Sensory-motor transformations in vestibular processing

Linear Systems

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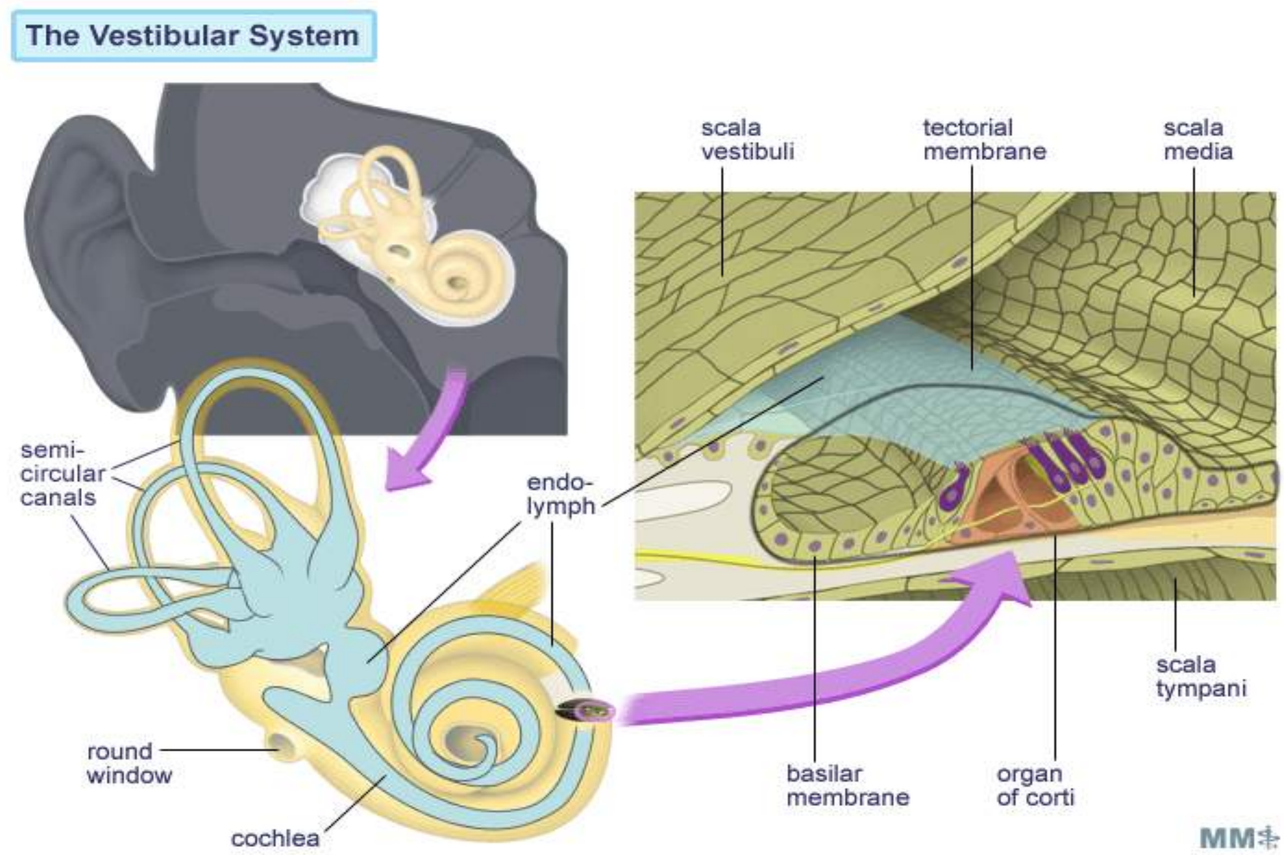
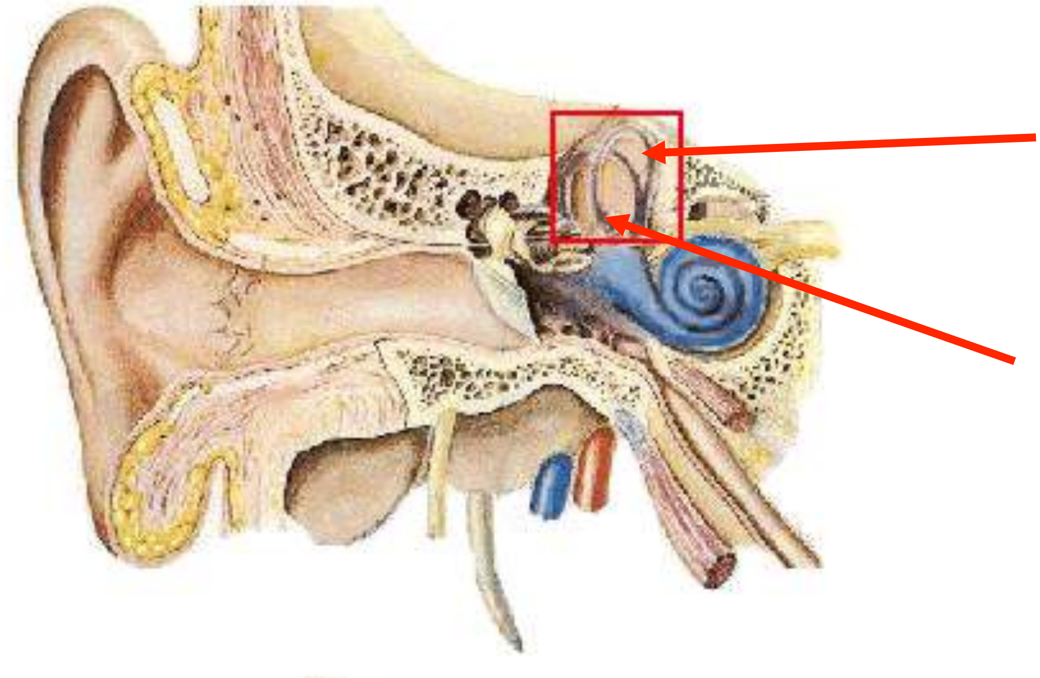
The Vestibular System

