Sensory-motor transformations in vestibular processing

Linear Systems

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The Vestibular System

The vestibular system is phylogenetically the oldest part of the inner ear:

It is situated in the petrous part of the temporal bone, and is not only in close proximity to the cochlea but is continuous with the scala media.
Function of the Vestibular System

Provide information about head motion relative to space and gravity to:

1) Stabilize the visual axis (VOR)
2) Maintain head and body posture (VCR and vestibulospinal reflexes)
3) Compute spatial orientation or ‘sense of balance’
4) Navigation

Semicircular canals - sense angular rotation
Otoliths - sense linear acceleration
Function of the Vestibular System

i. The VOR,
ii. Posture and balance, and
iii. Higher order vestibular processing
What would the world look like if you had to walk home without a vestibular system?
The Vestibulo-Ocular Reflex (video)

Central Vestibular Processing for the VOR
Central Pathways: Vestibular Nuclei

Slow phase direction = left
Quick phase direction = right
So, head velocity direction = right
Sensorimotor transformations: VOR

1. Overview of Eye Movements - VOR
2. Motor Control of Eye Movements: Mechanical Constraints
3. The Vestibular System
   3.1) Signal Processing by Vestibular Sensors
       i. Mechanical Analysis of the Semicircular Canals
       ii. Hair Cells and Afferent responses
   3.2) Central Vestibular Processing for the VOR
       i. Central Pathways (Vestibular Nuclei)
       ii. Neuronal Pathway: Model of the VOR
How does the brain generate appropriate motor commands to move the eyes to stabilize the axis of gaze during head motion?
How does the brain generate appropriate motor commands to move the eyes to stabilize the axis of gaze during head motion?

What are mechanical properties of the eye and surrounding tissues?

Why Study Eye Movements?
- No joints in system
- Constant inertia (negligible)
Mechanics of Eye Movements

What are the mechanics of the Oculomotor Plant? 
*Plant*: devise which produces the final output
For eye movements = 1) eye muscles, 2) orbital tissues, 3) globe

What is the output? Eye Movement
What is the input? Muscle tension
Control System Analysis

A system is represented as:

Where $x(t)$ is the input, and $y(t)$ is the output. These are signals that vary as a function of time.

1) The goal of an engineer is to design $S$, so that $x$ results in $y$.
2) The Neurobiologist already has $S$, and controls $x$, observes $y$.
   Then tries to guess what $S$ is.
The VOR as an Example System

What is the output? Eye Velocity
What is the input? Head Velocity

And the problem, is to find the system (S), for the VOR
The VOR as an Example System

Note:

\( \dot{H}(t) \) is head velocity: here a step of velocity and \( \dot{E}(t) \) is slow-phase eye velocity

(note \( \dot{H}(t) \) and \( \dot{E}(t) \) are short hand for \( dH/dt \), \( dE/dt \))
Mechanical System Analysis

For example, to understand how you move your eye,

First, consider some examples of mechanics to relate force to eye movement:

1) Apply a force $F$ to a spring of stiffness $K$, stretch it to length $L$.

![Diagram of a spring with force $F$, stiffness $k$, and length $L$.]

Hooks Law says: $F = kL$
Mechanical System Analysis

2) Apply a force \( (F) \) to a system characterized by a pure viscosity (of coefficient \( r \)). A good example is a hypodermic syringe.

If you push at a constant force, the plunger moves at a constant velocity \( \frac{dL}{dt} \), such that:

\[
F = r \frac{dL}{dt}
\]
3) Put these 2 elements in series (this is a simplified muscle model):

This is called a visco-elasticity. The force is shared by the elasticity ($kL$) and the viscosity ($r \frac{dL}{dt}$) so:

$$F = kL + r \frac{dL}{dt}$$

This is a first order differential equation and if our “system” was a visco-elasticity, solving this equation for a given input should produce the observed output.
Mechanical System Analysis:

4) Now add a mass to the system:

From Newton’s second law of motion
\[ F = m \frac{d^2L}{dt^2}, \text{ where } \frac{d^2L}{dt^2} \text{ is acceleration} \]

The system is now described by:

\[ F = kL + r \frac{dL}{dt} + m \frac{d^2L}{dt^2} \]

(i.e. a second order differential equation)
Mechanics of Eye Movements

How does mechanical analysis in the previous slides relate to the Oculomotor Plant?

*Plant*: devise which produces the final output
For eye movements = 1) eye muscles, 2) orbital tissues, 3) globe

What is the output?  Eye Movement
What is the input?  Muscle tension, but hard to measure.
We can measure motoneuron drive to muscles
How does the brain generate appropriate motor commands to move the eyes to stabilize the axis of gaze during head motion?

