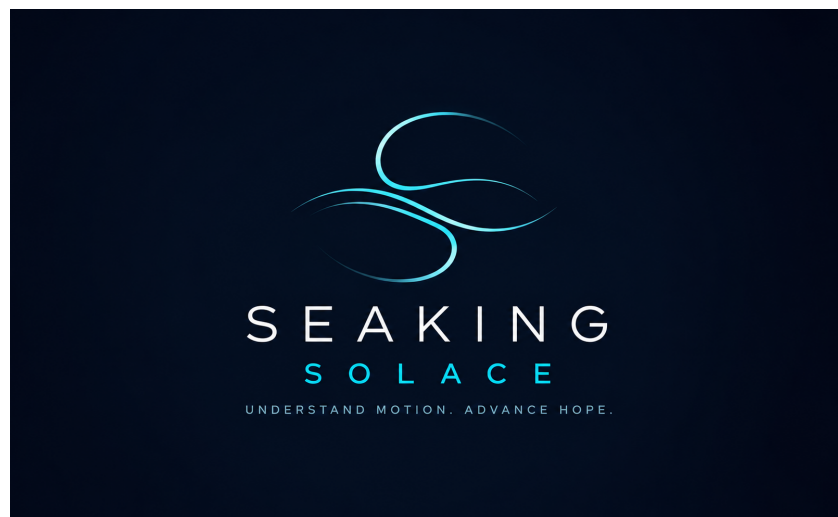




# Vestibular System & Motion

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*Scientific Review*

## 1. Abstract

The vestibular system provides the central nervous system with continuous information about head motion and orientation through the coordinated activity of the semicircular canals and otolith organs. Vestibular stimulation is often described broadly as exposure to “motion,” but the physical input is neither unitary nor adequately characterized by magnitude alone. Natural vestibular input comprises time-varying rotational and translational components across multiple axes, with statistical and spectral properties that differ substantially from simplified laboratory stimuli. Measurements of natural self-motion demonstrate activity across all six dimensions of head movement, while neurophysiological studies show that regular and irregular vestibular afferents differ in their encoding of naturalistic stimuli. [1-2]

The biological representation of motion is further shaped by central integration. Semicircular canal and otolith signals interact rather than simply summing, and otolith signals encode gravito-inertial acceleration, requiring central mechanisms to distinguish translation from changes in orientation relative to gravity. [3,6] Higher vestibular pathways also incorporate behavioral context and predictions associated with self-generated movement. Axis, frequency, temporal structure, combinations of rotational and translational inputs, head orientation, and the origin of motion are therefore potentially relevant characteristics of a vestibular stimulus.

A critical methodological distinction exists between motion of an external platform or environment and motion received at the head. Because the labyrinth senses head motion, voluntary or compensatory head movement can alter the vestibular exposure produced by a moving vessel or platform. Contemporary head-centric motion-platform methods address this distinction by tracking head motion and defining stimulation relative to head-fixed coordinates. [4]

This review examines vestibular motion sensing, peripheral encoding, central integration, natural multidimensional motion, externally imposed versus self-generated movement, individual variability, repeated exposure, adaptation, and stimulus structure. The literature establishes that vestibular responses depend on multiple characteristics of physical motion. It does not establish that natural multi-axis motion is therapeutically superior, that externally applied motion produces beneficial autonomic effects, or that any particular motion profile has clinical efficacy.

Within the SeaKing Solace research framework, the resulting methodological question is whether reproducible physiological responses during externally applied rhythmic motion can be related to identifiable characteristics of the received motion. The literature supports measuring natural motion with

sufficient dimensional and temporal resolution to investigate that question before selecting a fixed controlled waveform.

## 2. Purpose and Scope

The purpose of this review is to examine the vestibular system as a biological sensor and processor of physical motion, emphasizing the characteristics of motion that may matter when externally applied movement is treated as an experimental stimulus. It is not a comprehensive review of vestibular pathology, perception, rehabilitation, autonomic physiology, neuroplasticity, or clinical efficacy.

The peripheral vestibular apparatus comprises three semicircular canals and two otolith organs in each labyrinth. The semicircular canals transduce rotational head motion, while the utricle and saccule respond to gravito-inertial acceleration. These peripheral signals are subsequently integrated with one another and with visual, proprioceptive, and internally generated estimates of head orientation, gravity, and self-motion. [5-6] Natural vestibular stimulation is therefore an integration problem rather than a collection of independent engineering axes.

Direct measurements of natural human head motion show simultaneous translational and rotational components across three dimensions, with non-Gaussian amplitude distributions and activity-dependent temporal structure. [1] For this reason, the review treats vestibular exposure as a multidimensional time series and distinguishes environmental motion from the head-centered motion that more directly determines the physical input to the labyrinth. [4]

The review addresses six linked questions: (1) what physical quantities are encoded by the semicircular canals and otolith organs; (2) how rotational and translational inputs are combined centrally during multi-axis movement; (3) how natural vestibular input differs from simplified laboratory waveforms; (4) how processing differs when motion is externally imposed rather than generated voluntarily; (5) how frequency, amplitude, orientation, individual sensitivity, and exposure history alter vestibular response; and (6) what these properties imply for studies using controlled or naturally occurring externally applied motion.

The scope deliberately stops short of treating autonomic regulation, vagal physiology, neuroplasticity, or clinical outcomes as primary subjects. Vestibular pathways reach motor, perceptual, cognitive, and autonomic targets, but detailed evaluation of those downstream domains belongs in separate reviews so that evidence concerning motion sensing is not conflated with evidence concerning downstream physiological or clinical effects. [5]

For SeaKing Solace, the relevance of this review is methodological rather than therapeutic. The literature supports treating externally applied motion as a structured physical exposure whose constituent characteristics should be measured before a controlled stimulus is selected. The specific SeaKing Solace inference is that natural motion should first be characterized with sufficient dimensional and temporal resolution to determine which features, if any, covary reproducibly with physiological response. That inference is a research question derived from the literature, not a finding established by it.

## 3. Vestibular Motion as a Physical Stimulus

The vestibular system is a mechanosensory system. Its peripheral receptors do not detect an abstract state called “movement.” Mechanical consequences of head motion and orientation act on specialized structures within the inner ear, producing hair-cell deflection and modulation of vestibular afferent activity. The relevant physical input therefore consists of time-varying rotational and gravito-inertial forces acting on the head, transformed by semicircular canal and otolith biomechanics into neural signals. [5]

A statement such as “the participant experienced motion” consequently provides little information about the vestibular exposure. Motion can differ in direction, rotational and translational composition, magnitude, velocity, acceleration, frequency content, duration, temporal envelope, and the relationships among simultaneous components. Because the end organs have distinct mechanical and neural dynamics, superficially similar exposures need not produce equivalent vestibular inputs.

### **3.1 Rotational motion and the semicircular canals**

Each inner ear contains three semicircular canals, conventionally described as horizontal, anterior, and posterior. Their approximately orthogonal arrangement provides sensitivity to rotations throughout three-dimensional space. Each membranous canal terminates in an ampulla containing the crista ampullaris, where vestibular hair cells project into the cupula. [5]

During angular acceleration, inertia produces relative motion between the canal and its endolymph. The resulting hydrodynamic force deflects the cupula and hair bundles, altering receptor potential, neurotransmitter release, and vestibular afferent discharge. [5] The relationship between physical rotation and neural activity is dynamic: afferents differ in spontaneous discharge regularity, sensitivity, gain, phase, and responses to stimulus amplitude and frequency. Thus, even single-axis rotation is incompletely described by peak angle or by the statement that rotation occurred.

### **3.2 Translational motion, gravity, and the otolith organs**

The utricle and saccule contain macular sensory epithelia whose hair bundles interact with an otolithic membrane weighted by calcium carbonate crystals, or otoconia. Changes in gravito-inertial force produce shear across the macula, deflecting hair bundles and altering afferent activity. [5]

The otolith organs are often described as linear-acceleration sensors, but their peripheral signal reflects both inertial acceleration associated with translation and the gravitational component associated with head orientation. Otolith afferent activity alone therefore cannot uniquely distinguish translation from tilt relative to gravity. Resolving this tilt-translation ambiguity requires central integration with semicircular canal and other sensory information. [5-6] In natural motion, translation, rotation, and orientation relative to gravity can change together.

### **3.3 Six physical degrees of freedom do not equal six biological channels**

Rigid-body motion can be represented by three translations and three rotations. In vessel-centered coordinates these are commonly termed surge, sway, heave, roll, pitch, and yaw. This six-degree-of-freedom representation is useful for engineering measurement, but it should not be mistaken for six independent vestibular channels.

The canals and otolith organs provide directionally organized information through anatomical geometry, receptor distributions, bilateral organization, and central convergence. [3,5] A vessel may undergo several engineering-axis motions simultaneously, while the resulting head motion produces overlapping canal and otolith stimulation whose biological representation depends on temporal relationships, head orientation, and peripheral and central dynamics.

### **3.4 Natural motion is a multidimensional time series**

Carriot and colleagues measured three-dimensional linear acceleration and angular velocity during everyday human activities using head-mounted inertial sensing. Motion varied across activities and across all six measured dimensions. Natural vestibular inputs showed non-Gaussian distributions with extended tails and behavior-dependent spectral structure. [1]

Natural vestibular exposure is therefore better represented as a multidimensional time series than as a scalar quantity. Two periods can have similar average acceleration yet differ in spectral content, rotational composition, temporal sequence, cross-axis relationships, or transient events. This does not establish that every measurable characteristic is important for every biological outcome. It establishes that deciding which characteristics can be discarded is an empirical question.

### 3.5 Environmental motion and head-centered vestibular motion

Environmental motion and vestibular motion are related but distinct. A vessel-mounted inertial sensor describes motion of the vessel at the sensor location. That measurement approximates the participant's imposed motion only to the extent that the participant's body and head remain fixed relative to the vessel.

In natural behavior, participants turn, tilt, stabilize, lean, change posture, stand, or recline. These actions transform vessel-frame motion into a different motion at the head and therefore at the labyrinth. For vestibular physiology, head-centered motion is the more proximal physical stimulus.

La Scaleia and colleagues demonstrated a six-degree-of-freedom platform system incorporating real-time head tracking so that desired vestibular stimulation could remain defined in head-centered coordinates while participants moved freely. [4] The methodological implication is direct: environmental motion describes the moving system, whereas head motion more directly describes the physical input presented to the vestibular organs. Both measurements can be valuable, but they answer different questions.

### 3.6 From physical exposure to neural stimulus

Figure 1 summarizes the measurement-to-biology chain from environmental motion to peripheral vestibular neural input.



**Figure 1. From environmental motion to vestibular neural input. Environmental motion is transformed by participant mechanics before reaching the head and then undergoes additional peripheral biological transformations. This conceptual figure does not imply that each transformation is directly measured in Phase 1.**

The transformation from environment to vestibular neural activity can be represented conceptually as:

*environmental motion → body and head mechanics → head-centered rotational and gravito-inertial motion → end-organ biomechanics → hair-cell transduction → vestibular afferent activity*

Each stage can alter the relationship between the original environmental waveform and the signal transmitted to the central nervous system. An inertial measurement unit describes motion in engineering coordinates. The labyrinth transforms head-centered motion through biological mechanics, receptor orientation, afferent dynamics, bilateral organization, and subsequent neural integration.

### 3.7 Experimental implication

Table 1 formalizes the measurement hierarchy implied by the physical-to-biological chain and clarifies what each measurement level can and cannot establish.

| Level         | Example measurement              | Scientific value                     | Does not directly measure                  |
|---------------|----------------------------------|--------------------------------------|--------------------------------------------|
| Environmental | Vessel/platform 6-DoF kinematics | Defines external mechanical exposure | Participant head motion or neural activity |

| <b>Level</b>           | <b>Example measurement</b>                    | <b>Scientific value</b>                            | <b>Does not directly measure</b>         |
|------------------------|-----------------------------------------------|----------------------------------------------------|------------------------------------------|
| Participant mechanical | Head 6-DoF kinematics and orientation         | Approximates received physical vestibular exposure | End-organ mechanics or afferent firing   |
| Physiological          | HR/HRV, pupil and other synchronized measures | Quantifies downstream physiological response       | Clinical benefit or vestibular mediation |
| Behavioral/contextual  | Posture, activity, visual context, symptoms   | Supports interpretation and confound control       | A unique causal mechanism                |

**Table 1. Measurement hierarchy for natural-motion characterization.**

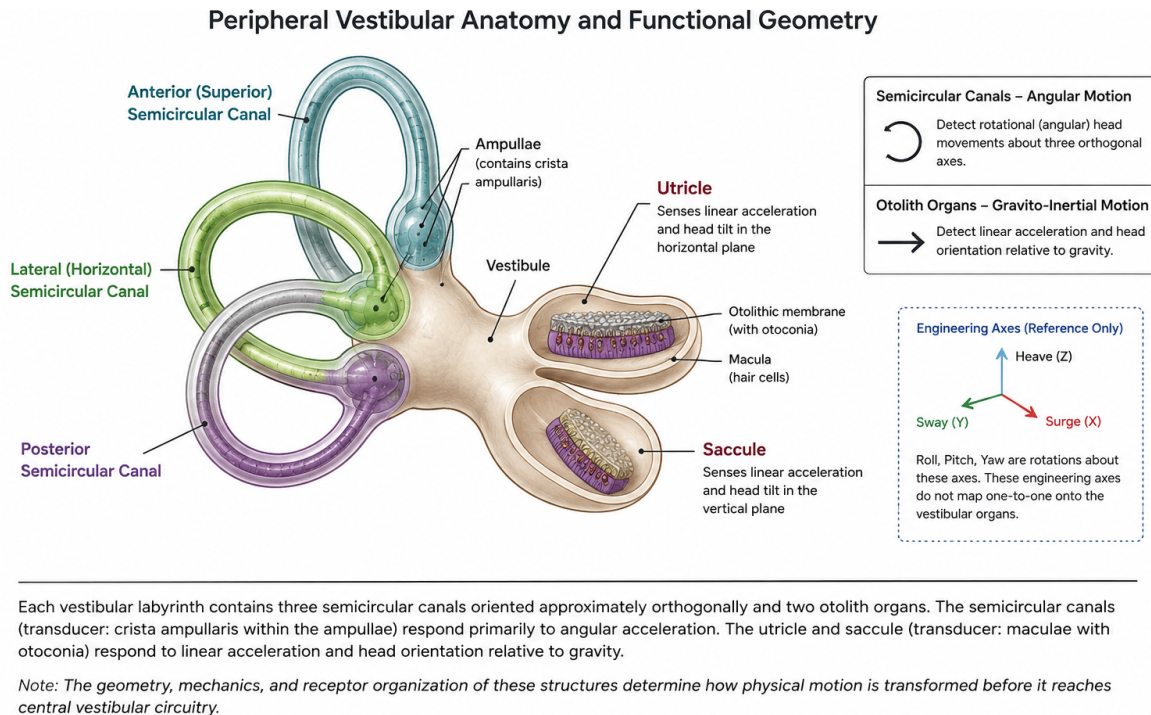
For studies of externally applied rhythmic motion, the independent variable should not initially be reduced to motion present versus motion absent. A more informative representation preserves time-resolved translational and rotational components and, where relevant, acceleration, angular velocity, frequency content, amplitude distribution, temporal envelope, duration, cross-axis structure, and head orientation.