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

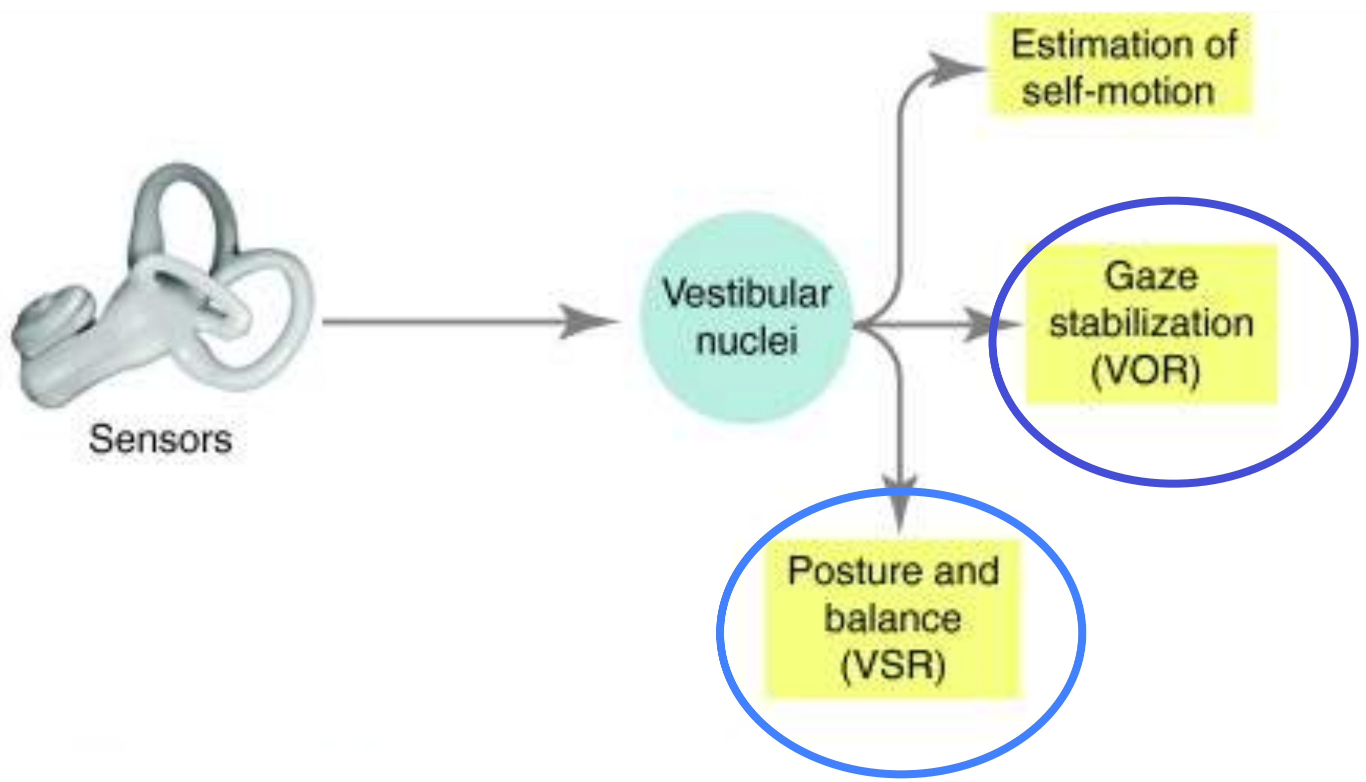


Provide information about head motion relative to space and gravity to:

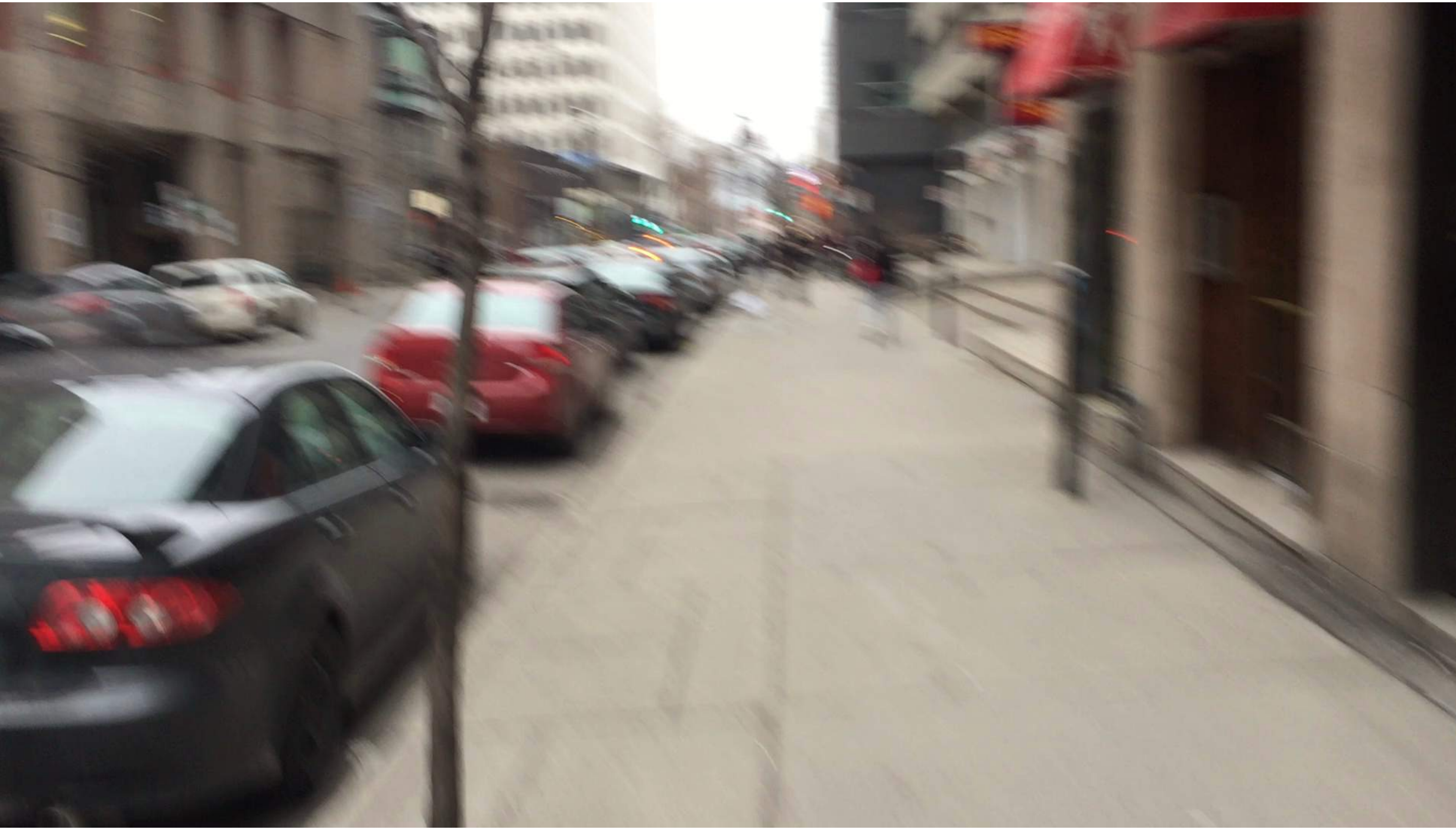
1) Stabilize the visual axis (VOR)
2) Maintain head and body posture (VCR and vestibulospinal reflexes)
3) Compute spatial orientation or 'sense of balance'
4) Navigation

