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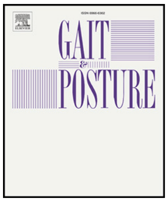

Review

Human vestibular perceptual thresholds — A systematic review of passive motion perception

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ABSTRACT

Background: The vestibular system detects head accelerations within 6 degrees of freedom. How well this is accomplished is described by vestibular perceptual thresholds. They are a measure of perceptual performance based on the conscious evaluation of sensory information. This review provides an integrative synthesis of the vestibular perceptual thresholds reported in the literature. The focus lies on the estimation of thresholds in healthy participants, used devices and stimulus profiles. The dependence of these thresholds on the participants clinical status and age is also reviewed. Furthermore, thresholds from primate studies are discussed.

Results: Thresholds have been measured for frequencies ranging from 0.05 to 5 Hz. They decrease with increasing frequency for five of the six main degrees of freedom (inter-aural, head-vertical, naso-occipital, yaw, pitch). No consistent pattern is evident for roll rotations. For a frequency range beyond 5 Hz, a U-shaped relationship is suggested by a qualitative comparison to primate data. Where enough data is available, increasing thresholds with age and higher thresholds in patients compared to healthy controls can be observed. No effects related to gender or handedness are reported.

Significance Vestibular thresholds are essential for next generation screening tools in the clinical domain, for the assessment of athletic performance, and workplace safety alike. Knowledge about vestibular perceptual thresholds contributes to basic and applied research in fields such as perception, cognition, learning, and healthy aging. This review provides normative values for vestibular thresholds. Gaps in current knowledge are highlighted and attention is drawn to specific issues for improving the inter-study comparability in the future.

1. Introduction

Our head is constantly in motion. Accelerations of up to 4.5 G can occur during everyday activities (e.g. jumping, sprinting). During active movements, the strongest accelerations typically occur along the vertical axis. Moving passively, the largest accelerations of up to 1 G occur in the for/aft direction (e.g. during a car or bus ride) [1]. In addition to these large accelerations, very small perturbations must also be detected to keep the body in balance. Active and passive movement must be constantly monitored to avoid a fall. This process depends on the perceptual thresholds for acceleration. It is not possible, however, to measure vestibular thresholds based on active motion stimulation. Therefore, all measurements of vestibular performance are based on passive motion. Because active and passive motions are indistinguishable for the sensory system, the thresholds measured for passive motion are also relevant within the active context (e.g. unrestricted body sway). Passive self-motion is omnipresent in life, when we ride trains, in cars or buses, or in airplanes. The peripheral vestibular organs detect accelerations of the head in six degrees of freedom (6DOF) using five direction specific sub-components. The three semicircular canals are oriented roughly perpendicular to each other and detect rotatory accelerations. Two otolith organs, the saccule and the utricule, provide the brain with information about translational accelerations in the horizontal and vertical plane. The otolith organs also provide information on the head orientation relative to the gravitational field of the earth. Combined information from the vestibular sub-components allow to capture head accelerations in 6DOF in three dimensional space. A functioning vestibular sense is crucial for keeping the body in balance and for allowing complex motions, such as bipedal walk. Linear [2] and angular [3] vestibular thresholds are correlated with posturographic measurements.

The vestibular system unfolds its full potential when combined with other sensory systems. It is a key supporter of the visual system as it enables keeping a fixed image on the retina during active head movements by means of the vestibular ocular reflex (VOR). Furthermore, the vestibular system helps to resolve the visual ambiguity regarding

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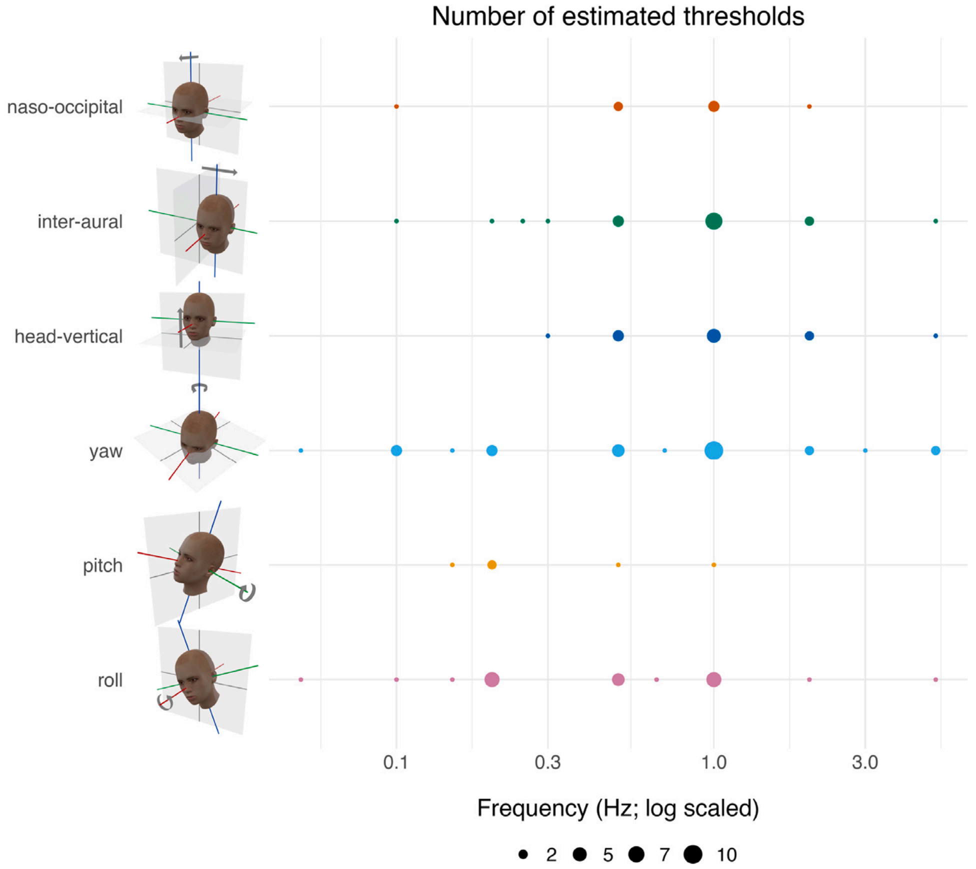

Fig. 1. Overview of the number of thresholds reported in the literature matching our inclusion criteria split by DOF and frequency. The motions corresponding to the 6 degrees of freedom are color-coded. The dof pictograms were created using a freely available 3D head model [7]. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

self- or world-motion and the distinction between active and passive self-motion.

One important feature that sets the vestibular system apart from other sensory systems is that it is, except for magnetic vestibular stimulation [4,5], never stimulated in isolation [6]. Changing the velocity of a body requires a force to act on it. This force can be generated either internally by the person's own motor activity, which also changes the proprioceptive input, or by an external force which must act on the body surface and thus activates the somatosensory system. This non-exclusivity might be the reason why a primary vestibular cortex has not yet been identified in humans.

In the clinic, vestibular function is usually assessed by methods which rely on mechanisms bypassing the cortex (e.g. reflex arcs), such as caloric vestibular stimulation (CVS), head impulse test (HIT) and vestibular evoked myogenic potentials (VEMPs). Vestibular perceptual thresholds have the great advantage of not relying exclusively on reflexive behavior. In contrast to the methods used in the clinic, thresholds measure a construct closer to conscious perception of motion. VEMPs, for example, contain no directional information. Often, patients report symptoms on a perceptual level, and, in some patients, no abnormalities can be found using clinical standard tests. Threshold measures allow for assessing all directions of motions separately. They also involve cortical processing of vestibular sensory information. For example, patients with Persistent Postural-Perceptual Dizziness (PPPD) report perceptual motion (dizziness) without a known organic/sensory cause. There are also patients who, despite having an intact vestibular system, have an attenuated perception of motion [8].

