowed substantial time for the afferent signal to decay, and (3) the inability to provide controlled stimuli (not as well as we can today, given modern electronics and computers). The vast majority of the earlier studies used triangular velocity motion profiles

[1] We use the term threshold as often defined by psychophysicists using signal detection theory, which is the level at which a signal becomes detectable relative to noise—where the noise includes noise inherent to the sensory system and may also include noise applied intentionally or incidentally via the stimuli.

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that, in "theory", included acceleration discontinuities (i.e. steps of acceleration), which could have easily influenced the measured thresholds via characteristics of the motion device acceleration step transients (e.g., "ringing", rise times, etc.). It is also possible that central processing (e.g., velocity storage) might have contributed to the large variability.[2]

Even though frequency is known to influence other vestibular responses like the VOR, we know of only one study (Benson et al. 1989) that investigated thresholds for yaw rotation direction detection across a range of frequencies (0.05–1.11 Hz). Benson and colleagues reported that the velocity thresholds at higher frequencies (circa $1° s^{-1}$ at 1.11 Hz) were lower than at lower frequencies (circa 3–5 deg $s^{-1}$ at 0.05 Hz). However, a complete understanding of thresholds as a function of frequency was not provided, since—as the authors wrote—"… the limited range of stimulus durations employed in the experiment were considered to be inadequate for a meaningful mathematical model of the sensory system to be developed".

Hence, our study was designed to provide fundamental information regarding perceptual yaw rotation thresholds about an earth vertical axis for healthy subjects across a broader range of frequencies—a two-decade range spanning from 0.05 to 5 Hz. One goal was to provide data to establish a vestibulogram—thresholds as a function of frequency—for the detection of the direction of yaw rotation. This will not only help to improve our understanding of vestibular perception dynamics but may also be useful in the context of clinical testing. In line with Benson et al. (1989) we hypothesized that velocity thresholds would be higher at low frequencies than at high frequencies. Moreover, based on the high-pass dynamics of the semicircular canals, we also hypothesized that a plateau in the velocity thresholds would be evident when higher frequencies were tested.

## Methods

### Subjects

Ten healthy volunteers (5 females, 5 males; 39 ± 13 years; 7 right-handed, 3 left-handed) were recruited to participate in this study. All were screened via a detailed vestibular diagnostic clinical examination to confirm the absence of undiagnosed vestibular disorders. Screening consisted of Caloric electronystagmography, Hallpike testing, angular VOR evoked via rotation and posture control measures. Furthermore, a short health history questionnaire was administered; subjects were asked to indicate any known history of dizziness or vertigo, back/neck problems, cardiovascular, neurological and other physical problems. Subjects were also asked about their motion-sickness susceptibility. In fact, screening yielded two potential subjects who did not meet our stringent criteria for inclusion in the study.[3] Acting conservatively, these two subjects—one female and one male—were excluded from our final data set. Informed consent was obtained from all subjects prior to participation in the study. The study was approved by the local ethics committee and has been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

### Motion stimuli

Motion stimuli (Fig. 1a) were generated using a MOOG motion platform (Fig. 1b). They consisted of single cycles of sinusoidal acceleration $(a(t) = A\sin(2\pi ft) = A\sin(2\pi t/T))$, where $A$ is the acceleration amplitude and $f$ is the frequency, which is the inverse of the period (and duration) of the stimulation ($T = 1/f$). Since the motion began at zero velocity, integration of the acceleration yields an oscillatory velocity, $v(t) = AT/(2\pi)[1 - \cos(2\pi t/T)]$, and a lateral displacement $\Delta p(t) = AT/(2\pi)[t - T/(2\pi)\sin(2\pi t/T)]$. Therefore, both the peak velocity ($v_{max} = AT/\pi$ ) and the total lateral displacement ($\Delta p = AT^2/2\pi$) are proportional to the peak acceleration ($A$). These motion profiles were chosen because they mimic the characteristic shape of natural volitional head movements, because they have been successfully utilized in the only other study quantifying perceptual yaw rotation thresholds as a function of frequency (Benson et al. 1989), and because these motion profiles contain no discontinuities in acceleration, velocity, or position.