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?



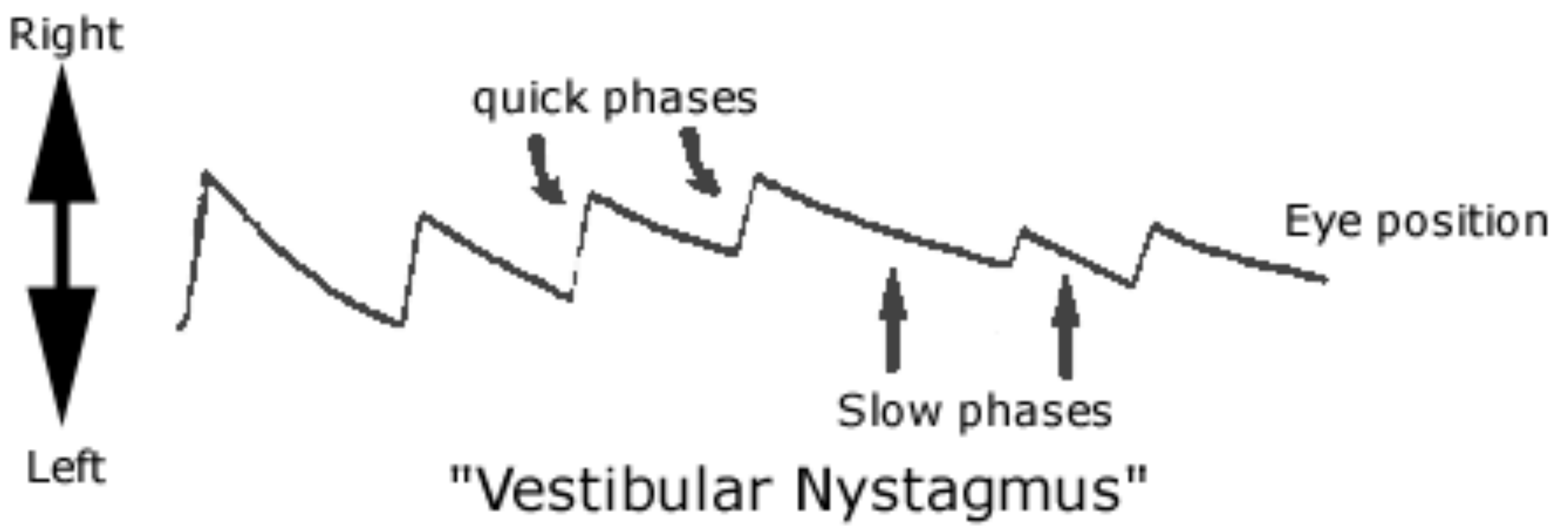
The Vestibulo-Ocular Reflex

(video)