The literature does not establish that all of these variables will predict a downstream physiological response. Determining which features matter, which are redundant, and which can ultimately be reduced to a simpler controlled stimulus is part of the experimental problem.

For SeaKing Solace, the vessel is therefore not assumed to provide an optimal or therapeutic stimulus. It functions initially as a natural motion-generating environment. If reproducible physiological changes occur, the relevant scientific task is to determine whether identifiable characteristics of the received motion covary with those responses and can later be reproduced, isolated, and manipulated under controlled conditions.

## 4. Peripheral Vestibular Anatomy and Encoding

Figure 2 provides a schematic orientation to the peripheral vestibular structures discussed in this section and emphasizes that engineering motion axes do not map one-to-one onto individual vestibular organs.



**Figure 2. Peripheral vestibular anatomy and functional geometry. Schematic depiction of the semicircular canals and otolith organs, with the distinction between engineering axes and biological sensors.**

The peripheral vestibular system provides the first biological transformation between physical head motion and neural information about self-motion and orientation. Each vestibular labyrinth contains five sensory organs: three semicircular canals and two otolith organs, the utricle and saccule. Their geometry, mechanics, receptor organization, and afferent innervation determine how a physical waveform is transformed before it reaches central vestibular circuitry. [5]

### 4.1 The bony and membranous labyrinth

The vestibular apparatus lies within the bony labyrinth of the temporal bone. The membranous labyrinth is an endolymph-containing system surrounded by perilymph and includes the semicircular ducts, utricle, and saccule. Sensory epithelia are localized to the cristae ampullares within the canal ampullae and the maculae of the otolith organs. [5]

These structures create two mechanically distinct forms of transduction. Semicircular canals couple head rotation to endolymph and cupular mechanics, while the otolith organs couple gravito-inertial force to displacement of an otoconial membrane. Natural head movement commonly engages both systems concurrently.

### 4.2 Semicircular canal anatomy and mechanics

Each labyrinth contains horizontal or lateral, anterior or superior, and posterior semicircular canals arranged in approximately orthogonal planes. Each membranous duct expands into an ampulla containing the crista ampullaris. Vestibular hair bundles project into the cupula, which couples endolymph mechanics to receptor deflection. [5,7]

During angular acceleration, endolymph inertia creates pressure and displacement that deform the cupula and alter hair-cell signaling. Physiological movements involve very small fluid displacements and cupular deformations, emphasizing the mechanical sensitivity of the system. [7]

### **4.3 Functional geometry and bilateral organization**

Functionally corresponding canals form approximately coplanar bilateral pairs. Head rotation tends to increase activity associated with one member of a pair while decreasing activity associated with the contralateral partner. This push-pull organization contributes directional information to central vestibular pathways.

Engineering coordinates such as roll, pitch, and yaw are not exact anatomical synonyms for individual canals. Canal activation depends on head orientation and anatomical canal planes. A platform command expressed as roll therefore does not, by itself, specify the resulting peripheral activation pattern.

### **4.4 Utricle and saccule**

The utricle and saccule detect gravito-inertial acceleration through macular epithelia containing vestibular hair cells beneath an otolithic membrane loaded with otoconia. Linear acceleration or changes in orientation relative to gravity produce shear between the membrane and sensory epithelium, deflecting hair bundles and changing afferent activity. [5]

The maculae are curved and contain hair cells with systematically varying directional preferences; they should not be represented as simple one-axis accelerometers. [5] The otolith organs therefore provide a distributed population representation of gravito-inertial force. During natural multi-axis motion, changing translation, rotation, and head orientation create evolving patterns of canal and otolith activation rather than sequential activation of independent engineering channels.

### **4.5 Hair cells and primary vestibular afferents**

Both canal and otolith transduction depend on polarized vestibular hair cells. Deflection of the hair bundle alters mechanotransduction, receptor potential, neurotransmitter release, and activity in primary vestibular afferents. These afferents have cell bodies in Scarpa's ganglion and project centrally through the vestibular division of cranial nerve VIII, principally to vestibular nuclei and cerebellar circuits. [5]

The vestibular nerve does not carry a uniform representation of motion. Differences in receptor orientation, innervation, and afferent physiology create population-level diversity before central processing begins.

### **4.6 Regular and irregular afferents**

Primary vestibular afferents are commonly classified by the regularity of spontaneous discharge. Regular and irregular afferents differ in sensitivity, response dynamics, morphology, and motion encoding.

Schneider and colleagues examined canal and otolith afferents during naturalistic motion in rhesus macaques and found greater sensitivity among irregular afferents. Naturalistic stimulation also revealed nonlinear behavior, including rectification and saturation, that was not adequately captured by conventional linear models at larger stimulus magnitudes. [2] Their analysis further suggested that irregular afferents were more closely matched to the distribution of natural vestibular stimuli, largely because of this greater sensitivity. [2]

These findings demonstrate that the transformation from physical motion to neural activity depends on both stimulus structure and the physiological properties of the afferent population. They do not establish that preferentially engaging irregular afferents is therapeutically advantageous; the experiments addressed sensory coding, not autonomic regulation or clinical efficacy.

## 4.7 Peripheral encoding as biological transformation

Physical motion is transformed through a sequence:

*head motion* → *labyrinthine mechanics* → *receptor displacement* → *hair-cell transduction* → *population-specific afferent activity*

The geometry and mechanics of the end organs shape the initial transformation, hair-cell orientation contributes directional selectivity, and afferent physiology adds differences in sensitivity and temporal encoding. Naturalistic stimulus magnitudes can reveal nonlinearities not evident under smaller conventional laboratory inputs. [2,5,7] By the time vestibular information reaches the brainstem, the original physical motion has already been biologically filtered and encoded.

## 4.8 Implications for motion characterization

Peripheral anatomy places several constraints on experimental description. Head orientation matters because labyrinth orientation relative to acceleration determines how the stimulus is distributed across the end organs. Rotation and gravito-inertial acceleration are encoded through mechanically different receptor systems. Simultaneous motion components can engage multiple receptor populations, and temporal characteristics matter because canal biomechanics and afferent dynamics vary across frequencies and amplitudes. [7] Naturalistic magnitudes can also expose nonlinear afferent behavior. [2]

These observations do not identify an optimal stimulus. They establish why physical characterization should precede assumptions about which parameters are biologically relevant.

For SeaKing Solace, this provides the foundational link between externally applied physical motion and structured vestibular neural input. If physiological responses are observed during natural motion, exposure should ultimately be related to motion received at the head rather than characterized only as time spent aboard a moving vessel. Even then, an observed motion-physiology association would not establish vestibular causation; later experiments would be required to test whether vestibular activation mediates the relationship.

## 5. Semicircular Canal Encoding of Angular Motion

The semicircular canals are the principal peripheral vestibular sensors for angular head motion. Their response is not a static readout of rotation. Canal biomechanics and afferent physiology transform angular motion according to direction, magnitude, frequency, and temporal structure, and the afferent population contains multiple response dynamics rather than a single transfer function. [7-8]

For experimental design, this means that roll, pitch, and yaw should be treated as time-varying angular inputs. Peak angle or peak acceleration alone cannot be assumed to specify the resulting vestibular signal.

### 5.1 Directional decomposition of angular head motion

The three canals in each labyrinth occupy different anatomical planes and together provide sensitivity to three-dimensional head rotation. The lateral canal is oriented approximately with head-centered yaw, while the anterior and posterior canals occupy oblique vertical planes. Complex rotation is therefore decomposed across canal planes rather than mapped one-to-one from engineering roll, pitch, and yaw coordinates. [7-8]

Actual canal stimulation depends on head orientation and bilateral canal geometry. A vessel undergoing roll does not activate a single biological “roll sensor”; it produces a distributed pattern of canal activity determined by the motion received at the head.

## 5.2 Canal biomechanics transform angular motion over time

Angular acceleration creates inertial effects in the endolymph, producing pressure across the cupula and altering hair-cell activity. The semicircular canal has commonly been approximated as a torsion-pendulum system whose response varies with stimulus frequency. [7-8]

At very low frequencies, cupular mechanics attenuate sustained or slowly changing rotation. Across an intermediate range relevant to ordinary head movement, canal output more closely reflects angular velocity. At higher frequencies, mechanical and neural dynamics again alter gain and phase. Thus angular acceleration initiates the mechanical response, but canal output over time cannot be reduced to instantaneous angular acceleration alone. [7-8]

## 5.3 Angular velocity, acceleration, and frequency are linked

For a sinusoidal angular displacement, position, velocity, and acceleration are mathematically related through frequency. Changing frequency while holding displacement amplitude constant changes both peak angular velocity and peak angular acceleration. This is why reporting only one motion descriptor can obscure biologically relevant differences between waveforms.

Frequency is therefore not a secondary engineering parameter. It changes the relationship between commanded motion, canal mechanics, and afferent output. The same nominal angular excursion delivered slowly and rapidly can constitute materially different vestibular stimuli. [7-8,10]

## 5.4 Regular and irregular afferents provide different temporal representations

Canal afferents differ in spontaneous discharge regularity and response dynamics. Regular afferents tend to provide comparatively tonic representations, whereas irregular afferents show greater sensitivity and more phasic behavior, particularly as stimulus dynamics increase. [9-11]

This heterogeneity means that angular motion is represented in parallel across afferent populations with different temporal characteristics. It also cautions against assuming that a single scalar measure of rotation predicts the complete peripheral neural response.

## 5.5 Naturalistic angular motion can expose nonlinear encoding

Natural head motion contains broadband, intermittent angular signals rather than a single repeated sinusoid. Carriot and colleagues demonstrated broad natural angular-motion statistics in humans, while Schneider and colleagues showed that naturalistic stimulation can reveal nonlinear features in vestibular afferents, including rectification and saturation, that are not adequately captured by simple linear models. [1-2]

This does not imply that naturalistic complexity is inherently beneficial. It means that neural responses inferred from small-amplitude laboratory stimulation may not fully predict responses to larger or more complex natural motion.

## 5.6 Sustained and repeated rotation change the response

Canal mechanics attenuate sustained constant-velocity rotation as the cupula returns toward its resting position, and vestibular responses can also change with repeated exposure. [10] The time history of angular stimulation therefore matters in addition to its instantaneous magnitude.

For later experimental work, duration and prior exposure should be retained as separate variables rather than treated as interchangeable with amplitude or frequency.

## 5.7 Implications for angular-motion measurement

A useful angular-motion record should preserve head-centered rotation through time, including angular velocity, acceleration, frequency content, amplitude distribution, axis relationships, duration, and transient events. The literature does not establish that each feature will predict the physiological endpoint of interest; it establishes that canal physiology is capable of distinguishing among them.

For SeaKing Solace, this supports measuring the received angular stimulus rather than describing exposure only as vessel roll, pitch, or yaw. Candidate relationships identified in natural data can later be simplified and manipulated under controlled conditions.

## **6. Otolith Encoding of Translation and Gravity**

The utricle and saccule encode gravito-inertial acceleration. Unlike a simple linear accelerometer, the otolith system does not provide an unambiguous peripheral separation between translation and gravity. Its output reflects the direction and magnitude of the gravito-inertial vector relative to the head, transformed by distributed receptor geometry and heterogeneous afferent dynamics. [5-6,12-13]

This makes otolith physiology particularly important for natural multi-axis motion, where translation, tilt, and rotation frequently occur together.

### **6.1 The utricle and saccule are distributed directional sensors**

The utricular and saccular maculae contain hair cells with systematically varying directional preferences. Their curved geometry and receptor organization create population representations of gravito-inertial force rather than simple one-axis measurements. [5,13]

Consequently, engineering labels such as heave and sway do not map directly onto isolated saccular or utricular activation.

### **6.2 Otoliths encode gravito-inertial force**

Otolith afferents respond to forces produced both by linear acceleration and by changes in head orientation relative to gravity. At the receptor level, these components are combined as gravito-inertial acceleration. [5,12]

A useful physical representation is a time-varying head-centered gravito-inertial vector. Its exact mathematical sign convention depends on the coordinate system, but the biological point is invariant: gravity and inertial acceleration are combined at the peripheral receptor.