Perceptual thresholds rely on the conscious evaluation of sensory information related to self-motion, and they are therefore closer to the subjective reports given by vestibular patients. This review provides an integrative synthesis of the accessible information provided by previous studies. Thresholds from primate and human studies are considered and discussed. We focus on each of the six individual degrees of freedom (inter-aural, naso-ocipital, head-vertical, yaw, pitch, roll; see Fig. 1), and we refrain from including more complex protocols (e.g. self-motion along multiple axes, cyclic profiles). We will see that the comparison of single-axis motion thresholds yields substantial variability already, and therefore, we have chosen to restrict ourselves to those studies with a simple and well-defined stimulus profile, allowing for straightforward comparisons. Particular emphasis is given to the estimation of thresholds based on behavioral data, used devices and stimulus profiles. Complementing the review by Kobel et al. [9], we also address technical aspects (software and hardware), the relationship to animal data and perceptual learning.

The databases of Pubmed, ISI Web of Science, and Google Scholar were searched using combinations of the keywords "*vestibular, thresholds, perception, psychophysics, sensory, motion platform*". Relevant references found in the identified articles were also considered. To be included in this review, an article must report (1) vestibular perceptual thresholds for passive self-motion in the dark. (2) The motion profiles must consist of single cycles of sinusoidal acceleration. (3) The thresholds must be estimated separately for each of the six degrees of freedom (inter-aural, naso-ocipital, head-vertical, yaw, pitch, roll). (4) The threshold values must be provided in cm/s respectively °/s or in units convertible to cm/s or °/s. And (5) the subjects in the samples studied must belong to one of the following two groups: non-expert healthy subjects or vestibular patients. In total, 22 articles reporting 92 distinct threshold values for healthy participants and four articles reporting 28 distinct threshold values for vestibular patients met these criteria and were included in this article. All articles were published

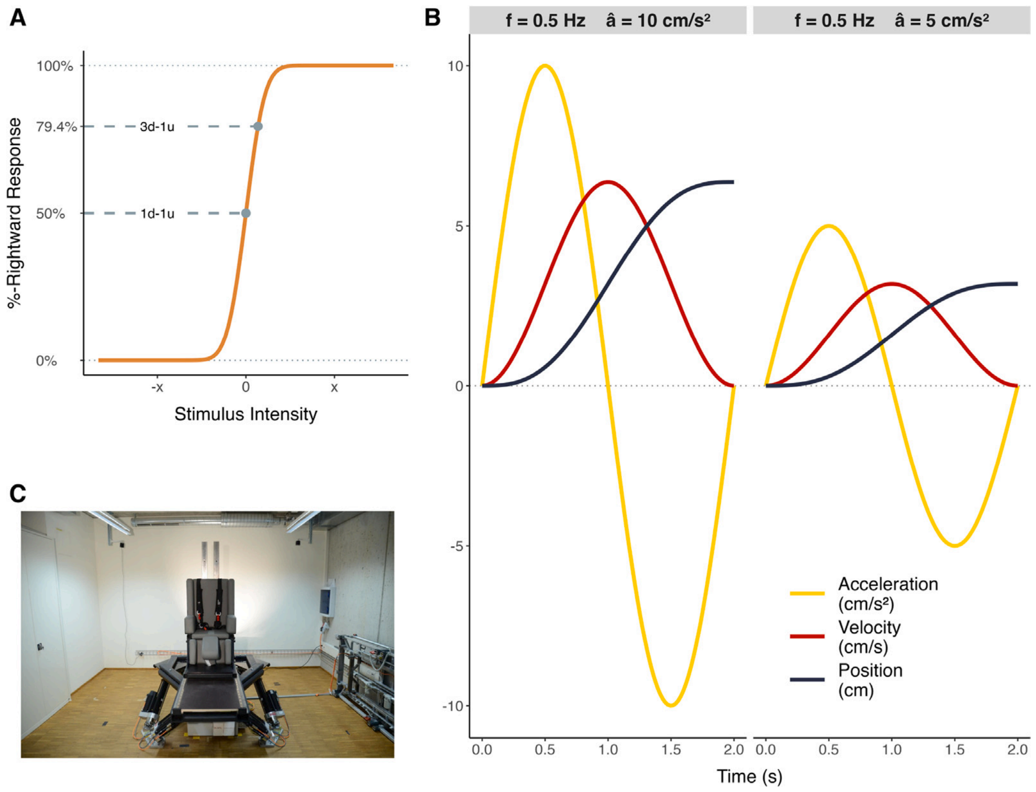

Fig. 2. A: The psychometric function relates observer performance (y-axis) to stimulus intensity (x-axis). In a discrimination task, the performance is given by the proportion of right answers (for a left right discrimination task along the inter-aural axis). In a detection task, the performance is given as the proportion of correct answers. Adaptive algorithms target fixed performance levels. For example a 1 up/3 down staircase targeting 79.4% and a 1 up/1 down staircase targeting 50% are shown. B: Acceleration, Velocity and Position are shown for a motion stimulus following a sinusoidal acceleration profile with a duration of 2 s. C: Image of a motion platform.

before June 2022. The data extracted from these articles and used in this manuscript can be found on the Open Science Framework (OSF: https://osf.io/ug6de/). Fig. 1 shows the available data, per frequency and movement axis. The figure also shows that more studies are needed with specific motion profiles; current knowledge is still scarce for frequencies below 0.3 Hz, and essentially for all linear accelerations above 1 Hz and for rotations in the pitch plane.

2. Technical aspects

2.1. Threshold estimation procedures

The psychometric function relates performance in a psychophysical task to some aspects of the motion-stimulus (e.g. acceleration strength) [10]. Estimating the psychometric function requires a large number of trials spanning the whole intensity range from chance to perfect performance, making this approach time consuming and inefficient for clinical use. In many cases, thresholds, describing a certain level of reliable discrimination (or detection depending on the task) performance are sufficient to answer the research question. Using adaptive estimation methods, test duration can be shortened substantially while maintaining accuracy by optimizing the placement of stimulus intensities. Using adaptive algorithms, either the threshold or the slope can be estimated. As described by Leek [11] there are several adaptive approaches, with staircase algorithms being the most popular in vestibular research. In typical staircase methods the target performance (threshold) is determined by the intensity update rule. A 1 up/1 down procedure results in estimating the 50% performance level. While a 1 up/3 down rule targets the 79.4% performance level (Fig. 2). A detailed description of the staircase procedure including a video can be found elsewhere [12]. Other estimation algorithms (e.g. PEST/QUEST) offer the possibility to freely choose the desired performance level.

In a detection task, motion stimuli are presented along or about one axis at a time. The stimulus intensity is determined by the selected algorithm trial by trial. The participant reports if a motion was detected. Vestibular stimulation is usually bidirectional [13]. A motion stimulus is always coupled to a direction. Any linear combination along or around the three main axes may be used. It is not possible, however, to combine multiple opposing directions in one stimulus. Instead of deciding whether a motion was present the subject has to discriminate between different motion directions. In a discrimination task, the stimulus intensity is still determined by the chosen algorithm for each trial. Given the intensity, motion direction is determined randomly. For a linear motion along the inter-aural axis the two directions correspond to left and right. The participant discriminates between the two possible motion directions. This binary choice, introduces the possibility of a directional response bias, where one option is favored over the other independent of the motion properties. With a bias present thresholds estimated by staircase procedures do not accurately describe discrimination sensitivity [14]. Because the psychometric function allows for a separate estimation of bias and threshold, this limitation can be overcome. This reflects the notion that a stimulus is represented in the brain as a random sample drawn from a distribution with a mean and variance [14].