Approach 1: Record Eye movements

Suction contact lens used to apply forces and loads to the eye to understand the Mechanical properties of the eye and surrounding tissue.

\[
FR(t) = b + kE(t - t_d) + rE'(t - t_d) + u\ddot{E}(t - t_d) - cFR'
\]
Summary of mechanical analysis:

**Experimental Results**

\[ F = a + bE + c\dot{E} \quad \text{(eq mech)} \]

\[ c/b = \sim 200 \text{ ms} \]

**Mechanical System Analysis**

The eye plant is viscous-elastic - force is shared by the elasticity (\(kL\)) and the viscosity (\(r \frac{dL}{dt}\)) as a result:

\[ F = kL + r \frac{dL}{dt} \]

Again, the combination of these 2 elements in parallel (visco-elasticity) is often used as a simplified muscle model.

**Important:** If \( MN \text{ fr} = \) proportional force then the ‘eq mech’ will also describe MNs.
How does the brain generate appropriate motor commands to move the eyes to stabilize the axis of gaze during head motion?

Approach 2: Record Motoneurons
Summary of all analyses:

**Experimental Results**

F = a + bE + cĖ

**Mechanical System Analysis**

Eye plant is viscous-elastic
force is shared by
the elasticity (kL) and the viscosity (r dL/dt)

F = kL + r dL/dt

**Description of MN**

Fr = Ro + KE + rĖ

Good news: The motoneuron equation that we described:
Fr = Ro + KE + rĖ also has the same form as our muscle-force/eye movement model (“eq mech”).

Note that: This implies that the relationship between muscle force and Fr is indeed ~ linear
### Standard Classification of 5 Types of Eye Movements

<table>
<thead>
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Classically eye movements grouped into 5 types

Extraocular motoneurons participate in all types of eye movements including the VOR, and their response dynamics can (largely) be predicted by the mechanics of the eye.
A given extraocular motoneuron participates in all classes of eye movements.
The Vestibulo-ocular reflex

A given extraocular motoneuron participates in all classes of eye movements.
Description of MN discharge rate

Recall:

1) \( Fr = Ro + KE + r\dot{E} \)

\[ \downarrow \]

In the Laplace domain:

\[
\text{Derivative: } \mathcal{L}\left[ \frac{df}{dt} \right] = sF(s) - f(0^+) \]

\[ \downarrow \]

2) \( Fr(s) = KE(s) + r\cdot s\cdot E(s) \)

\[
H(s) = E(s)/Fr(s) = (1/K)/ [(r/K)s + 1] \]

The time constant: \( \tau_e = \frac{r}{k} \)
Description of MN discharge rate

3) \( \text{Fr} - \text{Ro} = KE + r\dot{E} \) if \( \tau_e = \frac{r}{k} \)

\[
E(t) = R \left(1 - e^{-t/\tau_e}\right)
\]

\[
E(t) = R \left(1 - e^{-1}\right) \text{ if } t = \tau_e
\]

\[
= R \left(1 - \frac{1}{e}\right)
\]

\[
= R \left(1 - \frac{1}{2.7}\right)
\]

\[
= R \times 0.63
\]

If \( r = 1, K = 5 \), then \( \tau_e = 250 \text{ ms} \).

Consider, eye dynamics if muscles received a step command of \( \text{FR} \) – they would be too slow. Saccades can be on target in less than 100ms.
Analysis of Motoneuron Signals

**Pulse**
Need an extra “burst” (pulse) in MN command signal in order to complete saccade in a shorter time (i.e. overcome viscous drag).

**Step**
Also need tonic activity after saccade (step) in order hold eye at new position (i.e. overcome elastic restoring forces).

*Note, The pulse resembles velocity + The step resembles position*
Neural Circuit: A simple form of memory
Tonic activity after saccade (step) generated by the oculomotor neural integrator

Similar integration is also performed in the VOR pathway, but the mechanism is somewhat different
Neural Circuit: Controlling Saccades
Tonic activity after saccade (step) generated by the oculomotor neural integrator

Current model of the neural integrator based on experimental findings in Species ranging from monkeys to Zebrafish.