### **6.3 The tilt-translation ambiguity**

Because translation and tilt can generate equivalent instantaneous otolith signals, otolith afferent activity alone cannot uniquely determine whether the head translated or changed orientation relative to gravity. This is the classical tilt-translation ambiguity. [6]

The ambiguity is not a defect of the otolith organs. It is a consequence of the physics of gravito-inertial sensing and creates a central computational problem addressed in Section 7.

### **6.4 Dynamic translation and static orientation are not encoded identically**

Although gravity and translation are physically combined at the otolith receptor, afferent populations do not necessarily encode static orientation and dynamic translation in identical ways. Experimental work indicates different coding strategies for these conditions. [13]

This distinction matters for controlled motion design. Changing platform tilt can alter gravitational loading without reproducing the same inertial translation, while translation can alter inertial acceleration without the same pattern of canal activation. Equivalent instantaneous gravito-inertial force should therefore not be assumed to mean equivalent whole-system vestibular stimulation.

### **6.5 Otolith afferents differ in temporal sensitivity**

Regular and irregular otolith afferents differ in sensitivity and temporal dynamics, as they do in the canal system. Experimental studies show that irregular afferents can emphasize more dynamic components of translation and can respond with greater sensitivity to naturalistic stimuli. [2,13]

Otolith sensitivity is also frequency dependent. The same translational amplitude delivered at different temporal rates can therefore produce different peripheral representations. [13]

## **6.6 Peripheral encoding and behavioral context**

Natural behavior adds voluntary movement and changing sensory context, but peripheral otolith afferents can continue to encode the physical motion itself without the context-dependent suppression seen at some central stages. Work during active and passive translation supports this distinction between peripheral encoding and later central interpretation. [14-15]

This helps separate two questions: what physical stimulus reaches the vestibular nerve, and how the central nervous system interprets that stimulus in relation to behavior.

## **6.7 Natural multi-axis motion creates a continuously changing otolith stimulus**

Natural human movement contains simultaneous translational and rotational components across multiple dimensions. [1] On a vessel, heave, sway, surge, pitch, and roll can change the gravito-inertial vector and the orientation of the head relative to gravity at the same time.

The otolith exposure is therefore vectorial and time varying. Magnitude, direction relative to the head, temporal structure, simultaneous angular motion, and preceding exposure can all contribute to the physical context in which the otolith signal is generated.

## **6.8 Engineering axes are not biological organs**

It would be scientifically inaccurate to equate vessel heave with isolated saccular stimulation or vessel sway with isolated utricular stimulation. The received stimulus depends on head orientation, vessel orientation relative to gravity, simultaneous rotations and translations, distributed macular sensitivity, and central canal-otolith integration.

Engineering coordinates remain necessary for measuring the external environment. Vestibular coordinates describe the biological transformation of that environment. The research problem is to relate the two, not to treat them as interchangeable.

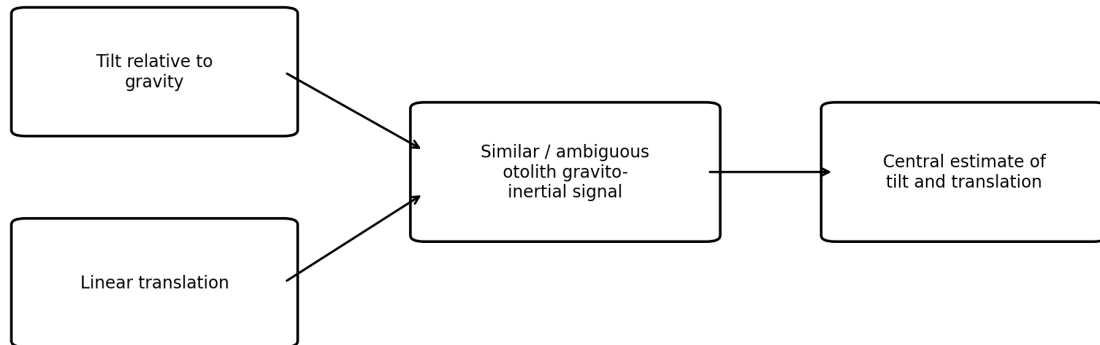
## **6.9 Implications for otolith-exposure measurement**

Vessel-mounted accelerometry is useful but insufficient for a complete participant-level otolith description when the head can move relative to the vessel. Participant-level head orientation and acceleration allow the gravito-inertial stimulus to be expressed in a head-centered frame, which is more proximal to the input received by the otolith organs.

For SeaKing Solace, the key methodological conclusion is that translational exposure should be preserved as time-resolved head-centered gravito-inertial data and interpreted together with simultaneous angular motion. The literature does not identify an optimal otolith stimulus or establish a therapeutic effect. It defines the measurement problem. [4,6,13-15]

## **7. The Tilt-Translation Problem**

Figure 3 illustrates the core ambiguity: different physical conditions can generate overlapping otolith gravito-inertial signals, requiring additional information for central interpretation.



**Figure 3. Tilt-translation ambiguity.** Tilt relative to gravity and linear translation can produce overlapping otolith signals; canal and other sensory information contribute to central estimates of orientation and translation.

The tilt-translation problem is a central example of why vestibular motion cannot be interpreted from isolated engineering axes. The otolith organs encode gravito-inertial acceleration, so identical or similar peripheral signals can arise from linear translation, changes in orientation relative to gravity, or combinations of the two. [6,16]

Central vestibular processing must therefore estimate the physical cause of an ambiguous peripheral signal.

### 7.1 Why the ambiguity exists

According to the equivalence principle, the otolith organs cannot distinguish gravitational acceleration from inertial acceleration using the instantaneous otolith signal alone. A head tilted relative to gravity and a head undergoing linear acceleration can produce overlapping gravito-inertial patterns. [16]

Any biologically meaningful estimate of translation must therefore incorporate information beyond the otolith signal itself.

### 7.2 Semicircular canal information helps disambiguate tilt and translation

Semicircular canals provide information about angular head motion that can be combined with otolith signals to estimate how gravity should change relative to the head during tilt. Comparing this estimate with the measured gravito-inertial signal helps separate translation from orientation. [6,16]

This computation illustrates why canal and otolith systems should not be analyzed as independent biological channels during natural motion.

### 7.3 Cerebellar processing contributes to the separation

Recordings from the cerebellar nodulus and uvula show neurons whose responses are consistent with transformations that distinguish translation from tilt. Yakusheva and colleagues demonstrated frequency-selective coding in this region, supporting a role for cerebellar computation in resolving the ambiguity. [17]

The result is not a single universal representation. Central vestibular populations remain heterogeneous, with different neurons emphasizing combinations of sensory and computed variables. [6]

## 7.4 Internal models provide a useful framework

Internal-model accounts propose that the nervous system combines sensory signals with estimates of physical dynamics to infer motion and orientation. In this framework, canal information, otolith information, gravity, and prior expectations are integrated over time rather than interpreted as isolated instantaneous measurements. [18]

Visual and proprioceptive information can also contribute to estimates of self-motion and orientation. [24] This multisensory contribution becomes important when later experiments attempt to distinguish a specifically vestibular effect from a broader sensory-context effect.

## 7.5 Natural vessel motion continuously presents the ambiguity

A moving vessel can translate and rotate simultaneously. Pitch or roll changes head orientation relative to gravity while heave, surge, or sway changes inertial acceleration. The otolith organs therefore receive a continuously evolving gravito-inertial signal while the canals simultaneously encode angular motion.

The timing between those components may matter because central disambiguation depends on their relationship over time. Frequency-selective cerebellar processing further supports treating temporal structure as part of the problem rather than as incidental noise. [17]

## 7.6 Why simplified laboratory motion remains essential

Single-axis laboratory paradigms are valuable precisely because they isolate variables that natural motion couples together. They have allowed investigators to characterize canal dynamics, otolith responses, and central computations with high interpretability.

The limitation is not that simplified experiments are unrealistic and therefore unhelpful. It is that their findings cannot automatically specify which combinations of variables matter in a prolonged natural exposure. Natural characterization and controlled reduction answer different questions.

## 7.7 Implications for motion parameterization

A future motion model should retain enough information to distinguish head-centered angular motion, gravito-inertial acceleration, orientation relative to gravity, and their temporal relationships. Reducing the exposure prematurely to vessel-axis acceleration risks obscuring the very signals central vestibular pathways use to interpret motion.

For SeaKing Solace, the tilt-translation literature supports a staged approach: characterize coupled natural motion first, identify candidate relationships, then manipulate tilt, translation, orientation, and timing independently under controlled conditions. [3,6,17-18]

# 8. Canal-Otolith Integration During Multi-Axis Motion

Natural motion stimulates canal and otolith systems concurrently, and central vestibular pathways combine these inputs. The resulting representation is not adequately described by adding an isolated rotational response to an isolated translational response. Integration is spatial, temporal, frequency dependent, and context sensitive. [3,6,19]

This section is therefore the primary home for the argument that relationships among motion components may be biologically relevant experimental variables.

## 8.1 Convergence begins early in central vestibular processing

Central vestibular neurons receive convergent canal and otolith input, creating response properties that reflect combinations of rotational and gravito-inertial information. [19] This convergence allows central pathways to construct representations more useful for estimates of orientation and self-motion than either peripheral system can provide alone.

## 8.2 Combined responses are not simple linear sums

Carriot and colleagues examined central vestibular responses during combined canal and otolith stimulation and found that responses to combined motion were subadditive relative to predictions based on simple summation of isolated components. [3]

Subadditivity should not be interpreted as meaning that combined motion is biologically weaker. It means that central integration is nonlinear enough that the response to a combination cannot be inferred reliably by adding the responses to its parts.

## 8.3 Relative weighting changes with frequency

The contribution of canal and otolith information to central responses can vary with stimulus frequency. [3] Frequency therefore affects not only peripheral transduction but also the way different vestibular signals are combined centrally.

This provides another reason to preserve spectral information when characterizing natural motion.

## 8.4 Integration contributes to perception and physical disambiguation

Canal-otolith integration contributes to resolving the tilt-translation ambiguity and to central estimates of orientation, translation, and self-motion. [3,6,16,18] The interaction therefore has perceptual and computational relevance, not merely anatomical significance.

## 8.5 Multi-axis integration is spatial and temporal

Central neurons can receive inputs associated with more than one canal or otolith direction, and natural motion presents these signals with continuously changing timing. [19] The biological stimulus is consequently shaped not only by the amplitude of each component but by when components occur relative to one another.

Two exposures with similar axis-specific averages can differ in phase, temporal coincidence, or sequence. Those relationships may be lost if each motion axis is summarized independently.

## 8.6 Natural motion presents the integration problem continuously

Human natural-motion measurements show simultaneous rotational and translational activity across multiple dimensions. [1] A natural marine environment therefore provides a continuously varying set of canal and otolith combinations rather than a sequence of isolated stimuli.

This complexity should not be assumed to be beneficial. Its scientific value in a discovery phase is that it supplies a broad, naturally occurring stimulus space from which candidate relationships can be identified.

## 8.7 Behavioral context adds another transformation

Central vestibular processing is influenced by whether motion is self-generated or externally imposed, while peripheral afferents can continue to encode the physical motion itself. The active-passive distinction is developed later in the review, but its relevance here is that identical or similar peripheral inputs need not produce identical central representations.

Thus multi-axis integration occurs within a system that also incorporates behavioral prediction and other sensory context.

## 8.8 Complexity does not establish therapeutic superiority

The finding that canal and otolith inputs interact does not establish that complex multi-axis motion is more beneficial than simple motion, or that any vestibular stimulus produces the physiological effect SeaKing Solace proposes to investigate.

It remains possible that a reproducible response, if one exists, could ultimately be generated by a much simpler controlled stimulus. The reason to preserve natural complexity initially is to avoid discarding potentially relevant structure before the data identify what can be removed.

## 8.9 A hierarchy of the measured and biological stimulus

The preceding sections support a useful hierarchy:

*environmental motion → vessel trajectory → participant mechanics → head-centered motion → peripheral canal and otolith encoding → central canal-otolith integration → central estimates of orientation and self-motion*

Each level is a transformation. A vessel IMU does not directly measure vestibular neural activity; an otolith signal does not directly equal translation; and combined canal and otolith activity cannot be assumed to equal the arithmetic sum of isolated responses.

## 8.10 Implications for experimental analysis

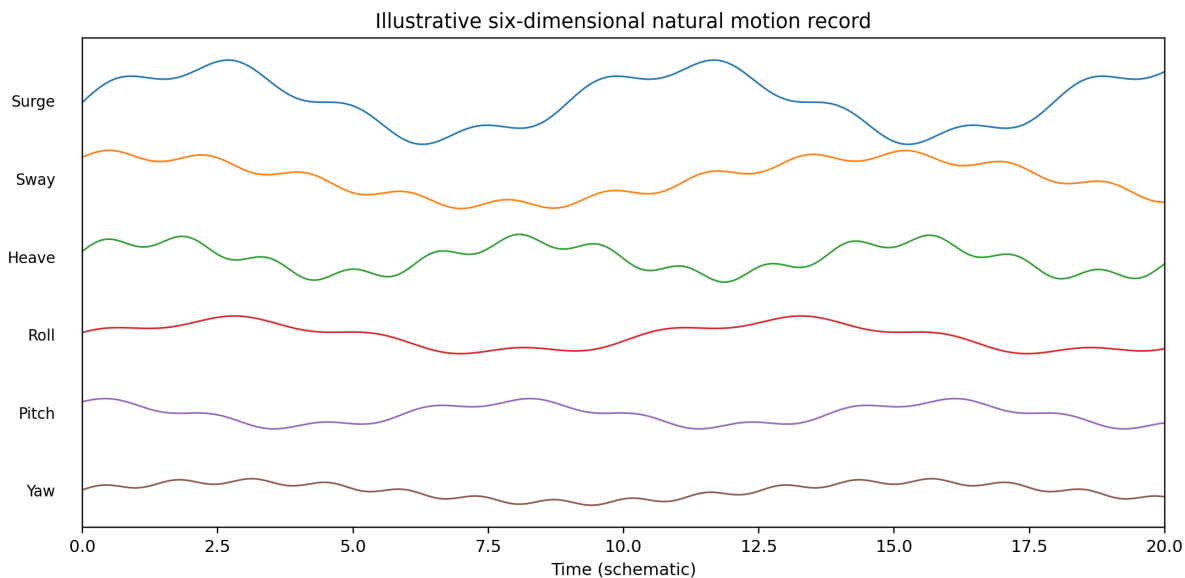
The initial dataset should preserve synchronized rotational and translational time series at sufficient resolution to examine individual axes, rotational-translational combinations, frequency-specific relationships, cross-axis timing, head orientation, and biologically plausible interaction terms.