2.2. Stimulation devices

The most frequently used devices are motion platforms/hexapods [3,15–27]. The popularity of hexapods is not surprising as they allow accelerating participants in all six degrees of freedom and therefore to estimate the vestibular perceptual threshold for each vestibular subcomponent separately. For the estimation of vestibular thresholds in the yaw plane rotatory chairs [28–30] offer a good alternative. Sleds on tracks have been used for studies on translational thresholds in the horizontal plane [31–34]. For roll and tilt translations a Tilt Translation Sled [35] was utilized. In some studies industrial robots [36,37], short-radius centrifuges [38,39], or hydraulic platforms [40,41] were used. There are also perceptual thresholds estimated based on galvanic stimulation [42–44]. Typically GVS is perceived as a rotation in the roll plane. However, galvanic stimulation is non-specific regarding the stimulated subcomponent of the peripheral vestibular organs. Despite the positive effect on posture [26] we do not consider GVS thresholds in this review because the link of GVS to perceptual vestibular thresholds is unclear.

2.3. Control software

Motion platforms are controlled by specialized software that is also able to synchronize with other hardware (e.g. VR-goggles, EEG-devices, screens). Though, most articles do not sufficiently specify the software used to control the motion platform and presentation of further stimuli. A systematic investigation showed that the software is only mentioned in eleven of the 37 articles included in this review. Of this eleven articles, six used custom-made programs which are not published and cannot be reused or analyzed [29,30,45–48]. Others [36,37,41,49,50] used proprietary, closed-source software solutions dedicated to particular hardware (e.g. D-Flow by Motex). No group published the code they used to generate the motion profiles and control the motion device, which hinders replications, collaborations and the identification of errors. To overcome the limitation, we recently published *PlatformCommander* [51], an open-source toolbox for interfacing motion platforms and synchronization with other devices (VR-goggles, screens, buttons).

2.4. Stimulation profiles

Multiple stimulation profiles with different properties have been used in vestibular threshold estimation experiments. Unfortunately, not all reports describe the used profile detailed enough, which hinders a systematic comparison of the results obtained by different laboratories. However, the most used class of profiles are trigonometric such as sinusoidal [18,20] functions. In Fig. 2 (pane B) acceleration, velocity and position are shown for two example stimuli over time. The formula for this sinusoidal acceleration a(t) is as follows [18]:

$$a(t) = A\sin(2\pi f t) = A\sin(2\pi t/T) \tag{1}$$

where A is the maximum acceleration and f denotes the frequency. The formula for the velocity v(t) and position p(t) can be obtained by integrating a(t) once, or twice respectively:

$$v(t) = AT/(2\pi)[1 - \cos(2\pi t/T)] \tag{2}$$

$$p(t) = AT/(2\pi)[t - T/(2\pi)sin(2\pi t/T)] \tag{3}$$

In most cases a single cycle of the oscillation was presented but some studies also used multi-cycle sinusoidal profiles [49,52]. Harmonic functions such as sine or cosine have the beneficial property that they can be described by two parameters (A,f) and can easily be integrated or derived. Based on these two parameters, properties like the duration $(T = 1/f)$ peak velocity $\left(v_{\max} = AT/\pi\right)$ or the total displacement $\left(\Delta p = AT^2/2\pi\right)$ of the motion profile can be calculated. Thresholds are usually estimated separately for different frequencies. Within each frequency block, peak acceleration is varied. Altering the peak acceleration and keeping the frequency constant affects peak velocity as well as the end position (Fig. 2 (pane B)). Vestibular thresholds are usually expressed as the peak velocity of the corresponding motion profile (e.g. Fig. 3). To ensure smooth motion profiles the manufacturers of motion platforms (high-pass) filter the requested position signal. This can lead to a considerable difference between the requested and the actual speed of the platform and distort the profile with respect to peak velocities or duration. Unfortunately, papers only report the mathematical description of the stimulus without mentioning the applied filter parameters of the platform. Future articles should disclose, at least in the supplementary material, the motion profile that was actually executed and reported by the platform.

Other profiles such as triangular [28], trapezoidal [36], or impulse like motion profiles [53], require more complex mathematical descriptions and their Fourier approximation contains multiple frequencies. Since vestibular thresholds are known to vary with stimulation frequency (see below), multi-frequency stimulation, like impulse or triangle profiles, could be inappropriate depending on the specific research question. Another benefit of sinusoidal profiles is that, for rotations, they roughly resemble voluntary, unrestricted motion profiles [54]. For passive translations, sinusoidal profiles are not an ideal approximation of profiles occurring in real-life. There is typically a period of constant velocity between the acceleration and deceleration. A bus, for instance, usually travels at a constant speed between accelerating and slowing. Acceleration profiles can be recorded in real life and played back on the motion device using *PlatformCommander*. This way, the external validity of the motion profiles can be increased.

A further obstacle to comparing values from different laboratories concerns the rotational axes of angular motion profiles. For rotations around the yaw axis, this seems to be less of an issue, as most devices (rotatory chairs, hexapods) typically aim to align the rotation axis with the head vertical. For roll and pitch rotations it is important to keep in mind, that the origin of the native coordinate system of hexapods is typically quite different from the position of the participants head and vestibular end-organs. Rotations around the native platform axis often result in a combination of rotation and translation. This can be overcome by adjusting the rotation axis individually. It is noteworthy, however, that an optimized rotation around an axis positioned at the height of the participant's vestibular organs leads to a substantial reduction of the desired motion range. Our literature review revealed that the rotational center for angular motion stimuli is often not reported, thus leading to ambiguities in the conclusions that can be drawn from the results.

3. Threshold data

The threshold values represent the peak velocity required for reliable discrimination of a motion stimulus. The level of reliability is expressed as % correct classification per stimulus intensity. The percentage depends on the method used to estimate the threshold (e.g. Fig. 2) and may differ between studies. A range of 70 to 84% can be observed among the included studies. However, there are two exceptions. van Stiphout et al. [50] tested patients using a 1 up 1 down staircase algorithm converging at 50%. Soyka et al. [36] used a discrimination task with 4 alternatives converging at 62.5%.

The thresholds reported by these studies are illustrated in Fig. 3. It is important to point out that a one-to-one comparison of the results reported by different studies is not easy because each lab used different approaches, including estimation algorithm, threshold definition, equipment, and reporting standards. Additionally, the platforms might apply different filters altering the requested profile. The thresholds of healthy controls are also summarized in Table 1. The data from this table can be used as norm values based on the literature.

3.1. Translation

A study [1] on head acceleration during daily activities reported that the mean accelerations sensed by the otolith organs are smaller than 1 G ($9.81\ \mathrm{m/s^2}$). During passive movements the largest forces can typically be registered in the fore/aft direction (e.g. 1.06 G: car ride) with very small vertical accelerations.