### Experimental procedures

Subjects were seated in a chair with a 5-point harness in an upright position, and were rotated in yaw about an earth-vertical axis. The subject's head was held in place via an adjustable helmet, and was carefully positioned relative to the axis of rotation using external landmarks. The head was centered left to right relative to the earth-vertical rotation axis. In addition, we identified the posterior edge of the external ear canal and located the rotation axis near this landmark in the fore-aft direction. To minimize the influence of non-vestibular cues regarding motion direction, trials were performed in the dark in a light-tight room. All skin surfaces except the face were covered (long sleeves,

[2] The concept of velocity storage (Raphan et al. 1977; Robinson 1977) was published after Guedry's (1974) review.

[3] A possible right side horizontal canal paresis was detected in one subject, and a slight VOR asymmetry in the other.

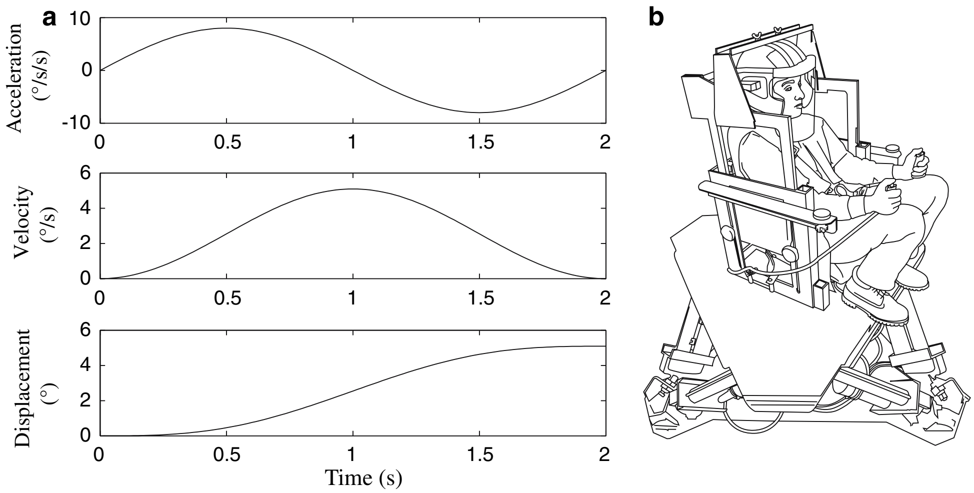


**Fig. 1** Example of motion stimulus and experimental set-up. **a** Illustration of acceleration (*top*), velocity (*middle*) and displacement (*bottom*) for a given motion stimulus (illustrated frequency is 0.5 Hz). Motion stimuli consisted of single cycles of sinusoidal acceleration. **b** Schematic illustration of the experimental set-up. Each subject was securely seated in a chair that was mounted on the motion platform (Moog 6DOF2000E). Subjects held a button in each hand to indicate the direction of their perceived yaw rotation

light gloves) and a visor attached to the helmet surrounded the face. Earplugs reduced external noise by about 20 dB and the remaining auditory motion cues were masked by white noise (circa 60 dB). Tactile cues were distributed as evenly as possible using padding. Figure 1b schematically illustrates the experimental set-up.

Thresholds were measured at seven different frequencies, namely at 0.05, 0.1, 0.2, 0.5, 1, 2, and 5 Hz. Each frequency was tested in a block of contiguous trials. These seven blocks of trials were grouped in four test-sessions: two blocks separated by a short break per session, with the only exception being the 0.05 Hz test block, which was assessed in a single test-session because we used a slightly different psychophysical method and wanted to avoid fatigue effects (this condition usually lasted the longest due to stimuli duration of 20 s). The order of blocks was randomized across subjects.

Subjects were rotated in yaw, either to the left or to the right. A brief low-pitch "warning" tone was administered 2 s before the onset of each motion stimulus. At the end of each trial a brief high-pitch sound was played to indicate that the subject needed to respond. The subject was instructed to push the button in their left hand if they perceived a leftward rotation or to push the button in their right hand for rightward rotation. In case the subjects were uncertain of the direction of motion, they were instructed to make their best guess by pressing one of the two buttons. Before each test-session a few supra-threshold practice trials were administered to assure that the subjects understood the task and to minimize training effects. The button pushes were noted by the experimenter and recorded via computer.