Rich time-series data also create a statistical hazard. Unrestricted feature mining can produce spurious correlations through multiple comparisons and overfitting. Candidate analyses should therefore be prespecified where possible, exploratory findings should be labeled as such, and candidate relationships should be validated in held-out participants, sessions, or later studies.

For SeaKing Solace, the methodological progression is: observe natural complexity → identify candidate structure → isolate that structure → manipulate it experimentally → determine whether it contributes causally to the response → simplify where the evidence permits. [3,6,19]

## 9. Natural Vestibular Input Is Six-Dimensional and Temporally Complex

Figure 4 illustrates why a natural exposure should be retained as synchronized time-series data rather than reduced immediately to a single amplitude or frequency.



**Figure 4. Illustrative six-dimensional natural-motion record.** Schematic traces show simultaneous translational and rotational components with differing temporal structure. These are illustrative signals, not SeaKing Solace participant data.

Natural vestibular input differs fundamentally from the simplified single-axis sinusoids commonly used to characterize vestibular physiology. Everyday head motion contains simultaneous translation and rotation across three dimensions, varies with behavior, and exhibits broad temporal and amplitude structure. Carriot and colleagues quantified this directly with head-mounted inertial measurements during natural activities, demonstrating activity across all six measured dimensions and distributions with extended, non-Gaussian tails. [1]

The significance of these findings is methodological. Natural motion provides a broad stimulus space in which amplitude, frequency, axis composition, timing, and transient events vary together. It does not follow that natural complexity is biologically superior or that all of this structure must be reproduced in a future intervention.

### **9.1 Six-dimensional motion is simultaneous, not sequential**

During natural behavior, rotational and translational components occur concurrently. A participant can experience angular velocity and linear acceleration in several directions at the same time. Because Sections 7 and 8 established that canal and otolith information is centrally integrated, these simultaneous components should not be treated as six biologically independent channels.

For analysis, six-degree-of-freedom measurement is therefore best understood as a high-resolution engineering description from which biologically relevant combinations can later be derived.

### **9.2 Natural amplitudes are non-Gaussian**

Carriot et al. found that natural vestibular inputs were not well described by simple Gaussian amplitude distributions. Most motion occurred within relatively modest ranges, but intermittent larger events produced extended tails. [1]

This matters because an average or root-mean-square value can conceal the occurrence and timing of transient events. If downstream responses are sensitive to peaks, transitions, or rare combinations, summary statistics alone could erase relevant exposure information.

### **9.3 Natural motion is broadband and behavior dependent**

The spectral content of natural head motion spans a range of frequencies and changes with activity. [1] Quiet behavior, walking, running, and other movements do not expose the vestibular system to the same frequency distribution.

Accordingly, frequency should be retained as part of the exposure description rather than inferred from an activity label. A natural vessel environment may contain dominant low-frequency oscillations together with higher-frequency components and transient events, and those components can vary over time.

### **9.4 Cross-axis relationships are part of the stimulus**

Two motion records can contain similar axis-specific amplitudes and spectra while differing in the timing among components. Because canal and otolith signals interact centrally, relative timing and phase can alter the combination of inputs presented to the nervous system. [3]

This does not establish that a particular phase relationship is important for the SeaKing Solace endpoint. It establishes that reducing each axis independently can discard information that the vestibular system is capable of integrating.

### **9.5 Temporal envelope and intermittency should be preserved**

Natural exposure is not defined only by repeated periodic motion. It contains onset, offset, changing amplitude, quiescent intervals, bursts, and transitions among motion regimes. These temporal envelopes may influence receptor dynamics, prediction, adaptation, or tolerability even when overall spectral content is similar.

The discovery dataset should therefore preserve continuous time series wherever feasible rather than storing only session-level summaries.

## **9.6 Natural complexity is useful because it can later be reduced**

The scientific value of a natural-motion phase is not that complexity should be preserved forever. It is that a broad naturally occurring stimulus space can be measured before investigators decide which variables are dispensable.

A later controlled platform can then reproduce candidate segments, remove axes or spectral components, alter timing, and test whether the response persists. Natural characterization and controlled reduction are complementary stages rather than competing philosophies.

## **9.7 Relevance to SeaKing Solace**

For SeaKing Solace, Section 9 strengthens the rationale for Phase 1 as a characterization study. The vessel supplies continuously varying motion rather than a predetermined dose. The research task is to measure that variation accurately enough to determine whether particular features covary reproducibly with physiology.

The boat is therefore a discovery environment, not evidence that boat motion itself is the required stimulus.

# **10. Neural Encoding of Naturalistic Motion**

Characterizing natural motion is only the physical half of the problem. The vestibular nervous system does not encode all portions of that stimulus equally. Peripheral afferent populations differ in sensitivity, regularity, temporal dynamics, and nonlinear response properties, and naturalistic stimulation can reveal coding behavior that simplified laboratory waveforms do not fully expose. [2,21-23]

This section asks how measured natural stimulus statistics are represented neurally, while preserving a strict boundary between sensory coding and downstream physiological or therapeutic significance.

## **10.1 Natural stimulus statistics interact with afferent physiology**

Schneider and colleagues compared canal and otolith afferent responses with the statistics of natural vestibular stimulation. Irregular afferents showed greater sensitivity and were more closely matched to the distribution of natural stimuli than regular afferents. Naturalistic inputs also revealed rectification and saturation that simple linear descriptions could miss. [2]

The implication is not that irregular afferents are a therapeutic target. It is that a physical waveform can be transformed differently across neural populations, particularly when stimulus magnitudes and dynamics extend beyond conventional small-amplitude laboratory conditions.

## **10.2 Sensitivity and information are not the same quantity**

Greater response sensitivity does not automatically mean that a neural population carries all information most effectively. Neural coding depends on signal gain together with variability, temporal precision, and the statistical structure of the stimulus.

Work examining vestibular coding under naturalistic conditions shows that different afferent classes can use different strategies to represent the same physical environment. [21-23] This population diversity is one reason an externally measured motion feature should not be equated directly with a single neural response.

## **10.3 Natural motion can evoke precise temporal coding**

Jamali and colleagues demonstrated that natural self-motion can evoke precise spike timing in primate vestibular afferents. [21] This finding is important because it shows that temporal structure in the

stimulus can be represented with high precision rather than being reduced entirely to average firing rate.

For experimental design, this supports preserving time alignment between motion and physiological measurements. A relationship that depends on stimulus timing could be obscured by aggressive temporal averaging.

#### **10.4 Neural variability helps determine coding strategy**

Naturalistic vestibular coding is shaped not only by the stimulus but by neural variability. Subsequent work showed that differences in variability influence how vestibular neurons encode natural self-motion. [22]

This reinforces a recurring theme of the review: there is no single universal transformation from physical motion to neural representation. Population identity and response variability are part of the biological system.

#### **10.5 Population coding extends beyond individual afferents**

Recent work examining early vestibular populations indicates that population-level representations are adapted to natural self-motion statistics. [23] This broadens the argument from individual afferent sensitivity to coordinated neural population coding.

Such findings strengthen the biological rationale for studying naturalistic motion, but they still do not identify which neural representation, if any, mediates a SeaKing Solace physiological response.

#### **10.6 Efficient encoding does not establish therapeutic importance**

A critical evidentiary boundary follows. A neural population that efficiently represents natural motion may support balance, gaze stabilization, perception, navigation, postural control, or other functions. Efficient encoding alone does not show that preferentially engaging that population is beneficial, regulatory, or clinically useful.

The coding literature should therefore be used to identify plausible stimulus dimensions and measurement requirements, not to infer efficacy.

#### **10.7 Implications for synchronized measurement**

Because naturalistic motion can be encoded with temporal precision and because afferent populations differ in sensitivity and nonlinear behavior, synchronized motion and physiological data should retain sufficient temporal resolution to examine lagged and feature-specific relationships.

For SeaKing Solace, the question is not whether the neural coding literature proves a desired downstream effect. It is whether a rich physical exposure can be represented in a way that allows reproducible motion-response candidates to be discovered and later tested causally.

### **11. Frequency, Amplitude, and Temporal Structure**

The preceding sections establish that vestibular stimulation is dynamic. Frequency, amplitude, temporal envelope, duration, and the relationships among simultaneous motion components can alter peripheral and central vestibular responses. A motion waveform therefore cannot be specified adequately by naming its axis or peak magnitude alone. [7-8,25-27]

This section consolidates those stimulus dimensions into an experimental framework without implying that the literature already identifies an optimal dose.

## 11.1 Frequency changes the biological stimulus

Semicircular canal biomechanics are frequency dependent, and vestibular perceptual thresholds also vary with stimulus frequency. [7,25-27] Frequency therefore changes both the mechanical transformation of rotation and the sensitivity with which motion can be detected.

A fixed angular displacement delivered at different frequencies also produces different angular velocities and accelerations. Frequency is thus intertwined with other physical descriptors rather than being an independent label.

## 11.2 Amplitude cannot be interpreted independently of frequency

For a sinusoidal displacement  $x(t)=A \sin(\omega t)$ , velocity and acceleration scale with frequency as well as amplitude. Two waveforms with the same displacement amplitude but different frequencies therefore impose different velocity and acceleration profiles.

Conversely, matching peak acceleration does not guarantee matching displacement, velocity, duration, or vestibular representation. This is why a future dose cannot responsibly be specified by one scalar such as degrees, meters per second squared, or hertz.

## 11.3 Thresholds depend on what is being measured

Human vestibular thresholds provide evidence that sensitivity varies with frequency, axis, age, and other factors. [25-27,36-38] But a perceptual threshold is not interchangeable with a receptor threshold, reflex threshold, autonomic threshold, or therapeutic threshold.

Threshold studies therefore help define variability and stimulus dependence. They do not provide a ready-made SeaKing Solace dosing rule.

## 11.4 Temporal envelope distinguishes waveforms with similar spectra

Stimuli with similar dominant frequencies can differ in onset rate, amplitude modulation, intermittency, transient peaks, and duration. These temporal characteristics can alter canal mechanics, neural firing, prediction, and adaptation.

Accordingly, spectral analysis should complement rather than replace the original time-domain record.

## 11.5 Duration is a separate stimulus dimension

A short exposure and a prolonged exposure to the same nominal waveform are not equivalent experimental conditions. Vestibular responses can adapt over time, and tolerability can change with cumulative exposure.

Duration should therefore be measured and later manipulated independently rather than absorbed into a general concept of dose.

## 11.6 Cross-axis timing may matter even when individual axes are unchanged

If two sinusoidal components have the same amplitudes and frequencies but differ in relative phase, the individual axis statistics can remain similar while their simultaneous relationship changes. Because canal and otolith signals interact centrally, such timing differences are biologically plausible experimental variables. [3]

The literature does not identify an optimal phase relationship. Controlled multi-axis experiments are needed to determine whether phase or other cross-axis timing contributes to any reproducible downstream response.

## 11.7 There is no established vestibular dose for the proposed endpoint

Table 2 summarizes the principal stimulus dimensions that the literature supports measuring without implying that any one dimension constitutes an established therapeutic dose.

| Stimulus dimension          | Why retain it                                                                  | Current evidentiary boundary              |
|-----------------------------|--------------------------------------------------------------------------------|-------------------------------------------|
| Amplitude                   | Changes displacement, velocity, acceleration, and receptor drive               | No established therapeutic amplitude      |
| Frequency                   | Changes vestibular dynamics and perceptual sensitivity                         | No established therapeutic frequency      |
| Temporal envelope           | Captures onset, offset, intermittency, modulation, and transients              | No established optimal envelope           |
| Duration / exposure history | Allows adaptation, habituation, and cumulative effects to be examined          | No established therapeutic duration       |
| Cross-axis timing / phase   | Preserves relationships among simultaneous rotational and translational inputs | No established optimal phase relationship |
| Head orientation            | Changes projection of gravity and motion into vestibular coordinates           | No established optimal orientation        |

**Table 2. Candidate stimulus dimensions to preserve during discovery.**

The existing literature cannot specify a SeaKing Solace waveform in the form of a particular amplitude, frequency, axis combination, and duration. Studies address different sensory, perceptual, reflex, adaptation, and motion-sickness endpoints under different conditions.

The appropriate conclusion is therefore not that the literature is insufficient to guide research. It is that the literature identifies the dimensions that should be measured and manipulated while leaving the relevant combination to empirical determination.