Regarding the nomenclature multiple terms are used to label the main axes of motion. All naming schemes are based on a head-centered rectangular Cartesian coordinate system and differ in the naming of the axes. Most authors use the terms naso-occipital (NO), inter-aural

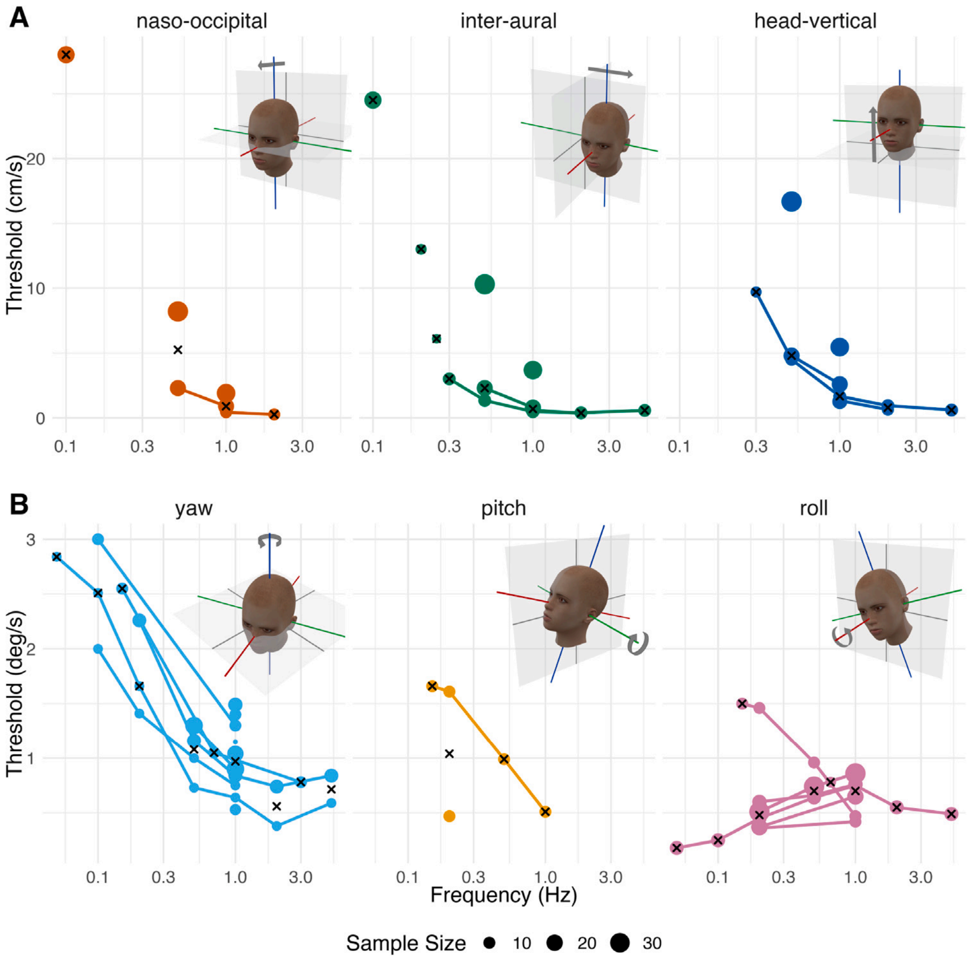

Fig. 3. Distinct thresholds are plotted over the tested frequencies for healthy controls. The crosses indicates the median threshold across all included studies at the respective frequency. The *x*-axis is scaled logarithmically. Thresholds estimated from the same sample at multiple frequencies are connected by a line. The motions corresponding to the 6 degrees of freedom are color-coded. A: Thresholds for linear translations along the naso-occipital (left), inter-aural (middle) and head-vertical axis (right). B: Thresholds for rotations in the yaw (left), pitch (middle), and roll (right) plane. The dof pictograms were created using a freely available 3D head model [7]. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
A summary of the median threshold, its range and the number of individual thresholds. These values are based on all included studies reporting thresholds for healthy controls (see Tables A.2 and A.3).

DOF	Median threshold	Range threshold	Unit	n Studies
Naso-occipital	1.91	0.27–28.01	cm/s	7
Inter-aural	0.80	0.35–24.51	cm/s	18
Head-vertical	2.13	0.61–16.7	cm/s	12
Yaw	1.10	0.38–3	deg/s	28
Pitch	0.99	0.47–1.66	deg/s	5
Roll	0.62	0.18–1.5	deg/s	22

(IA), or head-vertical (HV) [22,24]. Using the anatomical landmark allows for an unambiguous and intuitive definition of the main motion axes. Others use the letters X, Y, and Z where X refers to the NO, Y to the IA and Z to the HV axis [25,55]. This labeling option seems little intuitive and could lead to erroneous interpretations and ambiguities when explicit definitions are lacking. Sometimes, the terms fore/aft, left/right, and up/down are used to refer to the main axes [53]. These terms might be easier to understand compared to NO, IA, and HV, but they can also cause ambiguities in experiments where the subject is not upright (e.g., supine position) [56], and it thus becomes unclear whether the terms refer to the motion direction of the platform or the participant's head. A summary of all included studies reporting vestibular thresholds in healthy participant for linear motions can be found in Table A.2.

3.1.1. *Naso-occipital (fore/aft)*

In the naso-occipital direction we identified five studies [19,22,24,32,56] reporting seven perceptual thresholds at frequencies between 0.1 and 2.0 Hz. Due to the small number of data points the relationship between the stimulation frequency and the threshold can only be interpreted with caution. Considering all data points it seems that the thresholds decrease with increasing stimulation frequency. This is supported by the two studies reporting threshold values at multiple frequencies [19,56].

3.1.2. *Inter-aural (left/right)*

Thirteen Studies reported 20 individual thresholds along the inter-aural axis [19,20,22–27,32,33,47,55,56]. They have been measured over the largest frequency range (0.1–5.0 Hz) compared to the other translation directions. Most data is available for the 1.0 Hz stimulation frequency. The median threshold across frequency follows a high pass characteristic as described for yaw rotations by Grabherr et al. [18]. The few data points available for low stimulation frequencies show a huge variance compared to other stimulation axes.

3.1.3. Head-vertical (up/down)

Along the head-vertical axis 12 thresholds have been reported in 6 studies [19,20,22,24,25,56]. One study [20] measured thresholds over the whole frequency span (0.3–5.0 Hz) within the same participants. Such within subject studies have the advantage of controlling for interindividual variance and avoiding noise due to differences in experimental setup (e.g. head fixation, estimation procedure). The results show a clear decrease of thresholds with increasing stimulation frequency. This is also consistent with other studies reporting head-vertical thresholds.

3.2. Rotation

During passive angular movements in everyday life accelerations from 73.96 to 334.02 °/s were measured [1]. These angular accelerations are sensed by the semicircular canals. While head rotations in the yaw and pitch plane are performed frequently with a great variance in velocity, start and end position. Rotations in the roll plane are performed more rarely. The terms yaw, pitch, and roll always refer to the body-centered rotation. It is important to keep in mind that switching to a platform-centered view or changing the center of rotation can greatly alter the motion experienced by the participant. A summary of all included studies reporting vestibular thresholds in healthy participant for angular motions can be found in Table A.3.