Miri et al,
Nature NS., 2011
For example, the MN equation added the results from 3 experiments, together. **Assumption:** The system is linear. If we put in 2 signals, the output is the same as the sum of the response of each alone.
The most direct VOR is a 3 neuron pathway – Example System

The problem is to now find $S$ for the VOR

[Diagram of a 3 neuron pathway]
A given extraocular motoneuron participates in all classes of eye movements.
Sensorimotor transformations: VOR

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Organization of the Vestibular System

Anatomy: there are 2 types of sensors on each side of the head.

1) Otoliths (linear acceleration)
   → saccule
   → utricle

2) Semicircular canals (angular acceleration)
   → horizontal
   → superior
   → posterior

Note: Entire system is continuous with scala media of the cochlea via the ductus reuniens.
Function of the Vestibular System

i. The VOR,
ii. Posture and balance, and
iii. Higher order vestibular processing
Function of the VOR

Gaze Stabilization via the Vestibulo-ocular Reflex

More effective than vision since response latency is very short!

Huterer and Cullen, 
*J. Neurophys.*, 2002
Function of the VOR

Gaze Stabilization via the Vestibulo-ocular Reflex

Accordingly, VOR is more effective than visually driven OKN at higher frequencies.
Vestibulo-ocular reflex (VOR) Dynamics:
The VOR is compensatory over a wide frequency range.

A.

B. Green line = expected increased phase lag given fixed pathway delays.
The Vestibulo-Ocular Reflex
(video)

Mechanical Analysis of the Semicircular Canals

- The 3 canals are ~ at right angles to each other.
- Each of the 3 planes lie approximately in the pulling direction of one of the pairs of extraocular muscles

Horizontal → horizontal for normal resting posture.
Superior → subtend 45° relative to the sagittal and frontal plane.
Posterior

Each canal consists of
1) A circular fluid path
2) Ampulla → crista – hair cells
   → cupula – elastic membrane (water tight)
Receptor Cells
All hair cells are oriented in the same direction for each canal.

Mechanism: Head rotates
   → fluid is left behind
   → ampulla pushes against it
   → bends cilia.
The cupula is deflected by the movement of the endolymph, which occurs during head motion. The following sequence of events occurs:

1) the head turns
2) the endolymph tends to remain stationary due to inertial forces
3) therefore the endolymph moves relative to the canal (in the opposite direction of head motion).
Mechanical Analysis of the Semicircular Canals

Stimulus = Angular acceleration

But Over the frequency range of normal head movements (i.e. > .01Hz).

The very small diameter (0.3mm) →↑viscous properties of the fluid

This is mathematically equivalent to \( \int \) (integration)

Thus, the system functions as an angular speedometer (hair cell output → rotational speed)

CNS → 3 canals = speed of head in 3D
Hydrodynamic analysis of the canals predicted that the relationship between the angular displacement of the endolymph \( \varepsilon(t) \) and the head’s angular acceleration \( \alpha(t) \) is:

\[
\theta \frac{d \varepsilon^2}{dt^2} + \Pi \frac{d \varepsilon(t)}{dt} + \Delta \varepsilon(t) = \theta \alpha(t)
\]

Where: \( \theta \) is the effective moment of inertia of the endolymph.

\( \Pi \) is a damping constant that reflects the viscous drag exerted by the canal wall as the endolymph flows past it, and

\( \Delta \) is an elastic restoring factor related

The dynamics of this equation are governed by two time constants,

1) a long one \( (\tau_1 = \frac{\Pi}{\Delta} = 5s) \) and
2) a short one \( (\tau_2 = \frac{\theta}{\Pi} = .004s) \).
Hydrodynamic analysis of the canals predicted that the relationship between the angular displacement of the endolymph ($\varepsilon(t)$) and the head’s angular acceleration ($\alpha(t)$) is:

$$\theta \frac{d^2 \varepsilon}{dt^2} + \Pi \frac{d \varepsilon}{dt} + \Delta \varepsilon(t) = \theta \alpha(t)$$

In the Laplace domain:

**Derivative:** $\ell \left[ \frac{df}{dt} \right] = sF(s) - f(0^+)$

$$\ell \left[ \frac{d^2 f}{dt^2} \right] = s^2 F(s) - s \cdot f'(0^+) - f(0^+)$$

Where: $\theta$ is the effective moment of inertia of the endolymph.

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The dynamics of this equation are governed by two time constants,

1) a long one ($\tau_1 = \frac{\Pi}{\Delta} = 5s$) and
2) a short one ($\tau_2 = \frac{\theta}{\Pi} = .004s$).
This equation says that the movement of the endolymph in the canals is opposed by two frictional forces

1) one which arises from the viscosity of the endolymph and 
2) a second which is due to the elasticity of the cupula.