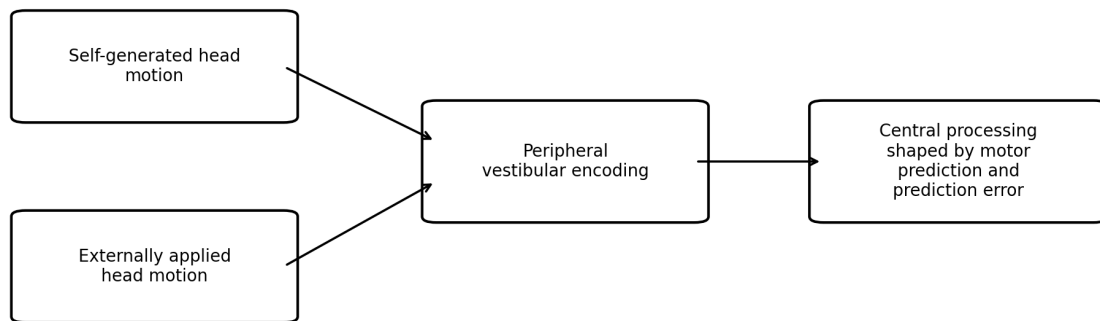
### 11.8 Implications for discovery and controlled testing

Phase 1 should preserve frequency content, amplitude distributions, temporal envelope, duration, cross-axis timing, and transient events rather than collapsing natural exposure into a single summary. Candidate relationships can then be reproduced under controlled conditions while one parameter is changed at a time.

For SeaKing Solace, this provides the bridge from descriptive natural-motion data to later dose-response experiments without pretending that the dose is already known.

## 12. Active Versus Externally Applied Motion

Figure 5 summarizes the distinction between peripheral encoding of physical head motion and the increasing influence of motor prediction and prediction error in central processing.



**Figure 5. Active versus externally applied motion. Peripheral vestibular encoding represents physical head motion in both conditions, while central processing is increasingly shaped by predicted versus unexpected sensory consequences.**

Physical head motion is not represented centrally without regard to how it was generated. Vestibular afferents strongly encode the mechanics of head movement, but central vestibular pathways increasingly distinguish expected sensory consequences of voluntary action from externally imposed or otherwise unexpected motion. [24,29-35]

This distinction gives externally applied motion a legitimate mechanistic meaning while also requiring caution: externally imposed does not mean therapeutically superior, and active and passive conditions are not simple opposites.

## 12.1 Reafference and exafference

Self-generated movement produces sensory reafference: sensory input arising from the organism's own action. Externally imposed movement contributes exafferent input that is not generated by the participant's motor command.

The nervous system can use internal predictions associated with voluntary movement to distinguish expected reafference from unexpected sensory consequences.

## 12.2 Peripheral afferents continue to encode active motion

Vestibular nerve afferents do not simply suppress self-generated head motion. Studies comparing active and passive movement show that peripheral afferents continue to represent the physical motion in both conditions. [14-15]

The major active-passive transformation therefore emerges centrally rather than being explained by a disappearance of peripheral vestibular input during voluntary movement.

## 12.3 Central vestibular neurons can attenuate expected self-generated input

Roy and Cullen demonstrated selective processing of vestibular reafference during self-generated head motion. [29-31] Central vestibular neurons can respond less strongly to predictable vestibular consequences of voluntary movement than to comparable externally applied motion.

This attenuation depends on the relationship between motor prediction and the actual sensory consequences of movement, not simply on whether muscles are active.

## 12.4 Proprioceptive agreement matters

Brooks and Cullen showed that active-motion attenuation depends on agreement between predicted and actual proprioceptive feedback. When the expected relationship is violated, central processing changes. [32]

This is important because the nervous system appears to evaluate whether incoming sensory information matches a learned prediction of the movement rather than labeling all voluntary motion identically.

## 12.5 Internal models can update rapidly

Cerebellar studies demonstrate that predictions of self-generated sensory consequences can adapt when the relationship between motor command and resulting motion changes. [33]

Thus expected versus unexpected motion is not a fixed property of a waveform. Experience and learning can alter how a repeated movement is interpreted centrally.

## 12.6 Externally imposed motion generates prediction error

When a boat, platform, vehicle, or other external force moves the head, there is no voluntary motor command that fully predicts the imposed motion. Vestibular afferents encode the physical movement, while central pathways compare that input with internal predictions. Unexpected components therefore generate sensory prediction error. [24]

This provides a mechanistic basis for distinguishing externally applied motion from otherwise similar self-generated kinematics.

## 12.7 The distinction persists in higher vestibular pathways

Differential processing of externally applied and active movement extends beyond the vestibular nuclei. Dale and Cullen reported preferential encoding of externally applied motion in the ventral posterior lateral thalamus, indicating that behaviorally relevant distinctions persist along pathways contributing to self-motion perception. [34]

The broad transformation is therefore from strong peripheral representation of physical motion toward central representations increasingly shaped by prediction and behavioral context.

## 12.8 Similar kinematics do not guarantee equivalent central conditions

Walking, self-rocking, being rocked, active swinging, passive swinging, horseback riding, mechanically driven riding simulation, actively controlling a vessel, and passively riding aboard one can all produce vestibular stimulation. They are not necessarily equivalent central vestibular conditions.

Even when head trajectories are similar, the proportion of motion that is voluntarily generated, externally imposed, predicted, unexpected, or actively compensated can differ.

## 12.9 Externally applied does not mean motionless participation

A participant aboard a vessel remains behaviorally active. Head turns, posture changes, bracing, walking, visual tracking, and anticipatory movements add self-generated components to the externally generated motion.

This is why behavioral context remains relevant even when head-centered kinematics are measured accurately. Sensors can describe what moved; they do not by themselves reveal which components the nervous system predicted from voluntary action.

## 12.10 Predictability can change with repeated exposure

Externally generated motion can become increasingly predictable. Repeated oscillation, visual cues, and prior experience can support anticipation and compensatory behavior. That does not make the environmental motion self-generated, but it can change central processing and behavior.

Repeated-session studies should therefore consider whether responses change as participants become familiar with the motion environment.

### 12.11 Evidentiary boundary

The active-passive literature establishes that origin and predictability of motion can influence central vestibular representation. It does not establish that externally applied motion produces stronger autonomic regulation, greater neuroplasticity, or better clinical outcomes.

Those propositions require direct downstream evidence.

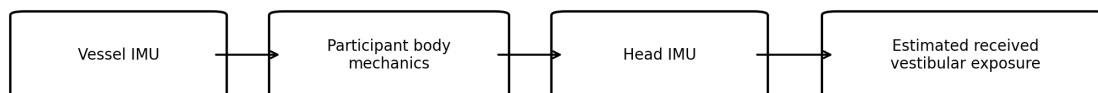
### 12.12 Relevance to SeaKing Solace

For SeaKing Solace, externally applied rhythmic motion should be treated as an experimentally meaningful descriptor rather than a synonym for passive therapy. The vessel supplies motion not generated by the participant's motor command, while the participant simultaneously contributes voluntary movement and adaptation.

A later controlled platform should therefore reproduce candidate head-centered kinematics while also documenting behavioral state and predictability. If the same physical motion produces different physiological responses under active, passive, predictable, or unexpected conditions, that difference would itself become part of the mechanism to investigate.

## 13. Head Motion Versus Platform Motion

Figure 6 summarizes the vessel-to-head transfer problem that participant-level sensing is intended to characterize.



**Figure 6. Vessel motion versus received head motion. Vessel-mounted sensing characterizes environmental motion; participant mechanics transform that input before it reaches the head. Simultaneous head sensing permits estimation of received head-centered exposure.**

The vestibular organs are fixed within the skull. The most proximal physical stimulus to the labyrinth is therefore the motion of the head, not the commanded motion of a vessel or motion platform. Environmental and platform measurements remain essential, but they do not by themselves establish the vestibular exposure received by an individual participant.

This distinction becomes especially important in natural settings, where participants can stabilize, rotate, tilt, translate, or reposition the head relative to the moving environment.

### 13.1 A rigid platform does not imply a rigid participant

A vessel-mounted or platform-mounted inertial sensor describes motion at the sensor location. A seated participant, however, is not mechanically rigidly coupled to that sensor. The trunk, neck, and head introduce additional degrees of freedom, and voluntary or compensatory movements can transform the imposed environmental motion before it reaches the labyrinth.

Two participants exposed to the same vessel trajectory can therefore receive different head-centered rotational and gravito-inertial inputs.

### 13.2 Head stabilization is itself part of the measured system

Humans actively stabilize the head and body during movement. Neck reflexes, postural responses, visual fixation, anticipation, and voluntary behavior can alter head motion relative to a moving support surface.

This means that the difference between vessel motion and head motion is not merely measurement error. It can contain information about how an individual mechanically and behaviorally interacts with the stimulus.

### 13.3 Head orientation changes vestibular geometry

Head orientation determines how gravitational and inertial vectors project onto the otolith organs and how rotations align with semicircular canal planes. The same platform trajectory can therefore generate different peripheral vestibular patterns when the head is held in different orientations.

Sections 5–8 established why this matters biologically: canal and otolith systems are directionally organized, gravito-inertial input is head centered, and central interpretation depends on their combined temporal relationship.

### 13.4 Head-centric motion control is technically feasible

La Scaleia and colleagues described a six-degree-of-freedom motion-platform approach in which head motion was tracked in real time and the commanded platform trajectory was adjusted so that the desired vestibular stimulation remained defined in head-centered coordinates despite voluntary head movement. [4]

This work is important because it demonstrates that the distinction between platform coordinates and vestibular coordinates can be handled as a measurable engineering-control problem rather than only as a theoretical concern.

### 13.5 Environmental and head sensors answer different questions

Environmental sensors characterize what the vessel or platform did. Participant-level head sensors characterize what motion reached the head after body mechanics and voluntary movement transformed that environmental input.

Neither measurement replaces the other. Their relationship can be informative: vessel-to-head transfer can vary by participant, posture, activity, frequency, axis, and time.

### 13.6 The vessel-to-head relationship can be modeled

With synchronized vessel and head kinematics, the research dataset can estimate how environmental motion is transmitted to the participant. This relationship may be simple in some conditions and strongly state dependent in others.

A useful conceptual chain is:

*vessel motion → body mechanics and behavior → head motion → vestibular end-organ stimulation*

The difference between the first and third terms is therefore a candidate explanatory variable rather than something to be discarded.

### 13.7 Head motion remains an engineering approximation of vestibular input

Head-mounted inertial sensing is more proximal to vestibular exposure than vessel sensing, but it is not a direct measurement of endolymph motion, hair-cell deflection, vestibular-nerve firing, or central neural representation.

Head kinematics should therefore be described as a physical approximation of received vestibular exposure. The biological transformations described earlier in this review still occur downstream.

### **13.8 Measurement introduces its own limitations**

Participant-level inertial measurement can be affected by calibration error, sensor drift, misalignment, synchronization error, magnetic interference, attachment movement, and participant discomfort. Instrumentation can also alter natural head behavior.

These limitations argue for careful calibration, synchronization, and quality-control procedures rather than abandoning participant-level measurement.

### **13.9 Implications for Phase 1**

For SeaKing Solace Phase 1, simultaneous vessel and participant head measurement would permit three distinct analyses: characterization of the natural environmental motion, characterization of the motion received at the head, and estimation of the transfer between them.

If physiological response tracks head-centered motion more closely than vessel-frame motion, that would materially change what should be reproduced in a later simulator. If vessel-frame variables predict response adequately, that would support a simpler engineering model. The study should allow the data to decide.

### **13.10 Implications for a controlled platform**

A later simulator should not assume that reproducing a recorded vessel trajectory automatically reproduces the vestibular stimulus experienced during the natural exposure. Head tracking can allow the system to compare commanded platform motion with actual head motion and, if justified, compensate in real time.

This creates a progression from open-loop playback toward head-centric stimulus control. Physiological closed-loop adaptation is a separate later question and should not be conflated with the more immediate problem of delivering the intended physical stimulus.

## **14. Individual Variability in Vestibular Sensitivity**

Vestibular sensitivity varies among individuals. Human psychophysical studies demonstrate substantial differences in motion-detection thresholds across people, and those thresholds can depend on stimulus axis, frequency, age, and testing method. [25-27,36-38]

This variability is relevant to experimental design because a single physical waveform does not guarantee an identical perceptual or neural state across participants.

### **14.1 Vestibular perceptual thresholds vary across people**

Threshold studies quantify the smallest motion that participants can reliably discriminate under controlled conditions. Across yaw rotation, translation, and other paradigms, investigators observe meaningful interindividual variability. [25-27]

Such variability supports treating participant identity as a major factor in repeated-measures analyses rather than assuming that all observations are exchangeable.

### **14.2 Frequency changes measured sensitivity**

Grabherr and colleagues demonstrated frequency dependence of yaw-rotation perceptual thresholds, and subsequent work has extended frequency-dependent threshold characterization across vestibular modalities. [25-27]

A participant who is relatively sensitive at one frequency should not automatically be assumed equally sensitive across the full spectrum of natural motion.

### 14.3 Age is an important source of variability

Bermúdez Rey and colleagues reported increasing vestibular perceptual thresholds above approximately age 40 across several motion conditions. [36] Age can therefore alter the distribution of sensitivity even among otherwise healthy adults.

Age should be considered as a potential covariate when characterizing healthy-adult response and when comparing later clinical populations.

### 14.4 Axis and modality matter

Thresholds differ among rotational and translational conditions and across vestibular tests. Reviews of vestibular perceptual testing emphasize that different paradigms probe different aspects of vestibular function rather than yielding one universal sensitivity value. [27,37]

Accordingly, a single vestibular threshold should not be used as a global participant descriptor without evidence that it predicts the stimulus-response relationship under study.

### 14.5 Perceptual threshold is not physiological-response threshold

A perceptual threshold indicates conscious discrimination performance under a defined psychophysical paradigm. It is not equivalent to the minimum stimulus that activates vestibular receptors, evokes a reflex, changes autonomic physiology, or produces a clinical effect. [27]

This distinction prevents an important inferential error: existing threshold literature can demonstrate variability and stimulus dependence without specifying a SeaKing Solace therapeutic dose.