http://www.nejm.org/doi/full/10.1056/NEJMicm031134

Central Vestibular Processing for the VOR

Central Pathways: Vestibular Nuclei



Slow phase direction = left

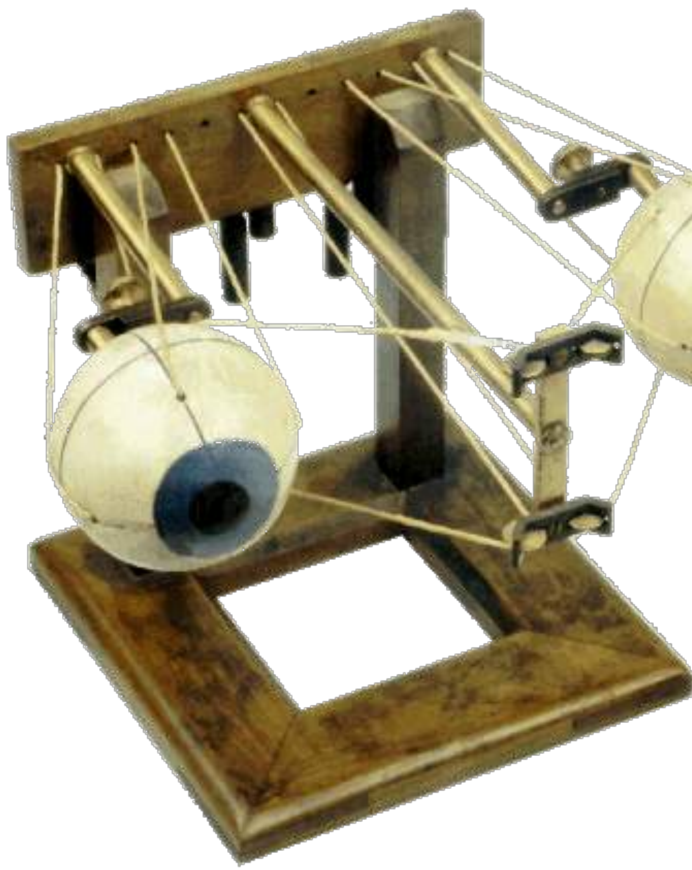
Quick phase direction = right

So, head velocity direction = right

Sensorimotor transformations: VOR

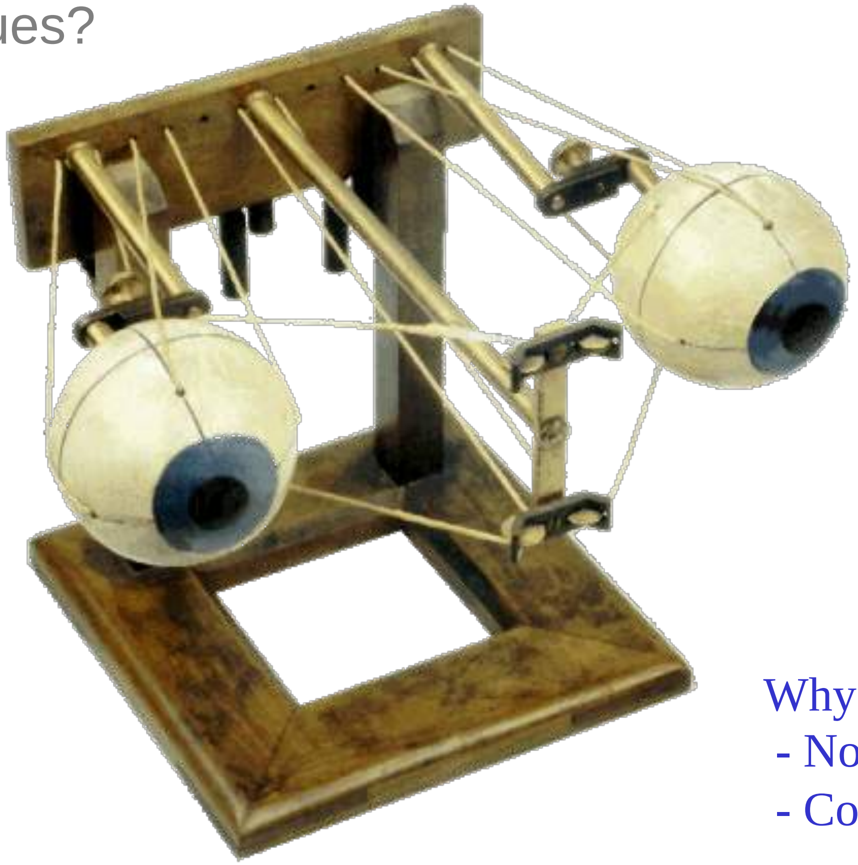
1. Overview of Eye Movements - VOR
2. Motor Control of Eye Movements : Mechanical Constraints
3. The Vestibular System
    - 3.1) Signal Processing by Vestibular Sensors
        - i. Mechanical Analysis of the Semicircular Canals
        - ii. Hair Cells and Afferent responses
    - 3.2) Central Vestibular 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 stabile the axis of gaze during head motion?



How does the brain generate appropriate motor commands to move the eyes to stabile the axis of gaze during head motion?

What are mechanical properties of the eye and surrounding tissues?



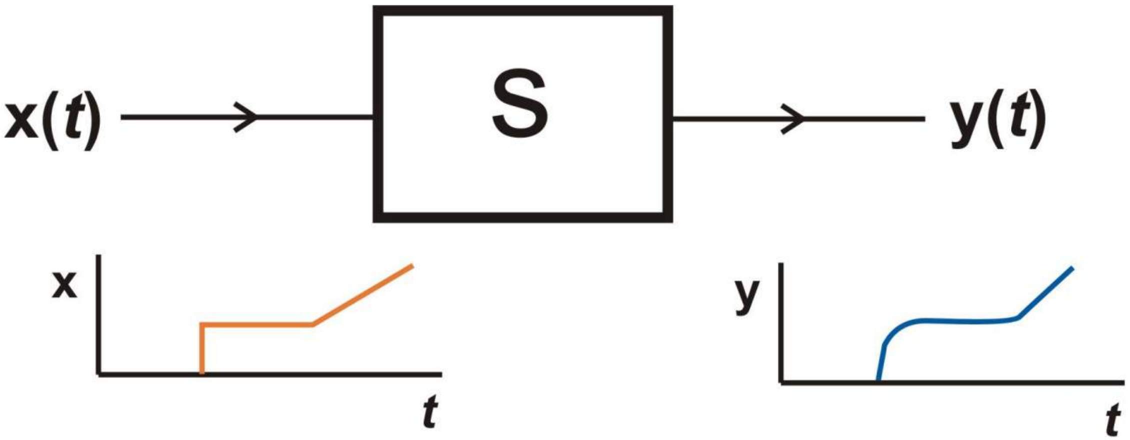
Why Study Eye Movements?
- No joints in system
- Constant inertia (negligible)