An adaptive two-alternative categorical forced-choice procedure (Treutwein 1995; Leek 2001) was used in all conditions except for 0.05 Hz, where a non-adaptive two-alternative categorical forced-choice procedure was used. For the adaptive procedure, thresholds were measured using a 3-down, 1-up staircase paradigm (e.g., Leek 2001), where 3-down means that the subject had to correctly detect the direction of motion for three motion stimuli in a row in order for the acceleration level to be reduced and 1-up means that the acceleration level is increased every time the subject makes a mistake. This 3-down, 1-up paradigm targets a threshold at which the subject correctly detects motion 79.4% of the time (Leek 2001), which we accepted as our threshold criteria. Typically, trials began well above threshold (starting values were 2.0 deg $s^{-1}$ for condition 5 Hz, 5.1 deg $s^{-1}$ for 2 and 1 Hz, 10.2 deg $s^{-1}$ for 0.5 Hz, 8.8 deg $s^{-1}$ for 0.2 Hz, and 4.1 deg $s^{-1}$ for 0.1 Hz). Testing continued until each test demonstrated nine direction reversals in the adaptive track: five minimum and four maximum direction reversals. Minimum reversals occur when the subject makes an error and the stimulus level goes up. Maximum reversals occur when the subject correctly detects motion at a given acceleration level three times in row immediately after incorrectly detecting motion on the previous trial. Threshold was defined as the mean of the last two—one minimum and one maximum—reversals.

The adaptive procedure could not be applied for the 0.05 Hz condition because the motion platform could not perform the long trajectories necessary to test well above the threshold level. We therefore used constant motion stimuli (Wichmann and Hill 2001), in total 36 motion stimuli (two directions × three levels × six trials each). The three levels tested were 3.8, 2.5, and 1.3 deg $s^{-1}$. We used the same threshold criterion, $p = 79.4\%$, as for the other frequencies.

## Results

On average, 48 trials were performed at each frequency that used the adaptive procedures, and each test-session lasted less than 30 min. One female subject had a threshold at 0.05 Hz that was above the highest level that we could test at this frequency. Acting conservatively, this subject's data are not included in the following data analysis.

Consistent with earlier findings (Benson et al. 1989), no significant gender effects were observed and motion-sickness susceptibility did not correlate with the thresholds measured at any of the seven frequencies tested. Analysis of the distribution of the velocity thresholds with the Kolmogorov–Smirnov as well as the Shapiro–Wilk test revealed significant departures from Gaussian distributions with distributions positively skewed. In accordance with the report of Benson et al. (1989), none of the conditions revealed a significant departure from a normal distribution when velocity thresholds were expressed in logarithmic units. Thus, averaging was performed using logarithmic units, but, for convenience, mean results were transformed back to be reported as velocity.

Mean (± SEM) yaw rotation velocity thresholds are shown in Table 1.

The data show that motion thresholds increase at 0.2 Hz and below and plateau at 0.5 Hz and above. These results are illustrated in Fig. 2.

## Discussion

One goal of this study was to establish a "vestibulogram", the vestibular equivalent of an audiogram quantifying thresholds as a function of frequency. Quantifying thresholds as a function of frequency is important as a step toward the development of clinical tests that focus on self-motion perception as compared to the present clinical tests, which focus upon reflexive responses (e.g., VOR and posture). In this light, the data from this study provide a better understanding of human yaw rotation thresholds and

**Table 1** Velocity direction detection thresholds for yaw rotation (mean ± SEM)

| | 5 Hz | 2 Hz | 1 Hz | 0.5 Hz | 0.2 Hz | 0.1 Hz | 0.05 Hz |
|---|---|---|---|---|---|---|---|
| Mean velocity (deg $s^{-1}$) | 0.59 | 0.38 | 0.64 | 0.73 | 1.66 | 2.51 | 2.84 |
| Positive SEM | 0.11 | 0.05 | 0.23 | 0.15 | 0.28 | 0.25 | 0.45 |
| Negative SEM | 0.09 | 0.05 | 0.17 | 0.12 | 0.24 | 0.23 | 0.39 |

Note that the standard errors (SEM) are not symmetric about the mean when expressed in units of degrees per second. This is because the mean and the standard error at each frequency were calculated using log units as discussed earlier. Data from seven normal subjects included