### 14.6 Within-person consistency may still be useful

Recent longitudinal work indicates that some vestibular perceptual thresholds show meaningful within-individual consistency over time. [38] This raises the possibility that certain vestibular characteristics behave partly as participant-level traits rather than pure measurement noise.

Whether physiological responses to externally applied rhythmic motion show comparable within-person stability remains unknown and is itself an empirical question.

### 14.7 Variability can arise from more than vestibular sensitivity

Individual differences in a motion-physiology dataset could reflect vestibular sensitivity, but also posture, head stabilization, autonomic baseline, medication, sleep, anxiety, physical conditioning, prior motion exposure, body mechanics, or other factors.

The research should therefore avoid labeling every participant-specific response pattern as a vestibular sensitivity phenotype.

### 14.8 Implications for study design

Repeated measurements within participants can help distinguish stable individual response patterns from session-to-session variability. Mixed-effects or other hierarchical analyses can preserve participant-level structure while estimating population effects.

For SeaKing Solace, individual variability is a reason to collect enough repeated exposure to characterize response, not evidence that a personalized closed-loop system is already required.

## 15. Adaptation, Habituation, and Repeated Exposure

Vestibular responses are not necessarily stationary across repeated exposure. Mechanical adaptation, central recalibration, habituation, sensory prediction, behavioral learning, and changing motion tolerance can all alter how a repeated stimulus is experienced or represented over time.

This makes exposure history a scientific variable rather than a scheduling detail.

### **15.1 Several different processes can produce a changing response**

The term adaptation is often used broadly, but repeated-exposure changes can arise at different levels. Peripheral receptor and reflex dynamics, central sensory recalibration, learned prediction, behavioral compensation, and habituation of symptom or postural responses are not interchangeable mechanisms.

Experimental interpretation should therefore describe the observed change first and assign mechanism only when the data support it.

### **15.2 Vestibular rehabilitation demonstrates experience-dependent change**

Vestibular rehabilitation relies on adaptation, substitution, and habituation principles to improve function after vestibular impairment. Reviews and clinical practice guidelines document that repeated, appropriately structured sensory and movement exposure can produce durable changes in gaze and balance function. [40-41]

These clinical findings establish vestibular plasticity and experience dependence. They do not show that repeated natural motion in healthy participants will produce the same mechanisms or outcomes.

### **15.3 Error signals can drive adaptation**

Vestibulo-ocular reflex adaptation depends on sensory error. Mahfuz and colleagues showed that retinal image slip must exceed a threshold to drive human vestibulo-ocular reflex adaptation. [42]

This illustrates a broader principle: repetition alone does not guarantee adaptation. The nervous system changes when repeated experience contains an error or mismatch signal capable of driving recalibration.

### **15.4 Repeated motion can alter motion-sickness susceptibility**

Repeated visual-vestibular exposure can reduce motion-sickness sensitivity, and changes in velocity-storage dynamics have been implicated in this process. [43-45]

Such findings demonstrate that tolerance to motion can change over time, but motion-sickness habituation should not be treated as evidence of beneficial autonomic regulation.

### **15.5 Near-threshold exposure can modify later thresholds**

Recent work indicates that prolonged near-threshold motion can alter vestibular perceptual thresholds, with effects that depend on vestibular status. [46]

This further supports treating prior exposure as a potential modifier of later response rather than assuming a fixed participant sensitivity throughout a longitudinal study.

### **15.6 Natural motion can produce persistent aftereffects**

Mal de débarquement provides a clinically important example of persistent motion-related aftereffects after prolonged passive exposure. [47] Its pathophysiology is distinct from the SeaKing Solace hypothesis, but it demonstrates that prolonged rhythmic motion can be followed by central perceptual consequences that outlast the stimulus.

The appropriate inference is not that prolonged motion is desirable. It is that duration and exposure history can matter beyond the period of active stimulation.

### **15.7 Habituation can occur in vestibular-evoked balance responses**

Repeated exposure can also reduce behavioral or postural responses to vestibular perturbation. Recent work on vestibular-evoked balance responses demonstrates habituation with repeated exposure under defined conditions. [48]

Again, the mechanism and endpoint matter. A reduced response can represent efficient adaptation, habituation, fatigue, or another process depending on the paradigm.

## **15.8 Repeated sessions create both opportunity and confounding**

Longitudinal sampling can reveal whether a motion-response relationship is reproducible within an individual and whether it changes systematically with exposure. At the same time, repeated sessions introduce familiarity, expectation, improved head stabilization, changing anxiety, changing tolerance, and ordinary day-to-day physiological variation.

Session number, cumulative exposure, time since prior exposure, and relevant behavioral context should therefore be retained in the dataset.

## **15.9 Implications for SeaKing Solace**

For Phase 1, repeated sessions should not be treated simply as duplicate observations. They can answer whether candidate motion-physiology relationships are stable, strengthen, weaken, or change form with exposure.

A later controlled program can then distinguish acute stimulus-response relationships from adaptation or habituation effects by manipulating exposure history deliberately.

## **16. Motion Sickness and Tolerability as Boundary Conditions**

Any program using externally applied vestibular stimulation must treat tolerability as a primary scientific and safety constraint. Motion sickness demonstrates that particular combinations of vestibular, visual, and predictive information can produce adverse autonomic and behavioral responses, and susceptibility varies substantially among individuals. [49]

The goal is not merely to avoid overt nausea. Physiological changes associated with emerging motion sickness can overlap with candidate biomarkers of autonomic response and can therefore confound interpretation.

### **16.1 Motion sickness is linked to sensory conflict and prediction**

Modern accounts of motion sickness emphasize conflict among sensed, expected, and internally estimated motion and orientation. Subjective-vertical conflict and related sensory-mismatch models explain many provocative conditions, although no single theory resolves every observation. [49]

This uncertainty argues for using motion-sickness theory as a guide to stimulus design and interpretation rather than as a complete mechanistic model.

### **16.2 Canal-otolith relationships can be provocative**

Stimuli that create unusual relationships between angular and gravito-inertial signals can be strongly motion provocative. Cross-coupled rotation and other paradigms demonstrate that the timing and geometry of combined vestibular inputs matter for tolerability. [49]

This reinforces the earlier conclusion that multi-axis structure is biologically meaningful while also showing that complexity can be harmful rather than beneficial.

### **16.3 Frequency strongly influences motion sickness**

Motion-sickness susceptibility varies with stimulus frequency. Studies of oscillatory motion show that relatively low-frequency motion can be particularly provocative under some conditions. [28,49]

These frequency-response relationships provide useful boundary information, but laboratory curves should not be treated as a complete prediction of tolerability during prolonged natural vessel exposure.

### **16.4 Velocity storage contributes to susceptibility**

Velocity storage is a central vestibular mechanism that extends and integrates rotational information beyond the immediate peripheral canal response. Its spatial-temporal properties have been linked to

motion-sickness susceptibility, and reducing velocity-storage time constants can accompany reduced susceptibility. [39,44-45]

This literature identifies a plausible central contributor to motion sickness without implying that velocity storage explains every adverse response to motion.

### **16.5 Visual context can increase or decrease conflict**

Visual information can either support an estimate of self-motion or conflict with vestibular input. Access to a stable horizon, visual fixation, optic flow, and enclosed visual environments can therefore change tolerability even when the physical motion is similar. [49]

Natural vessel studies should document visual context because it can modify both symptoms and physiological response.

### **16.6 Motion-sickness physiology can mimic the signal of interest**

Motion sickness is accompanied by autonomic changes. Heart rate, heart-rate variability, pupil dynamics, sweating, respiration, and other physiological variables can change as symptoms develop. [49]

A measured physiological change during motion should therefore not automatically be interpreted as beneficial regulation. It may represent an adverse response, especially if it precedes subjective symptoms.

### **16.7 Symptoms and physiology should be synchronized with motion**

Tolerability measurement is most informative when symptom reports and objective physiological signals can be aligned with the motion time series. This allows investigators to determine whether particular motion features precede discomfort and whether candidate physiological responses occur within or outside adverse-response trajectories.

Session-level labels such as tolerated versus not tolerated would lose much of this temporal information.

### **16.8 Susceptibility varies among participants**

Motion-sickness susceptibility differs substantially across individuals and can change with prior exposure. A stimulus that is well tolerated by one participant may be provocative for another.

This variability should be treated as a participant-level characteristic and safety constraint rather than as noise to be averaged away.

### **16.9 Natural vessel exposure differs from laboratory provocation**

Marine exposure can include horizon visibility, fresh air, voluntary posture changes, anticipation, social interaction, and prolonged low-level motion. Laboratory paradigms often isolate particular provocative stimuli under tightly controlled conditions.

Laboratory motion-sickness findings therefore provide mechanistic and boundary information but cannot substitute for direct tolerability characterization in the natural environment.

### **16.10 Tolerability defines a usable stimulus space**

A future controlled platform should search for reproducible physiological effects within a stimulus region that remains acceptably tolerated. A larger physiological response is not automatically preferable if it is coupled to discomfort or motion-sickness physiology.

This creates an optimization problem in which candidate efficacy-related signals, if later established, must be considered together with tolerability rather than maximized independently.

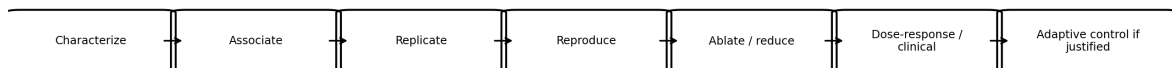
### 16.11 Implications for Phase 1 and later controlled testing

For SeaKing Solace Phase 1, motion exposure, physiological response, symptoms, and participant behavior should be synchronized closely enough to distinguish candidate desired responses from adverse motion-sickness trajectories.

Later controlled studies can deliberately test candidate motion profiles near, but not beyond, empirically established tolerability boundaries. The literature supports mapping that boundary; it does not provide a universal safe or effective waveform.

## 17. Implications for Characterizing Controlled Multi-Axis Motion

Figure 7 summarizes the evidence-gated progression from natural characterization to increasingly controlled and potentially adaptive stimulation.



**Figure 7. Discovery-to-control research sequence. Progression from natural characterization through controlled causal testing and, only if justified by prior evidence, clinical and adaptive-control stages.**

The literature reviewed in Sections 3–16 converges on a practical conclusion: a controlled vestibular stimulus cannot be specified adequately by platform displacement alone. Environmental motion is transmitted through the participant to the head, transformed by canal and otolith biomechanics, encoded by heterogeneous afferent populations, integrated centrally, and interpreted in relation to behavioral context and prior exposure.

A controlled system must therefore distinguish physical reproduction from biological reproduction. Physical reproduction means generating a desired mechanical trajectory. Biological reproduction means delivering a received vestibular exposure sufficiently similar to the target condition to test whether the biological response can be reproduced. These goals are related but not necessarily equivalent.

### 17.1 Controlled motion enables causal manipulation

Natural motion provides ecological richness but limited causal control because many stimulus dimensions vary simultaneously. Once Phase 1 identifies a candidate relationship, a controlled platform allows the relevant feature to be reproduced while other variables are held constant or manipulated deliberately.

The purpose of controlled stimulation is therefore not simply to replay an interesting vessel trace. It is to convert candidate associations into variables that can be tested for necessity, sufficiency, dose-response behavior, and interaction.

### 17.2 Six-degree-of-freedom capability supports both reproduction and reduction

A six-degree-of-freedom platform can generate translational and rotational motion across multiple axes and can reproduce combinations resembling natural motion. Its scientific value is not that every experiment should use all six axes simultaneously. Its value is that complexity can be reconstructed and then reduced systematically.

Candidate profiles can be tested with individual axes removed, amplitudes or frequencies changed, phase relationships altered, or broadband components simplified. If a response survives reduction, the minimum sufficient stimulus may be substantially simpler than the natural exposure.

### **17.3 Reproducing platform motion is not enough**

Section 13 established that the vestibular organs receive head-centered motion. Replaying a vessel trajectory on a land-based platform does not guarantee reproduction of the original head motion because seat geometry, posture, head stabilization, visual context, and voluntary behavior can differ.

Controlled reproduction should therefore distinguish commanded platform motion, delivered platform motion, and received head motion. Where necessary, real-time head tracking can allow control to be defined in head-centered coordinates. [4]

### **17.4 Validation should precede optimization**

The first controlled-platform question should be whether a candidate natural exposure can be reproduced sufficiently to recreate the associated physiological response. Optimization should follow only after reproducibility has been demonstrated.

Beginning immediately with an optimized waveform would risk fitting a controller to assumptions that have not yet survived experimental reproduction.

### **17.5 Dimensional reduction should be experimental**

Once reproduction is established, controlled experiments can remove or alter candidate components. This creates direct tests of whether roll, heave, translation, frequency bands, cross-axis timing, duration, or other features are necessary for the response.

Reduction should continue until further simplification weakens or eliminates the reproducible response, subject to tolerability and measurement precision. The resulting stimulus need not resemble a boat trajectory visually or mechanically if it preserves the biologically relevant structure.

### **17.6 Orthogonal manipulation can separate correlated natural variables**

Natural environments often couple variables that a platform can manipulate independently. Frequency can be changed while holding another parameter approximately constant; phase relationships can be altered; visual context can be modified; duration can be varied independently of waveform.

Such orthogonal manipulation is essential for distinguishing causal variables from features that merely covary in the natural environment.

### **17.7 Mechanical and control-system limits define the realizable stimulus space**

Every motion platform has finite stroke, velocity, acceleration, jerk, payload, bandwidth, and safety limits. Motion-cueing algorithms used in simulation illustrate that a platform may reproduce selected perceptually important components without physically reproducing an unrestricted real-world trajectory.