3.2.1. Yaw

We identified 12 studies reporting 30 individual threshold values [18–20,23,25,27,30,37,45–48]. Yaw rotation thresholds are the most frequently investigated vestibular thresholds. They are documented for frequencies ranging from 0.05 to 5 Hz. The reasons for this is that most available devices (hexapods, rotatory chairs or centrifuges) are able to perform rotations around the vertical axis. Another advantage of yaw rotations is that less adjustment is needed for positioning the participant's vestibular organs relative to the rotation axis, as the motion device is typically aligned with the rotation axis. This is of course not the case for centrifuges, which do not lead to pure rotations only sensed by the semicircular canals. Based on the results reported by two studies [18,57]. Grabherr and colleagues suggest that the thresholds follow a high pass filter characteristic with a time constant of 0.70 s (cut-off frequency = 0.23 Hz) and a threshold plateau of 0.71 deg/s. In the light of yaw thresholds available, this pattern remains robust.

3.2.2. Pitch

We could only find three studies reporting seven vestibular thresholds for the pitch plane [35,47,55]. These thresholds are documented for stimulation frequencies from 0.15 to 2 Hz. Despite the uncertainty due to the small number of data points, the threshold frequency relationship appears to be similar to the one observed with yaw rotations.

3.2.3. Roll

We found 8 studies reporting 24 perceptional threshold values for the roll plane [20,21,25,26,35,47,55,58]. Thresholds are available for frequencies between 0.05 and 5 Hz. A clear relationship of thresholds and frequency cannot be seen. There are studies reporting decreased [35,47] or increased [3,25,26] thresholds for higher frequencies. Data reported by Valko et al. [20] suggest a more complex relationship. In summary, roll threshold data is inconclusive and further data is needed to reveal the true relationship. The discrepancy between these reports might be due to variance in the positioning of the rotational axis. This information is not reported adequately by all of the studies. Another important point is that roll tilts in upright participants inevitably involve a stimulation of the otoliths, and, eventually, other sensory systems as this type of movement has shown a comparatively small difference between bilaterally impaired vestibular patients and healthy participants [50].

3.3. Age effects

Based on individual findings there is a consensus that thresholds increase with age [3,25]. To test this conclusion on a meta-level we plotted the relationship between thresholds and age (Fig. 4). Data is available for the development of vestibular thresholds within adulthood. Among all included studies participants from 23.5 years to 74.6 years were included. For subjects younger than 20 years there is very limited threshold data reported in literature Hartmann et al. [47]. We included thresholds at 0.5 and 1 Hz for linear motion profiles (NO, IA, HV) and thresholds at 0.2 and 1.0 Hz for rotational motion profiles (yaw, pitch, roll). These frequencies were selected because they contain the most data points across age. The information about the age of the participants is available either in the form of a mean or as a range.

Although age-range contains less information these data points were included because studies on age effects typically group their participants by decades. This overview confirms the conclusion of the individual studies. Where enough data is available thresholds increase with age. A summary of all included studies reporting vestibular thresholds and the age in healthy participants can be found in Tables B.4 and B.5.

3.4. Further individual factors

Besides age, other factors could potentially impact vestibular perceptual thresholds. We found five studies comparing thresholds between female and male participants [18,19,22,32,41]. None of these studies found gender-effects. A further potential factor is handedness. Imaging studies [59] suggest that the cortical vestibular network possesses a handedness dependent asymmetry. This could also influence vestibular perception. Surprisingly only two studies [18,19] reported the handedness of the tested participants, but none of them analyzed it systematically.

Frequent exposure to a specific acceleration environment (e.g. sailors, figure skaters) could also influence vestibular thresholds. Furthermore, physical properties of the body (e.g. absolute mass, mass distribution) might have an influence. In the available data, the influence of these factors on vestibular thresholds was not considered. A few studies investigated vestibular perception in expert groups such as artistic gymnasts [47] or pilots [60]. The results suggest small effects specific to certain types of motion.

3.5. Vestibular disorders

Vestibular perceptual thresholds have been investigated in the context of vestibular disorders and a dedicated review can be found elsewhere [9]. Here we show the available data points (Fig. 5). Data are available for patients with bilateral vestibulopathy (BVP) [16,22,31,45,61], Menieres disease (MD) [24], vestibular migraine (VM) and vestibular schwannomas (VS) [20]. The limited available data on patients are restricted and relevant factors like the impaired side could not be reliably analyzed. The disorders are therefore grouped under the category vestibular disorders (VD). Vestibular migraine thresholds are considered their own group because of their different pathogenesis [24]. It has been reported that vestibular thresholds are lower in patients with (vestibular) migraine compared to healthy controls because of the common symptom motion hypersensitivity, although not significantly [24]. This pattern of lower thresholds in patients compared to the within-study control group does not emerge when patients are compared to all healthy controls. Additionally, two studies investigated migraine patients but did not mention the estimated thresholds [62,63].

First data investigating PPPD is available, reporting reduced thresholds for yaw-rotations compared to healthy controls [64]. Due to the uncommon test procedure this study is not included in this review. The included threshold values for vestibular disorders are consistently higher than the median threshold of the respective healthy controls. A summary of all included studies reporting vestibular thresholds in patients can be found in Table C.6.

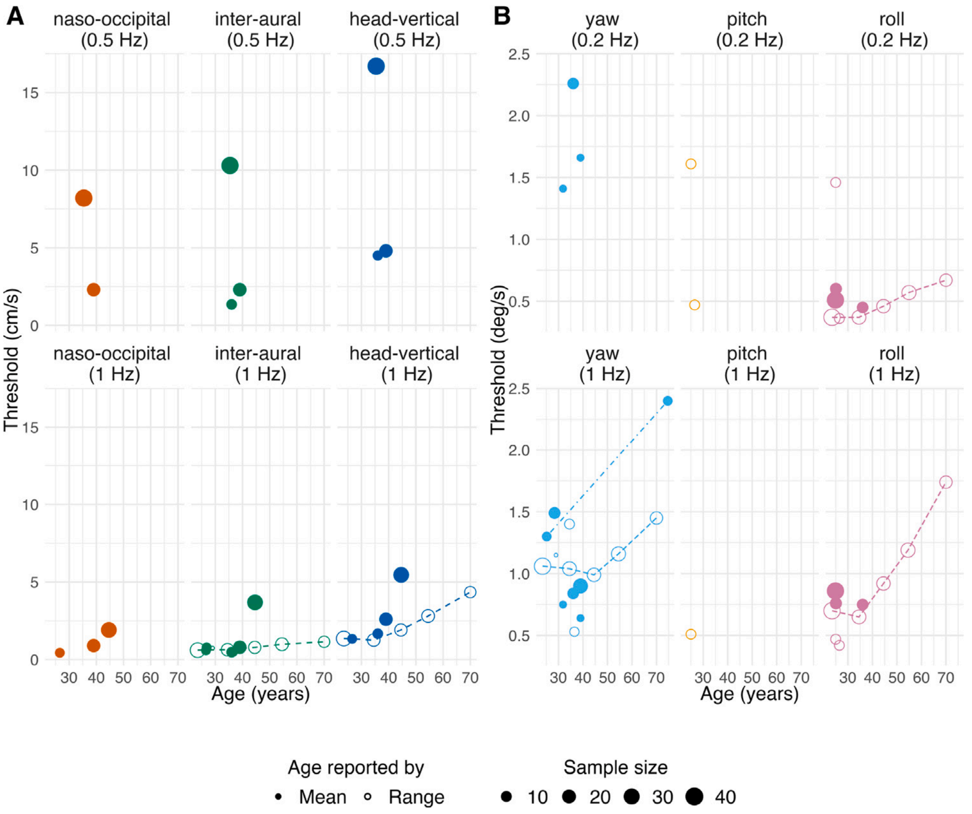

Fig. 4. Threshold values at different ages estimated from the same sample are connected by a line. Solid dots represent studies that report mean age. The open dots represent those that report the samples age range. In this case, the midpoint of the given range was used for the plot. The motions corresponding to the 6 degrees of freedom are color-coded. A: Thresholds for 0.5 and 1 Hz along the three main axes. B: Thresholds for 0.2 and 1 Hz about the three main axes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Vestibular thresholds in humans vs. primates