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

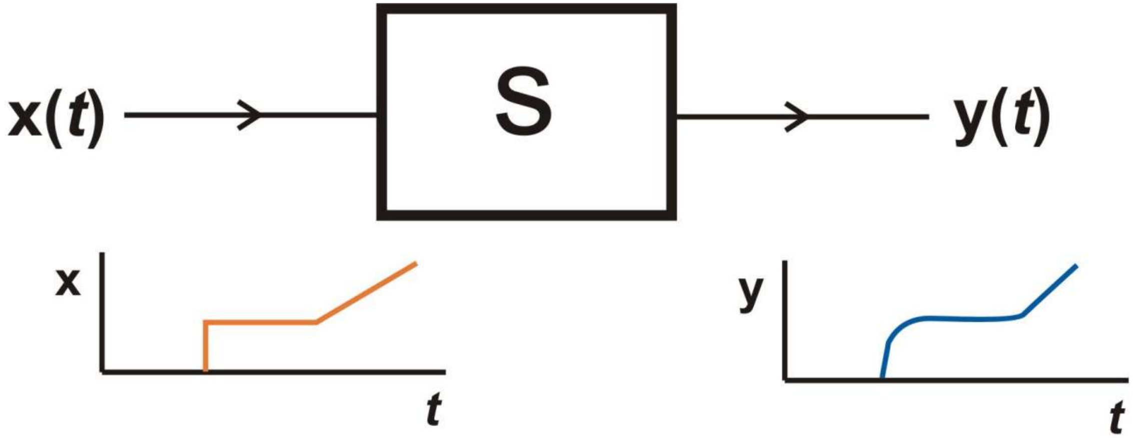


What is the output? Eye Movement

What is the input? Muscle tension

Control System Analysis

A system is represented as:

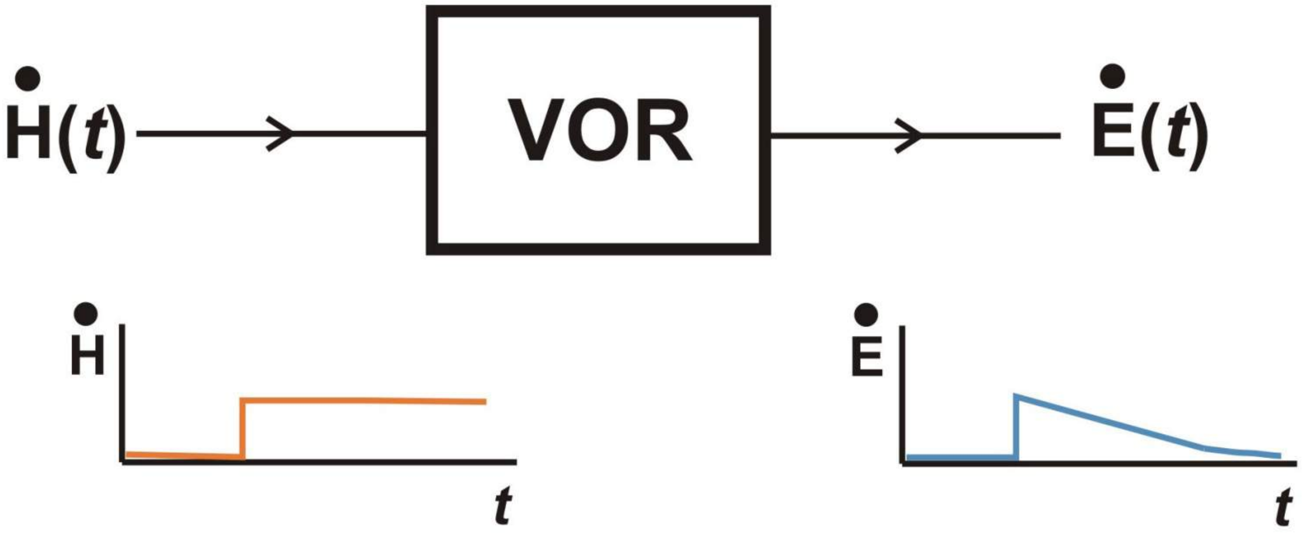


Where x(t) is the input, and y(t) is the output. These are signals that very as a function of time.

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.