These opposing forces cause the movement of the endolymph (relative to the cupula) to lag head acceleration (as would be the case if the only the inertia of the endolymph were significant).

Thus the receptor cells which deflect the movement of the cupula are primarily sensitive to head velocity (rather than acceleration) during most natural head movements (i.e. frequency = 0.05-20Hz).

• This is shown in the next slide………..
Mechanical Analysis of the Semicircular Canals

Frequency Response

System is characterized in terms of gain and phase (Bode Plots).

Note, in this graph a phase of 0 deg is in phase with head velocity, and -90 and +90 deg are in phase with head acceleration and position.
Sensorimotor transformations: VOR

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Hair Cells and Afferent Responses

Two types of Hair cells

Type I Hair Cells
Characterized by calyx like endings of the sensory fibers.

Type II Hair Cells
Characterized by more conventional (bulbous) cell fiber synapses.
Hair Cells and Afferent Responses

Exhibit a constant resting discharge when not stimulated

1) **Bending cilia towards** kinocilia
   
   excites hair cell:  \( \uparrow \) action potential, VIII nerve.

2) **Bending cilia away from** kinocilia
   
   inhibits hair cell:  \( \downarrow \) action potential, VIII nerve.

Thus, the resting discharge (spontaneous discharge) allows the CNS to sense stimulation in 2 directions (opposite via the change in activity).
Mechanism of Mechano-Neural Transduction: similar to auditory system Role of Efferent system: not yet understood
Hair Cells and Afferent Responses

Regular Versus Irregular Afferents

Afferent innervation patterns
- type II haircells - regular afferents
- type I haircells - irregular afferents

Regulars:
- More regular action potentials spacing
- Lower Afferent gain and phase
- Lower Efferent response magnitude
- Lower Galvanic sensitivity
Vestibular afferent Dynamics:
Afferents show a response gain increase with frequency

Sadeghi, Minor, and Cullen; J Neurophys, 2007
Vestibular afferent Dynamics:
Afferents (particularly irregular afferents) also show a response phase increase with frequency

Sadeghi, Minor, and Cullen; J Neurophys, 2007
Vestibular-Nerve Afferents: Response to Sinusoidal Rotation

Vestibular-Nerve Afferents: Response to Sinusoidal Rotation

Vestibular-Nerve Afferents: Response to broadband stimulus

\[ G(f) = \left| \frac{P_{rs}(f)}{P_{ss}(f)} \right| \]

Massot, Schneider, Chacron, Cullen, *Plos Biology*, 2012
Vestibular-Nerve Afferents: Response to broadband stimulus

\[ G(f) = \left| \frac{P_{rs}(f)}{P_{ss}(f)} \right| \]

Mutual Information: reduction in uncertainty about one random variable given knowledge of another

\[ MI = -\log_2(1 - C(f)) \]
\[ C(f) = \frac{|P_{rs}(f)|^2}{[P_{ss}(f)P_{rr}(f)]} \]

Massot, Schneider, Chacron, Cullen, *Plos Biology*, 2012
Prediction:
What should the VOR response to a step input look like?
Vestibular afferents response to “velocity trapezoid” inputs as predicted by the torsion-pendulum model

\[ \theta \ddot{\varepsilon} + \Pi \dot{\varepsilon}(t) + \Delta \varepsilon(t) = \theta \alpha(t) \]

Dominant time constant is 5 sec

In contrast, the VOR has a time constant of ~20 s.
Sensorimotor transformations: VOR

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Central Vestibular Processing for the VOR

Central Pathways: Vestibular Nuclei

4 subdivisions:

Superior/Medial predominantly canal

Lateral canal and otolith

Descending predominantly otolith
For the Horizontal rotational VOR:
Afferents project to neurons in the vestibular nuclei which in turn project to the
1) Abducens and
2) Medial Rectus subdivision of the oculomotor nucleus
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Central Vestibular Processing for the VOR
Central Pathways: Vestibular Nuclei

For the Horizontal rotational VOR:
Afferents project to neurons in the vestibular nuclei which in turn project to the
1) Abducens and
2) Medial Rectus subdivision of the oculomotor nucleus
Central Vestibular Processing for the VOR
Central Pathways: Vestibular Nuclei

Time constant is ~20 sec rather than 5 sec as for The Vestibular Afferents.
The slow time constant of the canals (5s) is represented in the discharges of vestibular afferents.

But for rotation in the dark at a constant velocity – slow phase eye velocity is initially compensatory, but then goes to zero with a time constant of 21 sec not 5 sec, as predicted by the dynamics of the afferents.