A comparison of perception thresholds between humans and other species is difficult to obtain. Primates can be trained to perform a psychophysical discrimination task [65]. The extensive training procedure of primates results in a higher level of expertise compared to verbally instructed and therefore task naive human participants. It is therefore unclear how this affects threshold comparisons across species [66]. A qualitative comparison can provide valuable insights. A few studies analyzed firing patterns and detection thresholds in setups similar to those used in human research. For example, [67] used firing rates to calculate detection thresholds in monkeys (macaca fascicularis) during passive whole-body yaw rotations with a sinusoidal acceleration profile. Detection thresholds were estimated for the frequency range between 0.5 and 15 Hz and for regular and irregular afferent signals. The latter show thresholds for lower frequencies. However, the thresholds again increased for frequencies larger than 5 Hz. This raises the question whether this is also the case in humans, where no threshold data is available for stimulation frequencies above 5 Hz.

Another aspect worth comparing are the relative thresholds between the axes. Yu et al. [66] reported detection thresholds in primates for regular and irregular otolith afferents and excitatory and inhibitory thresholds for 1 Hz stimulations. Three out of the four thresholds showed the largest value for translations in the naso-occipital direction and smallest for head-vertical translations. Interestingly, within subject comparisons of the perception thresholds estimated in healthy human participants for the three main axes consistently also reported the largest thresholds in the head-vertical direction [19,20,22,24,25]. The difference between thresholds in the inter-aural and naso-occipital direction is less consistent and typically small. For rotations the thresholds about the yaw axis are comparable to those of humans [20,68], and thresholds for pitch are typically larger than for the roll axis [35,55,68]. We are not aware of corresponding data in other species. To summarize, the threshold order in primates is $NO > IA > HV$ while it differs for humans $HV > NO \sim IA$.

The discrepancy between the thresholds measured on a neural level in monkeys and thresholds estimated on a perceptual level in humans could reflect differences in evolutionary adaptation to the natural motion spectrum. An alternative explanation could be that this difference reflects the cognitive influence on perception.

5. Perceptual learning

When dealing with vestibular thresholds, their stability on different time scales is a crucial issue. Vestibular perception declines with age, and the thresholds increase. The emerging domain of vestibular perceptual learning (PL) is focusing on altering thresholds as a function of training. There is evidence of improved direction discrimination. Klaus et al. [55] found decreased 0.2 Hz roll thresholds after six training days. Wagner et al. [69] reported lower roll thresholds for 0.2 and 0.5 Hz after only 5 training days. They also provide preliminary evidence, that perceptual learning might influences balance. While there is evidence that vestibular thresholds relate to other postural parameters, the impact of training is not yet understood. PL is defined as the lasting improvement in sensory function elicited by practice or repeated exposure to stimuli [70–72]. Though, there is evidence that perceptual improvements can also happen in the absence of physical stimulation (e.g. by mental imagery [73]. PL is best studied in the visual domain,

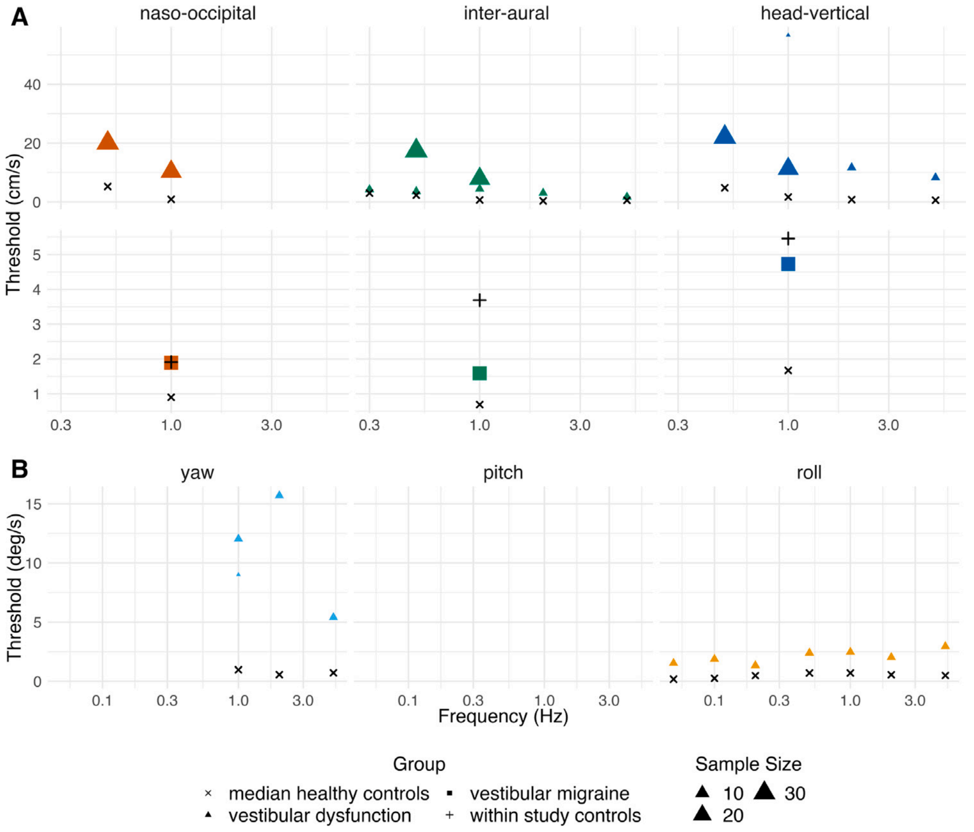

Fig. 5. Thresholds are plotted over the tested frequencies for patients. The median of the respective healthy controls is marked by the x. The *x*-axis is scaled logarithmically. The motions corresponding to the 6 degrees of freedom are color-coded. A: Thresholds for linear translations along the three main axes. Thresholds from vestibular migraine patients are visualized separately and supplemented with the thresholds from the within-study control group. B: Thresholds about the three main axes. There are no angular thresholds reported for vestibular migraine patients. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

where learning effects have been documented for features such as orientation [74], contrast [75,76], or texture [77]. PL has also been demonstrated in the auditory domain [78,79], the tactile domain [80,81], and in the chemical senses [82,83]. In the vestibular domain PL has been addressed only by a few studies. In two recent reports [55,69] roll/tilt direction discrimination improved after a few days of training thereby providing first evidence of PL by passive self-motion. However, an earlier study on yaw-rotations and inter-aural translations failed to demonstrate PL in darkness [68]. Klaus et al. [55] argue that PL might only occur in the vestibular system, when the semicircular canals and otoliths are stimulated jointly by the passive motions and that the learning effect is most likely related to an optimization of the signal integration. Regardless of whether the interpretation is correct or not, the question regarding the occurrence of PL in the vestibular system can, at this point in time, not be answered with the same certainty as for the other sensory systems.