For SeaKing Solace, this is a caution rather than a prescription. A vestibular research platform should be designed around the biological variables identified experimentally, not around the assumption that conventional simulator fidelity is the relevant objective.

### **17.8 Biomimetic engineering provides a useful precedent**

Vestibular prosthesis research demonstrates a broader engineering principle: artificial stimulation can be designed around known neural coding and then refined through physiological validation. The precedent is conceptual rather than directly therapeutic. A motion platform and an implanted vestibular prosthesis use different stimulation modalities and address different clinical problems.

The relevant lesson is that neuroscience and engineering can be iterated together rather than treating the mechanical device as fixed before the biological response is understood.

### 17.9 Necessity and sufficiency should be tested separately

If removing a motion component abolishes a response, that component may be necessary within the tested condition. If presenting a component alone reproduces the response, it may be sufficient under that condition. These are different claims and require different experiments.

Controlled testing should therefore avoid declaring a feature causal merely because it predicts response in natural data.

### 17.10 Individual variability becomes experimentally actionable

Once a candidate stimulus can be reproduced, between-person and within-person differences can be tested directly. Participants can receive the same controlled input, and stimulus parameters can be adjusted systematically to determine whether response functions differ.

This is the stage at which personalization can become an empirical question rather than an assumption.

### 17.11 From open-loop reproduction to system identification

The long-term engineering problem can be framed as system identification: determine how controlled motion inputs relate to measurable physiological outputs within individuals and across populations. Early experiments should use predefined open-loop stimuli because they are easier to interpret causally.

If reproducible input-output relationships are established, adaptive controllers can later be tested. A physiology-driven closed loop should emerge from validated system identification, not precede it.

### 17.12 Closed-loop control remains conditional

A closed-loop platform would add another layer of scientific risk because the controller changes the stimulus in response to the participant. That can improve personalization, but it can also create unstable feedback, obscure causal interpretation, or overfit transient physiology.

*The appropriate progression is therefore: reproduce → validate → manipulate → reduce → characterize individual response functions → test adaptive control. Each step should be evidence gated.*

### 17.13 Tolerability remains part of the control problem

Controlled optimization cannot maximize a physiological signal without regard to adverse responses. Motion-sickness physiology can overlap with candidate autonomic biomarkers, and tolerability varies among participants.

The usable stimulus space is therefore bounded by both the desired experimental response and evidence of discomfort or adverse physiology.

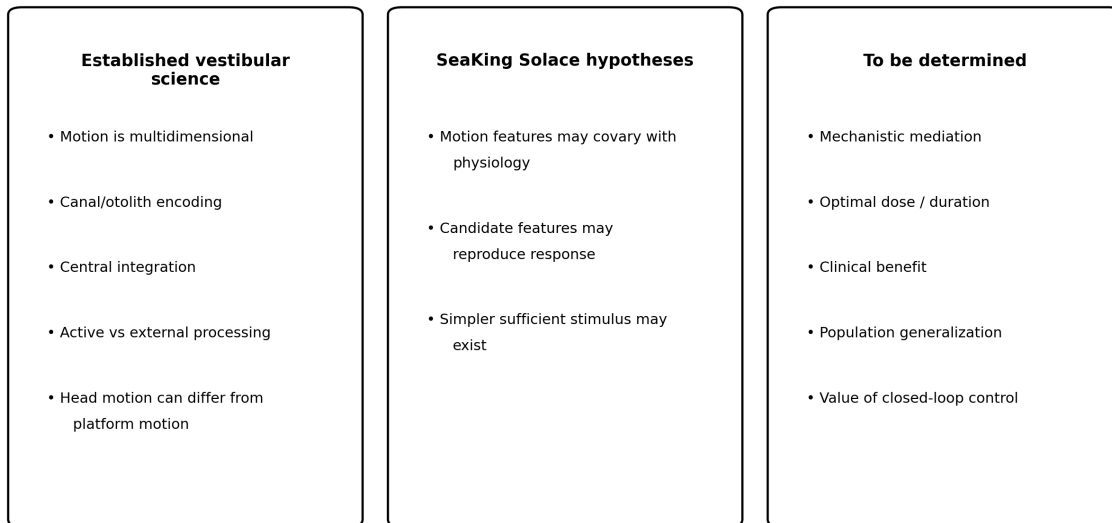
### 17.14 Central implication

The controlled platform is not the endpoint of the scientific argument. It is the instrument that allows a natural association to be converted into a causal, reducible, and eventually controllable stimulus-response model.

For SeaKing Solace, the strongest engineering strategy is therefore to let the biological data determine what the simulator must reproduce rather than deciding in advance what a therapeutic motion waveform should look like.

## 18. Relevance to the SeaKing Solace Hypothesis

Figure 8 separates established vestibular science from the SeaKing Solace hypotheses and the questions that remain to be determined experimentally.



**Figure 8. Evidentiary architecture of the SeaKing Solace hypothesis. Established vestibular findings support testable hypotheses but do not establish downstream mechanism, clinical benefit, optimal dosing, or the value of closed-loop control.**

The SeaKing Solace hypothesis emerged from observations made in natural motion environments, but the scientific hypothesis is not that boats are therapeutic. It is that identifiable characteristics of externally applied rhythmic motion may produce reproducible physiological responses and that, if such relationships exist, the responsible stimulus features may be isolated, reproduced, and tested under controlled conditions.

The vestibular literature reviewed here does not establish that downstream response. It establishes that motion is a biologically meaningful, multidimensional physical exposure that can be measured, parameterized, and manipulated.

### 18.1 The hypothesis concerns the physical stimulus rather than the experiential wrapper

Boat travel, horseback riding, swinging, rocking, and other motion-rich activities differ dramatically as experiences. From the vestibular perspective, however, each can expose the head to structured angular and gravito-inertial motion.

This does not prove that motion explains reported outcomes from those activities. It identifies motion as a separable candidate variable whose contribution can be tested rather than assuming the surrounding activity is an indivisible intervention.

### 18.2 Externally applied and rhythmic are empirical descriptors

Externally applied is biologically meaningful because central vestibular processing distinguishes expected self-generated sensory consequences from externally imposed or unexpected motion. Rhythmic should not be interpreted as a single sinusoid; natural rhythmic motion can contain variable amplitude, frequency, phase, and intermittency.

Whether either property is relevant to the proposed physiological endpoint remains an experimental question.

### **18.3 The hypothesis is a stimulus-response hypothesis**

A rigorous formulation is:

*measurable characteristics of externally applied motion → reproducible physiological response*

This formulation deliberately stops short of asserting mechanism. A motion-response association would not by itself prove vestibular mediation, vagal mediation, therapeutic benefit, or clinical efficacy.

### **18.4 The hypothesis can be decomposed into testable claims**

The program can test whether: natural externally applied motion produces reproducible acute physiological changes; those changes covary with identifiable motion features; the relationship is more strongly explained by received head motion than by coarse environmental labels; candidate features can reproduce the response under controlled conditions; removing or altering those features changes the response; and response functions remain sufficiently stable to support later individualized control.

Each claim can succeed or fail independently. Failure at one stage should modify or terminate the corresponding branch of the hypothesis rather than being explained away by the broader product vision.

### **18.5 Alternative explanations remain active competitors**

Observed physiological changes during natural vessel exposure could arise from visual input, posture, expectation, novelty, relaxation, social context, respiratory changes, temperature, motion sickness, self-generated movement, or other environmental factors.

The research program should therefore be designed to make these explanations increasingly separable rather than treating vestibular mediation as the default interpretation.

### **18.6 The hypothesis makes falsifiable predictions**

If motion is a meaningful driver, physiological response should show reproducible relationships with measurable stimulus characteristics beyond nonspecific time-on-boat effects. Candidate relationships should survive replication and should respond predictably when the relevant stimulus features are manipulated under controlled conditions.

If these predictions fail, the motion-centered hypothesis should weaken accordingly.

### **18.7 Multi-axis motion is relevant without being presumed superior**

Natural multi-axis motion is worth preserving during discovery because vestibular systems integrate simultaneous rotational and gravito-inertial inputs. Nothing in the reviewed literature establishes that multi-axis stimulation is therapeutically superior to a simpler waveform.

A successful research program may ultimately discover that only a small subset of the natural stimulus is required.

### **18.8 The closed-loop concept follows only conditionally**

If reproducible stimulus-response functions exist and differ meaningfully among individuals or across time, adaptive control may eventually provide a way to maintain a desired physiological state while respecting tolerability constraints.

If stable individual response functions do not exist, closed-loop personalization may add complexity without benefit. The product concept is therefore downstream of the scientific result, not evidence for it.

## **18.9 What this review establishes and does not establish**

This review establishes a mechanistic and methodological basis for treating externally applied motion as a structured vestibular exposure, measuring it in biologically relevant coordinates, and testing it through controlled manipulation.

It does not establish autonomic benefit, vagal activation, neuroplasticity, therapeutic efficacy, an optimal waveform, a clinical dose, superiority of natural or multi-axis motion, or the validity of a closed-loop therapeutic platform. Those questions require separate evidence.

## **18.10 Central inference**

The strongest conclusion supported by the vestibular literature is therefore modest but consequential: the SeaKing Solace motion hypothesis is sufficiently grounded in established sensory physiology to be formulated as a rigorous, falsifiable experimental program.

## **19. Implications for the SeaKing Solace Research Program**

The vestibular literature does not prescribe a SeaKing Solace protocol. It identifies the physical, biological, and methodological dimensions that should be preserved long enough to determine whether they matter. The research program should therefore begin with characterization and progressive reduction of uncertainty rather than with a predetermined therapeutic waveform.

### **19.1 Phase 1 is a stimulus-discovery study**

Phase 1 should characterize natural vessel motion, participant-level received motion, acute physiology, tolerability, and repeated-session variability in healthy adults. Its purpose is not to establish clinical efficacy.

The core question is whether reproducible relationships exist between measured motion and physiological response and, if so, which features warrant controlled testing.

### **19.2 Healthy adults establish the initial measurement framework**

Beginning with healthy adults allows the program to characterize the stimulus, normal response distributions, measurement performance, and tolerability before adding the heterogeneity of clinical populations.

Healthy-adult results should not be treated as surrogates for autism, POTS, or other clinical groups. Their role is to establish a cleaner first-stage physical and physiological model.

### **19.3 Repeated sessions are scientifically informative**

Repeated exposure allows the program to distinguish acute response, within-person reproducibility, adaptation or habituation, and between-person variability. Session number, cumulative exposure, and time since prior exposure should remain explicit variables rather than being absorbed into sample size.

### **19.4 The primary exposure should remain time resolved**

Raw or minimally transformed synchronized motion data should be retained so that later analyses can examine axes, frequency content, temporal envelopes, transients, cross-axis timing, and head-centered transformations. Session-level summaries alone would prevent many of the questions identified in this review from being tested.

### **19.5 Vessel and participant motion should be measured together**

Simultaneous environmental and participant-level sensing allows the program to determine what the vessel did, what motion reached the head, and how the relationship between them varies across participants and sessions.

This is particularly important for deciding what a later controlled platform must reproduce.

## **19.6 Synchronization is a core measurement requirement**

Motion, physiological signals, symptom reports, and relevant behavioral events should share a common or accurately aligned time base. Candidate relationships may involve short or delayed responses, and timing error can create false lags or erase real ones.

Synchronization quality is therefore part of measurement validity, not merely data engineering.

## **19.7 Physiological response should remain multivariate but interpretable**

Multiple physiological signals can provide complementary information, but each additional biomarker increases analytical flexibility and the risk of overinterpretation. Measures should be selected for defined physiological reasons, quality controlled, and interpreted within their known limitations.

A biomarker change should not be treated as a clinical outcome or proof of mechanism.

## **19.8 Discovery and confirmation should be separated**

High-dimensional motion and physiology data can generate many candidate associations. Exploratory analyses should be labeled as discovery, with prespecified or independently validated analyses used for confirmation.

Held-out participants, sessions, sites, or later controlled studies can provide increasingly strong tests against overfitting.

## **19.9 Natural variability is information, but also confounding**

Variation in sea state, vessel heading, participant posture, visual context, behavior, and other environmental factors broadens the observed stimulus space. That variability can help discover candidate relationships, but it also prevents simple causal interpretation.

Relevant context should therefore be recorded when feasible and incorporated into analysis rather than ignored or assumed harmless.

## **19.10 The two-site design can support external validation**

If the two sites differ meaningfully in environmental conditions while using harmonized instrumentation and procedures, one site can provide a partial test of whether candidate relationships generalize beyond a single vessel environment or location.

This value depends on adequate protocol consistency and should not be overstated as formal replication unless the analysis is designed accordingly.

## **19.11 Phase 1 should identify candidates, not declare a waveform**

The output of Phase 1 should be a prioritized set of candidate motion-response relationships, estimates of reproducibility and variability, tolerability information, and explicit null findings.

A single optimized therapeutic waveform would be premature at this stage.

## **19.12 Null results are decision-relevant**

If physiology changes during vessel exposure but does not track measurable motion features, the motion-centered hypothesis weakens. If motion-response relationships are inconsistent within participants, personalization may be difficult. If responses track motion-sickness symptoms, the interpretation changes substantially.

A useful Phase 1 dataset should therefore support falsification as readily as discovery.

### 19.13 Phase 2 should test reproduction before optimization

Candidate natural exposures should first be reproduced on a controlled platform with verification of delivered and received motion. Only after the associated physiological response is reproduced should investigators optimize amplitude, frequency, timing, duration, or axis composition.

### 19.14 Controlled ablation tests mechanism more directly

Once reproduction is established, individual components can be removed or altered to test necessity, sufficiency, and interaction. This is the experimental step that can distinguish a causal stimulus feature from a natural correlate.