1) The central mechanism responsible for lengthening the afferent time course is referred to as "velocity storage".

2) Reciprocal projections between the cerebellum and vestibular nuclei mediate velocity storage. After lesions of the cerebellar uvula and nodulus the VOR decay time constant (as well as the response of central vestibular neurons) returns to 5 ms.
Central Vestibular Processing for the VOR

Central Pathways: Vestibular Nuclei and Velocity Storage

1 ms 1 ms 1 ms 4 ms

Head motion

vestibular

VN

ABD

Nodulus/uvula of the cerebellum
Central Vestibular Processing for the VOR
Central Pathways: Vestibular Nuclei and Velocity Storage

1 ms  1 ms  1 ms  4 ms  = 7 ms delay

1 ms  1 ms  1 ms  4 ms  = 7 ms delay

Head motion → vestibular nerve → VN → ABD → eye movement

Nodulus/uvula of the cerebellum

Time constant returns to ~5 s.
Central Vestibular Processing for the VOR
Neuronal Pathway: Model of the VOR

\[ Fr = Ro + kE + r\dot{E} \]
Sensorimotor transformations: VOR

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System Dynamics and Levels of Analysis
1) Behavior, 2) Neural Circuits, 3) Neurons.
Neuronal Processing for the VOR
Central Pathways: Intrinsic Cellular Properties

Considerations:
1) Neuronal dynamics and limits (cut-off and saturation)
2) Intrinsic Processing and Membrane Properties
3) Compensation for pathway delays
Cellular Properties shape the dynamics of the VOR
Central Pathways: Intrinsic Processing and Membrane Properties

\[ 1 \text{ ms} \quad 1 \text{ ms} \quad 1 \text{ ms} \quad 4 \text{ ms} \]
Neuronal Processing for the VOR
Central Pathways: Intrinsic Processing and Membrane Properties
Neuronal Processing for the VOR
Dynamics of Mechanical-Neural Transduction

Bode Plots reveal:

1) Gain tuning narrows at each stage

2) Increased phase lag $> 20$ Hz at each stage; spiking adds a large phase lead below 20 Hz
Central Vestibular Processing for the VOR
Central Pathways: Intrinsic Cellular Properties
Serafin et al. 1991a,b

Summarized properties of 170 MVN neurones

**Type A neurones**
- Wide action potential
- 32.3%
- Large single AHP
- Single range firing
- A-type rectification
- Small high threshold calcium (HT–Ca$^{2+}$) spikes

**Type B neurones**
- Thin action potential
- 47.1%
- Early fast and delayed slower AHP
- Secondary range in the first intervals
- Large HT–Ca$^{2+}$ spikes and Ca$^{2+}$ plateau potentials
- And – 55.0% Na$^+$ plateau potentials (Na(P))
- – 16.5% Low threshold Ca$^{2+}$ spikes (LTS)
- – 16.5% LTS and Na (P)
- – 12.0% Absence of LTS and Na (P)

**Type C neurones**
- 20.6%
Central Vestibular Processing for the VOR
Intrinsic Cellular Properties: Input-Output Analysis

Sinusoids

Trapezoids

Ris et al. 2001
Central Vestibular Processing for the VOR

Intrinsic Cellular Properties: Input-Output Analysis

Ris et al. 2001
Central Vestibular Processing for the VOR
Central Pathways: Intrinsic Cellular Properties

**Type A** Vestibular Nuclei Neurons are modulators
- More linear
- Less sensitive to current
- Less phase lead, regular
- follow up mode

**Type B** Vestibular Nuclei Neurons are detectors
- Non linear (more overshoot, FRA)
- Very sensitive to current,
- Phase Lead, Irregular
- trigger mode
Vestibular Nuclei Neuron Dynamics:
Afferents show a response gain increase with frequency

Type B
Type A
Central Vestibular Processing for the VOR

Central Pathways: Pathway Delays – Phase compensation

Considerations:
1) Neuronal limits (cut-off and saturation)
2) Intrinsic Processing and Membrane Properties
3) Compensation for pathway delays
Vestibulo-ocular reflex (VOR) Dynamics:
The VOR is compensatory over a wide frequency range

A.

B. Green line = expected increased phase lag given fixed pathway delays

Huterer and Cullen, JNP 2000
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Intrinsic membrane properties as well as inputs shape response dynamics
Central Vestibular Processing for the VOR
Neuronal Pathway: Model of the VOR

IV (plant transfer function)
$Fr = Ro + kE + r\dot{E}$