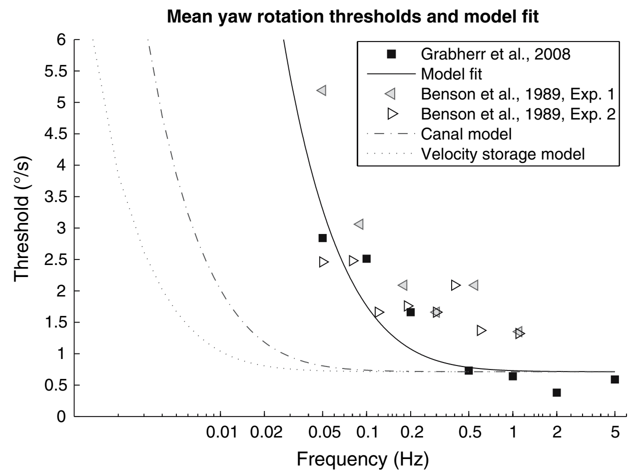


**Fig. 2** Velocity thresholds as a function of frequency. Mean velocity thresholds (*filled square*) are shown ($N = 7$). Velocity is the peak velocity achieved during a single cycle of sinusoidal acceleration. For comparison, data extracted from Benson et al. (1989, Fig. 4) are shown as well (*left triangle* Exp. 1: $N = 6$ and *right triangle* Exp. 2: $N = 8$). Note the qualitative similarity between our data and Benson's data. Relatively small quantitative differences are explained by methodological differences (e.g., different motion devices). The *solid line* shows the model fit to our data while the *dashed lines* show the theoretical threshold dynamics for the semicircular canals and for central processing via velocity storage

more specifically, how these perceptual thresholds vary with frequency.

Two main characteristics could be observed. First, direction detection thresholds for yaw rotation plateau at frequencies of 0.5 Hz and above. In fact, this appears to be one solid finding beyond that reported by Benson et al. (1989), whose data did not extend to a high enough frequency to demonstrate this plateau. Note that it was impossible for Benson et al. (1989) to identify the plateau in Fig. 2 in the absence of data at 2 and 5 Hz. This plateau is indicative of a velocity threshold (as opposed to an acceleration threshold or a minimal displacement threshold). This is consistent with the finding that the semicircular canals work as integrating angular accelerometers at physiological frequencies (Fernandez and Goldberg 1971) yielding afferent signals proportional to angular velocity at physiologic frequencies. Second, velocity thresholds increased at frequencies of 0.2 Hz and below. These increasing thresholds at lower frequencies reflect high-pass characteristics, analogous to the high-pass dynamics of the semicircular canals. In fact, the yaw velocity sensitivity was modelled with a simple first-order high-pass filter of the form $\frac{K\tau s}{\tau s+1}$ that mimics the high-pass characteristics of the horizontal canals, where $\tau$ is the high-pass filter time constant and $K$ is the plateau value. Because thresholds are inversely related to sensitivity, the actual model fit minimized the mean squared error between the average data and $\frac{\tau s+1}{K\tau s}$. The fit was performed using a

Nelder–Mead simplex method (MATLAB "fminsearch"). The fitted time constant was 0.70 s, which corresponds to an average cut-off frequency of 0.23 Hz, and the fitted threshold plateau was 0.71 deg $s^{-1}$. This model fit is illustrated in Fig. 2. For comparison, theoretical threshold dynamics for the semicircular canals and for velocity storage are illustrated as well. Theoretical threshold dynamics for the semicircular canals and velocity storage were calculated in the same manner as the model fit, except that different "theoretical" time constants were used. For velocity storage of yaw rotation perception, a theoretical time constant of 16 s was assumed (Young and Oman 1969), which corresponds to a cut-off frequency of 0.01 Hz. For the canal dynamics, a time constant of 6 s was assumed, which corresponds to a cut-off frequency of about 0.03 Hz. The 6 s time constant measured in squirrel monkeys (Fernandez and Goldberg 1971) probably provides the lowest value expected for the human canal time constant (Ifediba et al. 2007), which has never been measured. The actual human canal dynamics presumably fall between the two theoretical curves shown.

Our data suggest that velocity storage does not affect rotation thresholds. In fact, given a canal time constant of at least 5 s, these threshold data appear to indicate a shortening of the time constant, which is opposite any influence of velocity storage. It is worth noting that a similar shortening of a vestibular response time constant below that of the semicircular canals is observed in vestibular patients (e.g., Okada et al. 1999) and has also been reported for monkeys chronically utilizing a vestibular prosthesis to provide yaw rotation signals (Merfeld et al. 2007).

Our findings show that yaw rotation thresholds have frequency characteristics consistent with high-pass filtering, which has not previously been demonstrated. This finding is important given the paucity of knowledge regarding vestibular psychophysics. Moreover, the data provided herein will guide future studies, including the assessment of thresholds for other dimensions of motion and for the development of "vestibulograms"—the vestibular analog of audiograms, which measure hearing thresholds as a function of frequency—for potential use in the clinic.

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