### 19.15 The program should seek the minimum sufficient stimulus

If a simpler stimulus reproduces the response, retaining unnecessary natural complexity would make engineering, safety, standardization, and later clinical testing harder without scientific benefit.

The desired endpoint is therefore not maximal resemblance to boat motion but the simplest well-tolerated stimulus that preserves the reproducible biological effect, if such an effect is established.

### 19.16 Clinical populations should enter after the stimulus is better defined

Later studies in autism, POTS, or other populations can ask whether the controlled stimulus produces reproducible physiological and ultimately clinical effects in those groups. Different disorders may require different stimulus-response models.

Physiological biomarkers can guide dose-finding and mechanism studies, but clinical efficacy must ultimately be demonstrated with clinically meaningful endpoints.

### 19.17 Progression should be evidence gated

Table 3 translates the evidence-gated logic into explicit research decisions without converting the review into a fixed clinical protocol.

| Stage                              | Primary question                                        | Evidence needed to progress                                          | Reason to stop or revise                                                             |
|------------------------------------|---------------------------------------------------------|----------------------------------------------------------------------|--------------------------------------------------------------------------------------|
| Natural characterization           | Are motion-physiology relationships reproducible?       | Measurement quality, tolerability, repeatable candidate associations | No reproducible relationship or response dominated by confounding/adverse physiology |
| Controlled reproduction            | Can candidate exposure reproduce the response?          | Verified delivered/ received motion and reproduced physiology        | Natural association fails under control                                              |
| Ablation / reduction               | Which features are necessary or sufficient?             | Predictable changes when components are removed or altered           | Candidate feature is noncausal or irreducibly confounded                             |
| Dose-response / population testing | Is response stable, tolerable, and clinically relevant? | Replicated response functions and appropriate clinical endpoints     | Poor tolerability, instability, or absent clinical relevance                         |
| Adaptive control                   | Does feedback improve performance over simpler control? | Stable input-output model and superiority to open-loop               | Added complexity without measurable benefit                                          |

**Table 3. Evidence-gated progression from discovery to adaptive control.**

Advancement between phases should depend on predetermined criteria such as measurement quality, reproducibility, tolerability, strength of candidate relationships, successful controlled reproduction, and evidence from ablation or dose-response testing.

Decision rules reduce the risk that an appealing long-term product vision drives progression despite weak intermediate evidence.

### **19.18 Data stewardship should preserve future testability**

Raw synchronized data, calibration information, preprocessing decisions, metadata, analysis code, and versioned derived datasets should be retained sufficiently to permit reanalysis and audit. High-dimensional discovery work is particularly vulnerable to analytical flexibility.

Transparent data provenance strengthens both internal decision making and external scientific diligence.

### **19.19 Closed-loop development should follow system identification**

Only after stable input-output relationships are demonstrated should the program test whether real-time physiological feedback improves stimulus selection. The controller should operate within empirically established safety and tolerability bounds and should be evaluated against simpler open-loop alternatives.

Personalization is a hypothesis to test, not a design requirement to assume.

### **19.20 Research-program summary**

The program can be summarized as:

*characterize → associate → replicate → reproduce → ablate → reduce → test dose-response → evaluate clinical populations → test adaptive control if justified*

This sequence progressively converts an observation in a complex natural environment into increasingly specific causal claims while preserving opportunities for the hypothesis to fail.

## **20. Limitations of the Current Evidence**

The evidence reviewed here provides a strong foundation for treating externally applied motion as a measurable vestibular stimulus. It does not provide a complete evidentiary bridge from vestibular sensory physiology to the downstream autonomic, neuroplastic, therapeutic, or clinical outcomes proposed for later SeaKing Solace research.

The limitations below define where inference should stop.

### **20.1 Translation from foundational physiology is incomplete**

Some of the most direct mechanistic evidence comes from invasive recordings in nonhuman primates. These studies are valuable for understanding afferent coding, central integration, prediction, and cerebellar computation, but quantitative human equivalence cannot be assumed.

Human vestibular studies often use modest samples, specialized equipment, and carefully selected participants. These designs can establish mechanisms and within-subject effects while providing limited estimates of population heterogeneity or uncommon responses.

### **20.2 Laboratory stimuli and natural exposure answer different questions**

Much of vestibular science intentionally uses artificial single-axis rotations, translations, tilts, darkness, sensory isolation, or brief repeated trials. These paradigms are powerful because they isolate variables. Natural vessel exposure is prolonged, multidimensional, behaviorally rich, and less controllable.

Findings from one context inform the other but do not substitute for direct characterization and controlled reproduction.

### **20.3 Naturalistic vestibular datasets remain comparatively limited**

Direct measurements of natural human motion and neural responses to naturalistic stimulation provide important evidence, but this literature is much smaller than the broader vestibular literature. The full statistical range of marine motion and participant-level head exposure is not established by existing studies.

Phase 1 therefore has a genuine descriptive role rather than merely repeating known stimulus statistics.

### **20.4 Sensory measurements do not define the proposed downstream endpoint**

Perceptual thresholds are not autonomic or therapeutic thresholds. Efficient neural coding is not evidence of therapeutic importance. Central distinction between externally imposed and self-generated motion does not establish a beneficial autonomic effect. Multi-axis integration does not establish superiority of multi-axis stimulation.

These are mechanistic facts that make the hypothesis testable, not evidence that the hypothesized downstream effect is true.

### **20.5 Head-centered measurement improves exposure characterization but remains indirect**

Head-mounted sensing is more proximal to vestibular input than vessel sensing, yet it remains an engineering measurement. It does not directly measure end-organ mechanics, vestibular-nerve activity, or central neural representation.

Sensor calibration, attachment, drift, synchronization, and participant behavior introduce additional uncertainty.

### **20.6 Time-series analysis creates substantial statistical risk**

Both motion and physiology are nonstationary, autocorrelated time series. Large numbers of axes, spectral features, lags, biomarkers, sessions, and interaction terms can produce apparently strong relationships by chance.

Prespecification, dimensionality control, correction for multiplicity where appropriate, held-out validation, and replication are therefore essential.

### **20.7 Natural environments are confounded and nonrandomized**

Sea state, weather, visual context, posture, activity, expectation, social interaction, fatigue, and other factors can change with motion. Natural vessel motion itself is not randomized.

Associations discovered in Phase 1 should therefore be treated as candidates for later controlled testing rather than causal effects.

### **20.8 Repeated exposure complicates interpretation**

Responses may change through adaptation, habituation, learning, anticipation, changing head stabilization, or ordinary physiological variability. A repeated-measures design can characterize these changes but cannot assume stationarity across sessions.

### **20.9 Motion-sickness physiology is a major competing explanation**

Motion sickness can alter heart rate, heart-rate variability, pupil behavior, respiration, sweating, and subjective state. These changes can overlap with candidate autonomic biomarkers. [49]

Physiological response must therefore be interpreted together with synchronized tolerability and symptom information.

#### **20.10 Dose, duration, and optimal waveform are unknown**

The current evidence does not specify the amplitude, frequency, axis combination, phase structure, duration, or repetition schedule relevant to the proposed SeaKing Solace endpoint. Laboratory thresholds and motion-sickness curves cannot be converted directly into a therapeutic dose.

Determining whether a useful dose-response function exists is part of the research program.

#### **20.11 Mechanistic mediation remains unproven**

Even if motion predicts physiology, vestibular mediation would still require additional evidence. Visual, proprioceptive, respiratory, psychological, postural, and other pathways remain plausible contributors.

Likewise, a physiological biomarker response would not establish vagal mediation, neuroplasticity, or clinical benefit.

#### **20.12 Generalization to clinical populations cannot be assumed**

Healthy adults and clinical populations can differ in sensory processing, autonomic physiology, medications, comorbidities, communication, tolerability, and behavior. A stimulus-response relationship established in healthy adults must be tested again in each target population.

Autism and POTS, for example, should not be assumed to share an identical mechanism or optimal stimulus.

#### **20.13 Individual response stability is unknown**

Existing vestibular literature demonstrates individual variability, but it does not establish that the proposed physiological response to rhythmic motion will be stable enough for personalized control. Apparent individual patterns can also be overfit when many parameters are available.

Closed-loop personalization should therefore be evaluated against simpler population-level or open-loop approaches.

#### **20.14 Engineering feasibility is not clinical utility**

A platform may be capable of reproducing head-centered motion, adapting in real time, and generating sophisticated multi-axis trajectories without producing a clinically meaningful effect. Engineering achievement cannot substitute for biological or clinical validation.

#### **20.15 The evidence base is heterogeneous and evolving**

The reviewed studies differ in species, apparatus, stimulus waveform, endpoint, sample size, analysis method, and purpose. Publication bias and incomplete reporting are possible, and future work may modify current interpretations.

The review should therefore be maintained as a living scientific synthesis rather than treated as a fixed proof.

#### **20.16 Central evidentiary boundary**

The current literature supports the plausibility of a rigorous research question and provides detailed guidance for measuring and manipulating the stimulus. It does not establish that SeaKing Solace's central physiological hypothesis is correct.

That uncertainty is not a defect in the program. It is the reason the proposed sequence of characterization, controlled reproduction, causal manipulation, and clinical testing is necessary.

## 21. Conclusions

The vestibular literature provides a coherent scientific basis for treating externally applied physical motion as a structured, measurable biological stimulus. Motion is decomposed across rotational and gravito-inertial components, transformed by semicircular canal and otolith biomechanics, encoded by heterogeneous afferent populations, integrated centrally, interpreted in relation to gravity and behavioral context, and modified by individual sensitivity and prior exposure.

Natural vestibular exposure is therefore not adequately described as motion present versus motion absent, nor by a label such as boating, rocking, or swinging. It is a multidimensional time-varying exposure whose biological relevance depends more directly on the motion received at the head than on the trajectory of the external platform alone. The reviewed literature also establishes that frequency, amplitude, temporal structure, cross-axis relationships, head orientation, behavioral origin, exposure history, and tolerability can alter vestibular representation or response.

These findings do not identify a SeaKing Solace therapeutic waveform. They explain why selecting one in advance would be scientifically premature.

### 21.1 The boat is a discovery environment

Within the SeaKing Solace framework, the vessel should initially be understood as a natural motion-generating environment. Its value is that it produces continuously varying combinations of translation and rotation over extended periods, allowing environmental motion, participant head motion, physiology, behavior, and tolerability to be measured together without specifying in advance which waveform deserves testing.

This is fundamentally different from asserting that the boat itself is therapeutic. If the motion-centered hypothesis is correct, the relevant stimulus should ultimately be separable from the environment in which it was first observed.

### 21.2 Phase 1 is justified by what remains unknown

Existing vestibular science identifies many variables that could matter, but it does not determine which natural motion features, if any, covary with the physiological response of interest; whether those relationships reproduce within or across individuals; whether they can be reconstructed on a controlled platform; whether the stimulus can be simplified; or whether any physiological modulation ultimately produces clinical benefit.

Those are empirical questions. Phase 1 is justified precisely because guessing the waveform would skip them.

### 21.3 Preservation before reduction

The central methodological principle of this review is preservation before reduction: retain enough of the original stimulus, participant-level response, repeated-session structure, and tolerability information to discover what matters before deciding what can be discarded.

This principle does not argue for permanent complexity. The purpose of later controlled experiments is to remove complexity deliberately. Simplification should be an experimental result rather than an assumption made before the relevant variables are known.

### 21.4 From natural observation to controlled causality

The scientific progression supported by this review is:

*natural externally applied motion → measured environmental and head-centered exposure → candidate physiological association → controlled reproduction → causal manipulation and reduction → clinical testing, if justified → adaptive control, if justified*

At each transition, the claim becomes stronger only if the preceding evidence survives. A controlled platform should therefore be defined by the biological relationships that emerge from the data, not by visual or mechanical fidelity to a boat.

Head-centric stimulus control and physiology-driven closed-loop control are separate stages. The first concerns whether the intended physical vestibular exposure is actually delivered. The second would adapt that exposure in response to measured physiology and should be considered only after stable input-output relationships have been demonstrated.

### **21.5 The hypothesis is falsifiable**

The SeaKing Solace motion hypothesis can fail. Motion may not predict the physiological response; candidate relationships may fail to reproduce; environmental or behavioral factors may explain the observations better; controlled reconstruction may fail; the required stimulus may be poorly tolerated; or physiological modulation may fail to translate into clinical benefit.

Such findings would constrain or reject parts of the hypothesis. That possibility is essential to the program's scientific character.

### **21.6 Evidentiary boundary**

This review establishes that the vestibular system provides a defined pathway through which externally applied motion is sensed; that natural vestibular input is multidimensional and temporally structured; that canal and otolith signals interact centrally; that central processing distinguishes expected self-generated motion from externally imposed motion; that received head motion can differ from platform motion; and that individual variability, exposure history, and tolerability can materially affect response.

It does not establish therapeutic efficacy, clinical benefit in autism, POTS, or any other condition, an optimal waveform or duration, superiority of natural over artificial motion, superiority of multi-axis over single-axis stimulation, a specific vestibular-autonomic mechanism, or a validated closed-loop control strategy.

### **21.7 Final synthesis**

The most defensible conclusion is not that the SeaKing Solace hypothesis has been proven. It is that the hypothesis can now be expressed as a rigorous and falsifiable experimental program.

The existing vestibular literature supports the early links in the proposed causal chain strongly enough to justify testing the later ones, while also explaining why the investigation should begin with measurement rather than prescription.

The literature does not tell SeaKing Solace what motion should become the intervention. It tells us why motion must first be measured well enough to determine whether a reproducible, controllable intervention exists within it.

## 22. References

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