6. Further considerations

6.1. Non-vestibular input

The fact that one finds the expected disorder-dependent changes in patient thresholds indicates that vestibular function mainly drives the measured perceptual thresholds. However, to set a body in motion a force (internal/external) has to act on it. This means every motion stimulus is accompanied by somatosensory input highly correlated to the motion itself. The forces acting upon the body in order to change its velocity cannot be removed by air bearings, non-motorized drives, or any other technological trick. Therefore, necessities such as head fixation and belts are an additional but typically ignored source of non-vestibular information. Moreover, changes in fluid distribution within the body can influence the perception of body position [84,85]. Jarchow et al. [86] studied the influence of non-visual extra-vestibular information on the perception of gravity during centrifugation in healthy and paraplegic participants.

In this context it would be interesting to see if the somatosensory or proprioceptive systems also show a frequency dependence. The availability of threshold data from nephrectomized patients [87] or from paraplegics would allow to estimate the contributions of non-vestibular perceptions more accurately.

In addition to the intended acceleration, the use of motion platforms introduces unavoidable background vibrations that can be correlated with the intensity of the motion [34,88]. The manufacturers of motion platforms try to counteract this by filtering the requested position signal. The exact filter parameters can differ between platforms which add to the undocumented differences in experimental setups between labs.

Motion platforms also generate a significant amount of auditory noise, which is correlated with the motion profiles. Typically, stronger accelerations cause larger auditory noise which could be used as an additional source of information during threshold experiments. To avoid this, white noise has been used to mask these auditory cues when intensity discrimination was part of the task [24,55,89].

6.2. Stimulation profiles

In this review we included studies using the standardized uni-cycle sinusoidal motion profile. However, there are studies using diverging profiles like multi-cycle sinusoidal or triangle which might be more suitable for specific questions. Non sinusoidal profiles might play bigger role in the future, because a recent study [90] in monkey revealed remarkable differences in the coding of natural compared to artificial stimuli on a thalamic level. At this point it is unclear, whether this also affects higher vestibular functions like perceptual decision making. Given the known function of the thalamus as a relay and filter hub, it might be worth investigating more naturalistic profiles (e.g. recorded during daily activities) in psychophysical tasks.

6.3. Stimulation axes

Most of the studies test vestibular perceptual thresholds along and around the three main axes while the participant is in the upright position with gravity pulling along the head-vertical axis. This traditional approach has been extended by two recent studies. Kobel et al. [56] investigated the impact of gravity on the perception on translational motion by comparing thresholds acquired in the supine, upright, and side-lying position. Wagner et al. [91] compared rotations in the roll and pitch planes to rotations in the planes aligned with the anatomic orientation of the vertical semicircular canals.

6.4. Perception and cognition

Most studies on vestibular thresholds focus on sensory aspects. This leads to the assumption that thresholds reflect properties of the sensory system. However, over the last years studies demonstrated that perception involves non-sensory components such as decision making. Cognitive processes influencing the decision making process were shown for implicit [92] or explicit [93] manipulations of participants expectations. This can lead to changes in response behavior independent of the physical properties of the motion stimulus [89].

7. Conclusion

The purpose of this review was to gather and describe all evidence concerning vestibular perceptual thresholds . Much is already known about threshold values for certain motion frequency combinations in healthy participants. In healthy participants thresholds have been measured in all six degrees of freedom (naso-occipital, inter-aural, head-vertical, yaw, pitch, roll) for frequencies ranging from 0.05 to 5 Hz. Most studies examined perceptual thresholds in the yaw plane followed by roll and the inter-aural axis. As demonstrated in this review the hyperbolic (Fig. 3) relationship between thresholds and frequency can only be concluded in five of the six main movements. For thresholds around the roll axis the literature does not present a consistent pattern and further studies are needed to explain the discrepancy across studies. This is important since roll rotation thresholds have been used frequently in recent studies.

There are clear gaps for the healthy older adult population and patients. As already shown by individual studies, thresholds are increasing with age. Our synthesis confirmed this phenomenon for all six main movements for healthy participants (Fig. 4). This emphasizes the importance of a balanced age distribution in comparative studies between groups.

Relatively few studies report data obtained in patients. No patient data are available for pitch rotations. The available data consistently reports increased thresholds in patients with peripheral vestibular disorders compared to healthy controls. Some of the studies reporting patient data suffer from confounds, e.g., a significantly younger control group [22] which hinders a clear interpretation of the data.

With only one study that measured vestibular thresholds in combination with anxiety measures in PPPD patients [64], the available information is still scarce and more research will be needed to better understand how personality traits can influence vestibular thresholds.

A qualitative comparison of primate and human vestibular thresholds yielded two interesting findings. First, in monkeys the head-vertical axis showed the lowest neural thresholds for translations among the three main directions. In humans the largest thresholds are typically observed for head-vertical translations. This might reflect an adaptation of the vestibular system to the reduced movement activity of humans along the vertical axis compared to monkeys. Second, the available data for frequencies up to 15 Hz in monkeys seem to indicate that thresholds might not reach a plateau for at about 1 Hz, but instead start increasing, resulting in a U-shaped frequency dependency. It is surprising that no data on higher frequency is available, as it is known that natural vestibular input in humans reaches up to 20 Hz. Therefore, future data targeting thresholds at higher frequencies than 5 Hz might be interesting in the context of the widely accepted high-pass model [18,94].

Vestibular thresholds continue to be used in the study of perception, cognition, learning, and balance. Furthermore, thresholds have considerable potential to complement the procedures used in clinical practice and to dig deeper into the perceptual aspect of vestibular disorders. In everyday life they can contribute to next generation screening tools for professional athletes (e.g. gymnasts, downhill mountainbikers). Or in professions such as high-rise construction or scaffolding, thresholds can facilitate the screening of potential workers and improve workplace safety.

Future developments such as an increased use of sleeper trains or self driving cars will make knowledge about human vestibular perceptual thresholds more important. Also manned spaceflight missions to the Moon or Mars will entail environments to which the vestibular system is not adapted to. Vestibular thresholds will inform how to re-adapt and how to best counteract the long-term effects of altered gravity.

Declaration of competing interest

none

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Appendix A. Tables healthy subjects

See Tables A.2 and A.3.

Appendix B. Tables age

See Tables B.4 and B.5.

Appendix C. Table disorders

See Table C.6.

Table A.2

A summary of all studies that have estimated thresholds for linear motion in healthy subjects. The frequencies tested and the corresponding sample sizes are listed.

Author	Year	Axis	Frequency	Nbsubjects
Kobel et al.	2021	Naso-occipital	1, 2	12, 12
Bremova et al.	2016	Naso-occipital	1	34
Agrawal et al.	2013	Naso-occipital	0.5	42
Roditi and Crane	2012	Naso-occipital	0.5, 1	24, 24
Kingma et al.	2005	Naso-occipital	0.1	28
Kobel et al.	2021	Inter-aural	1, 2	12, 12
Keywan et al.	2020	Inter-aural	1	9
Klaus et al.	2020	Inter-aural	0.2	10
Keywan et al.	2019	Inter-aural	1	12
Bermudez Rey et al.	2016	Inter-aural	1	20
Bremova et al.	2016	Inter-aural	1	34
Agrawal et al.	2013	Inter-aural	0.5	42
Chaudhuri et al.	2013	Inter-aural	1	4
Roditi and Crane	2012	Inter-aural	0.5, 1	24, 24
Valko	2012	Inter-aural	0.3, 0.5, 1, 2, 5	14, 14, 14, 14, 14
Zupan and Merfeld	2008	Inter-aural	0.25	7
Kingma et al.	2005	Inter-aural	0.1	28
Kobel et al.	2021	Head-vertical	1, 2	12, 12
Bermudez Rey et al.	2016	Head-vertical	1	20
Bremova et al.	2016	Head-vertical	1	34
Agrawal et al.	2013	Head-vertical	0.5	42
Roditi and Crane	2012	Head-vertical	0.5, 1	24, 24
Valko	2012	Head-vertical	0.3, 0.5, 1, 2, 5	10, 13, 14, 14, 14

Table A.3

A summary of all studies that have estimated thresholds for angular motion in healthy subjects. The frequencies tested and the corresponding sample sizes are listed.

Author	Year	Axis	Frequency	Nbsubjects
Keywan et al.	2020	Yaw	1	9
Lee et al.	2020	Yaw	1	15
Shayman et al.	2020	Yaw	0.1, 0.2, 0.5, 1	7, 7, 7, 7
Shayman et al.	2018	Yaw	1	10
Bermudez Rey et al.	2016	Yaw	1	20
Peters et al.	2016	Yaw	0.1, 1	10, 10
Chaudhuri et al.	2013	Yaw	1	4
Roditi and Crane	2012	Yaw	0.5, 1	24, 24
Soyka et al.	2012	Yaw	0.15, 0.7, 3	10, 10, 10
Valko	2012	Yaw	0.2, 0.5, 1, 2, 5	14, 14, 14, 14, 14
Grabherr et al.	2008	Yaw	0.05, 0.1, 0.2, 0.5, 1, 2, 5	7, 7, 7, 7, 7, 7, 7
Klaus et al.	2020	Pitch	0.2	10
Suri & Clark	2020	Pitch	0.15, 0.2, 0.5, 1	10, 10, 10, 10
Wagner et al.	2021	Roll	0.2, 0.5, 1	33, 33, 33
Klaus et al.	2020	Roll	0.2, 1	10, 10
Suri & Clark	2020	Roll	0.15, 0.2, 0.5, 1	10, 10, 10, 10
Keywan et al.	2018	Roll	1, 0.5, 0.2	15, 15, 15
Bermudez Rey et al.	2016	Roll	0.2, 1	20, 20
Cran	2012	Roll	0.66	8
Valko	2012	Roll	0.05, 0.1, 0.2, 0.5, 1, 2, 5	14, 14, 14, 14, 14, 14, 14

Table B.4

A summary of all studies that have assessed age in relation to thresholds for linear movements in healthy subjects. The relevant frequencies, the age groups and the corresponding sample size are shown.

Author	Year	Axis	Frequency	Age_plot	Nbsubjects
Agrawal et al.	2013	Naso-occipital	0.5	35.4	42
Roditi and Crane	2012	Naso-occipital	0.5, 1	39, 39	24, 24
Kobel et al.	2021	Naso-occipital	1	26.57	12
Bremova et al.	2016	Naso-occipital	1	44.6	34
Agrawal et al.	2013	Inter-aural	0.5	35.4	42
Roditi and Crane	2012	Inter-aural	0.5, 1	39, 39	24, 24
Valko	2012	Inter-aural	0.5, 1	36, 36	14, 14
Kobel et al.	2021	Inter-aural	1	26.57	12
Keywan et al.	2020	Inter-aural	1	36.5	9
Keywan et al.	2019	Inter-aural	1	26.8	12
Bremova et al.	2016	Inter-aural	1	44.6	34
Chaudhuri et al.	2013	Inter-aural	1	29	4
Bermudez Rey et al.	2016	Inter-aural	1, 1, 1, 1, 1	23.5, 34.5, 44.5, 54.5, 70	29, 20, 19, 21, 16
Agrawal et al.	2013	Head-vertical	0.5	35.4	42
Roditi and Crane	2012	Head-vertical	0.5, 1	39, 39	24, 24
Valko	2012	Head-vertical	0.5, 1	36, 36	13, 14
Kobel et al.	2021	Head-vertical	1	26.57	12
Bremova et al.	2016	Head-vertical	1	44.6	34
Bermudez Rey et al.	2016	Head-vertical	1, 1, 1, 1, 1	23.5, 34.5, 44.5, 54.5, 70	29, 20, 19, 21, 16

Table B.5
A summary of all studies that have assessed age in relation to thresholds for angular movements in healthy subjects. The relevant frequencies, the age groups and the corresponding sample size are shown.

Author	Year	Axis	Frequency	Age	Nbsubjects
Shayman et al.	2020	Yaw	0.2, 1	31.86, 31.86	7, 7
Valko	2012	Yaw	0.2, 1	36, 36	14, 14
Grabherr et al.	2008	Yaw	0.2, 1	39, 39	7, 7
Keywan et al.	2020	Yaw	1	36.5	9
Lee et al.	2020	Yaw	1	28.4	15
Shayman et al.	2018	Yaw	1	34.5	10
Chaudhuri et al.	2013	Yaw	1	29	4
Roditi and Crane	2012	Yaw	1	39	24
Peters et al.	2016	Yaw	1, 1	74.6, 25.2	10, 10
Bermudez Rey et al.	2016	Yaw	1, 1, 1, 1, 1	23.5, 34.5, 44.5, 54.5, 70	29, 20, 19, 21, 16
Klaus et al.	2020	Pitch	0.2	26.5	10
Suri & Clark	2020	Pitch	0.2, 1	25, 25	10, 10
Bermudez Rey et al.	2016	Roll	0.2, 0.2, 0.2, 0.2, 0.2, 1, 1, 1, 1, 1	23.5, 34.5, 44.5, 54.9, 70, 23.5, 34.5, 44.5, 54.5, 70	29, 20, 19, 21, 16, 29, 20, 19, 21, 16
Wagner et al.	2021	Roll	0.2, 1	24.9, 24.9	33, 33
Klaus et al.	2020	Roll	0.2, 1	26.5, 26.5	10, 10
Suri & Clark	2020	Roll	0.2, 1	25, 25	10, 10
Valko	2012	Roll	0.2, 1	36, 36	14, 14
Keywan et al.	2018	Roll	1, 0.2	25.1, 25.1	15, 15

Table C.6
A summary of all studies that have estimated thresholds for vestibular patients. The frequencies tested and the corresponding sample size are shown. There are studies on the following disorders: bilateral vestibulopathy (BVP), Menieres disease (MD), vestibular migraine (VM), vestibular schwannomas (VS).

Author	Year	Axis	Group	Frequency	Nbsubjects
Bremova et al.	2016	Naso-occipital	VM, MD	1, 1	20, 27
Agrawal et al.	2013	Naso-occipital	BVP	0.5	33
Bremova et al.	2016	Inter-aural	VM, MD	1, 1	20, 27
Agrawal et al.	2013	Inter-aural	BVP	0.5	33
Valko	2012	Inter-aural	VS, VS, VS, VS, VS	0.3, 0.5, 1, 2, 5	3, 3, 3, 3, 3
Bremova et al.	2016	Head-vertical	VM, MD	1, 1	20, 27
Agrawal et al.	2013	Head-vertical	BVP	0.5	33
Valko	2012	Head-vertical	VS, VS, VS	1, 2, 5	1, 3, 3
Shayman et al.	2018	Yaw	BVP	1	3
Valko	2012	Yaw	VS, VS, VS	1, 2, 5	1, 3, 3
Valko	2012	Roll	VS, VS, VS, VS, VS, VS, VS	0.05, 0.1, 0.2, 0.5, 1, 2, 5	3, 3, 3, 3, 3, 3, 3

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