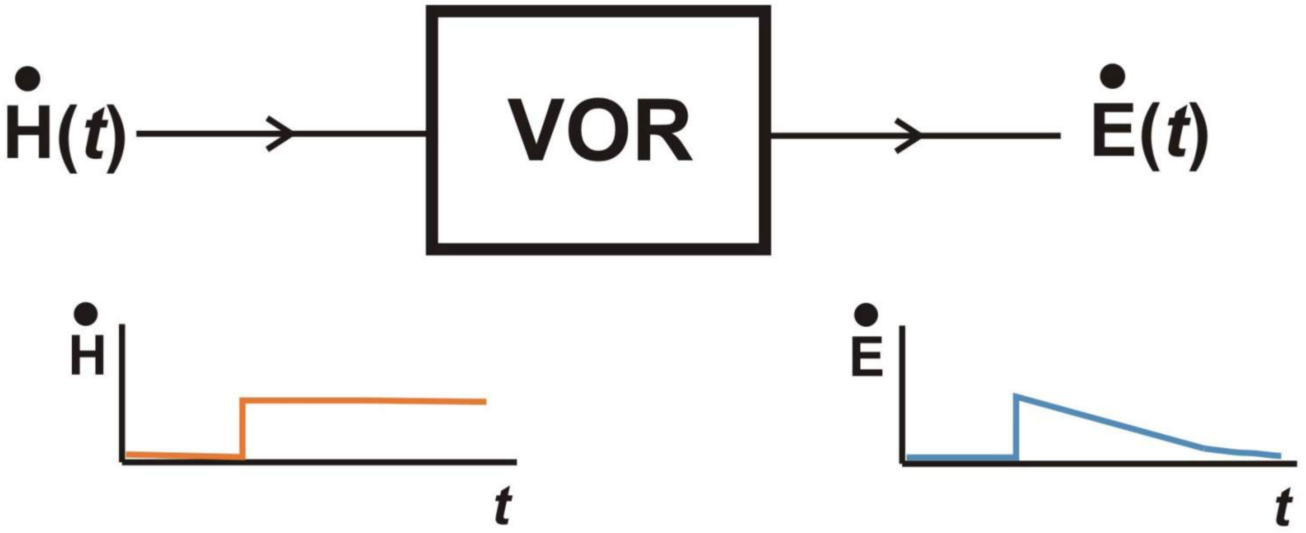
The VOR as an Example System



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

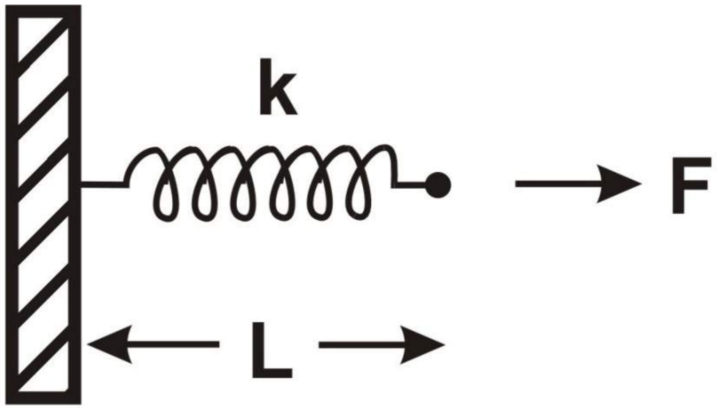
(note $\dot{H}(t)$ and $\dot{E}(t)$ are short hand for dH/dt, dE/dt)

Mechanical System Analysis

For example, to understand how you move your eye,

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

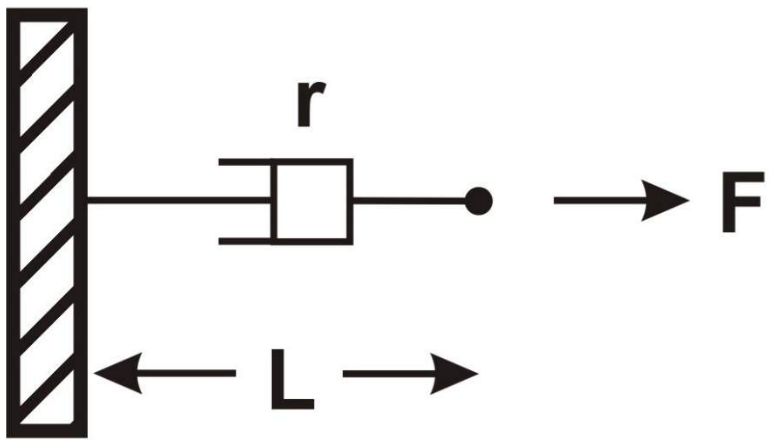
1) Apply a force F to a spring of stiffness K, stretch it to length L.



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.

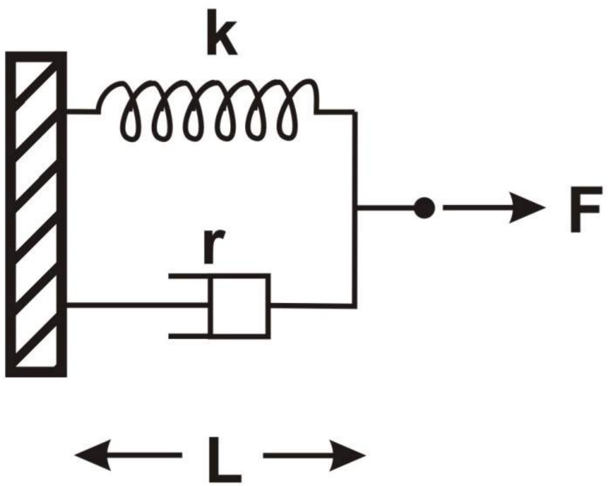


If you push at a constant force, the plunger moves at a constant velocity dL/dt, such that:

$$F = r \quad dL/dt$$

Mechanical System Analysis

3) Put these 2 elements in series (this is a simplified muscle model):

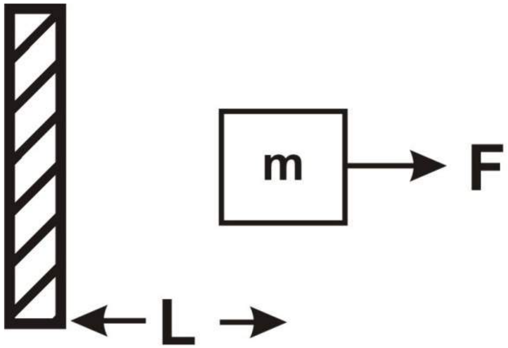


This is called a visco-elasticity. The force is shared by the elasticity (kL) and the viscosity ($r\ dL/dt$) so: $F = kL + r\ dL/dt$

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.

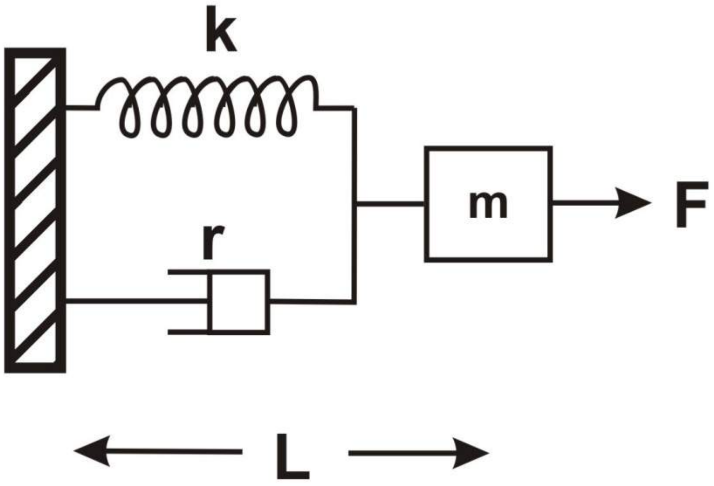
Mechanical System Analysis:

4) Now add a mass to the system:



From Newton's second law of motion

$F = m\, d^2L/dt^2$, where d^2L/dt^2 is acceleration



The system is now described by:

$$F = kL + r\ \ dL/dt + m\, d^2L/dt^2$$

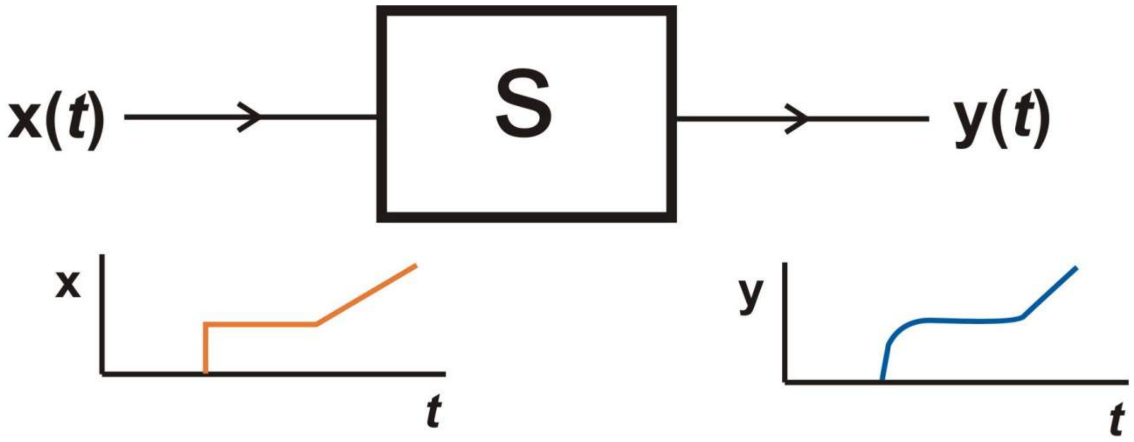
(i.e. a second order differential equation)

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

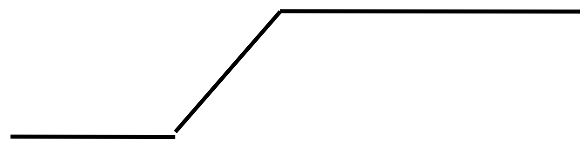


What is the output? Eye Movement

What is the input? Muscle tension, but hard to measure.

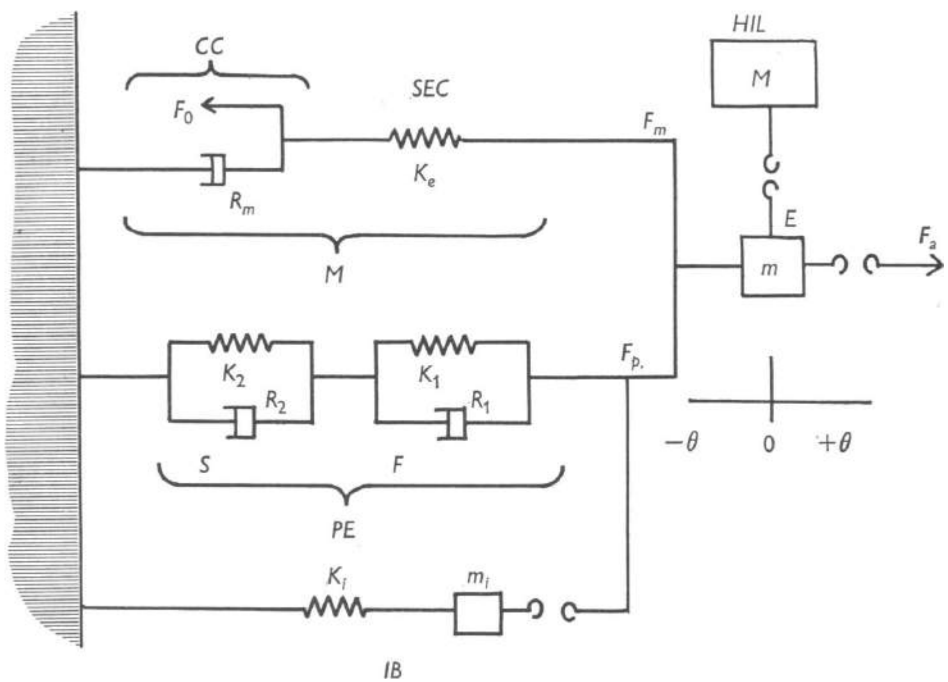
We can measure motoneuron drive to muscles

How does the brain generate appropriate motor commands to move the eyes to stabile 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.

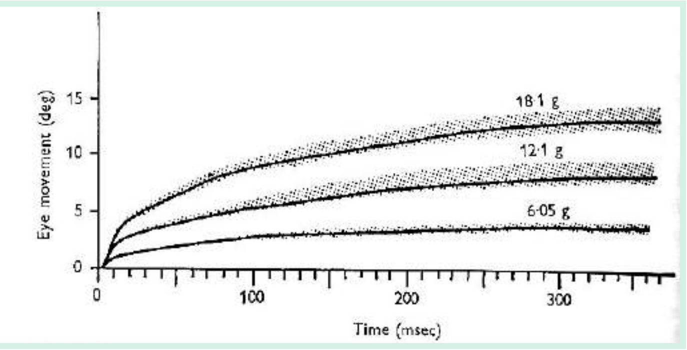


$$FR(t) = b + kE(t - t_d) + r\dot{E}(t - t_d) + u\ddot{E}(t - t_d) - cFR'$$

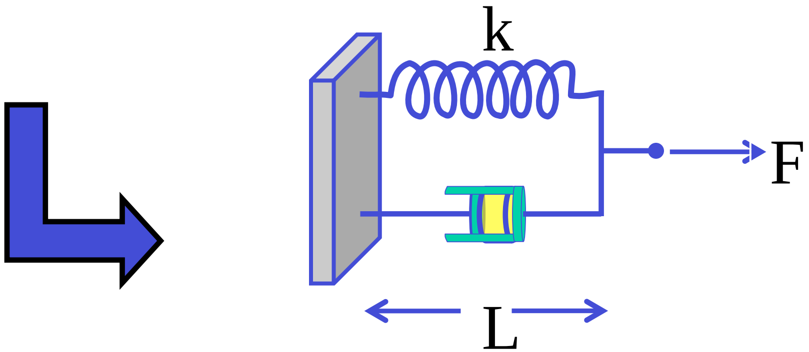
David Robinson 1964

Summary of mechanical analysis:

Experimental Results



Mechanical System Analysis



$F = a + bE + c\dot{E}$ (eq mech)

$c/b = \sim 200$ ms

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

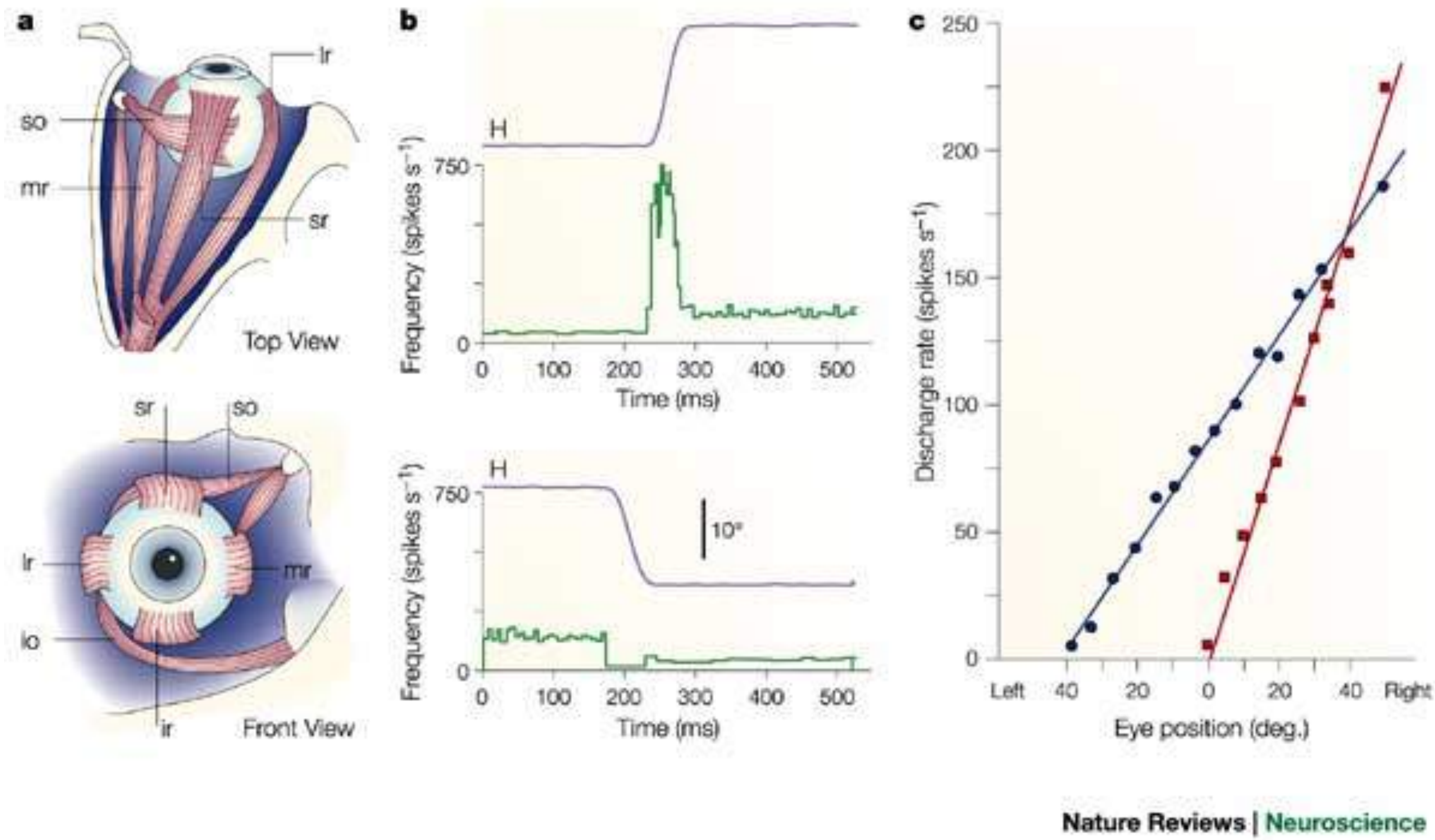
as a result: $F = kL + r\ dL/dt$

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

Important: If MN fr = proportional force then the 'eq mech' will also describe MNs.

How does the brain generate appropriate motor commands to move the eyes to stabile the axis of gaze during head motion?

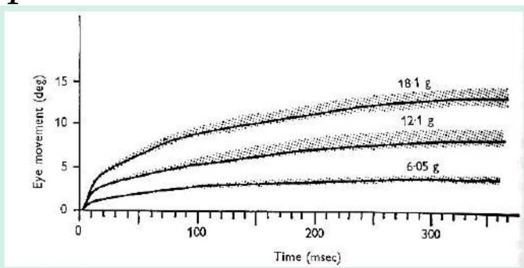
Approach 2:
Record Motoneurons



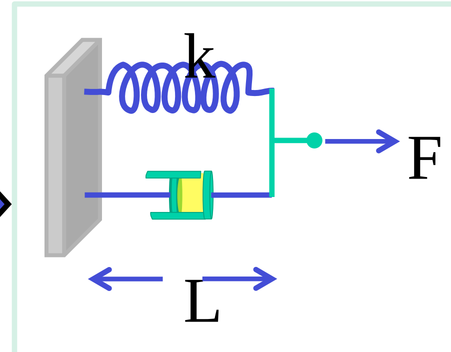
Dave Sparks 2002

Summary of all analyses:

Experimental Results



Mechanical System Analysis



Description of MN

$Fr = Ro + KE + r\dot{E}$

$F = a + bE + c\dot{E}$

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

Good news: The motoneuron equation that we described:
$Fr = Ro + KE + r\dot{E}$ 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

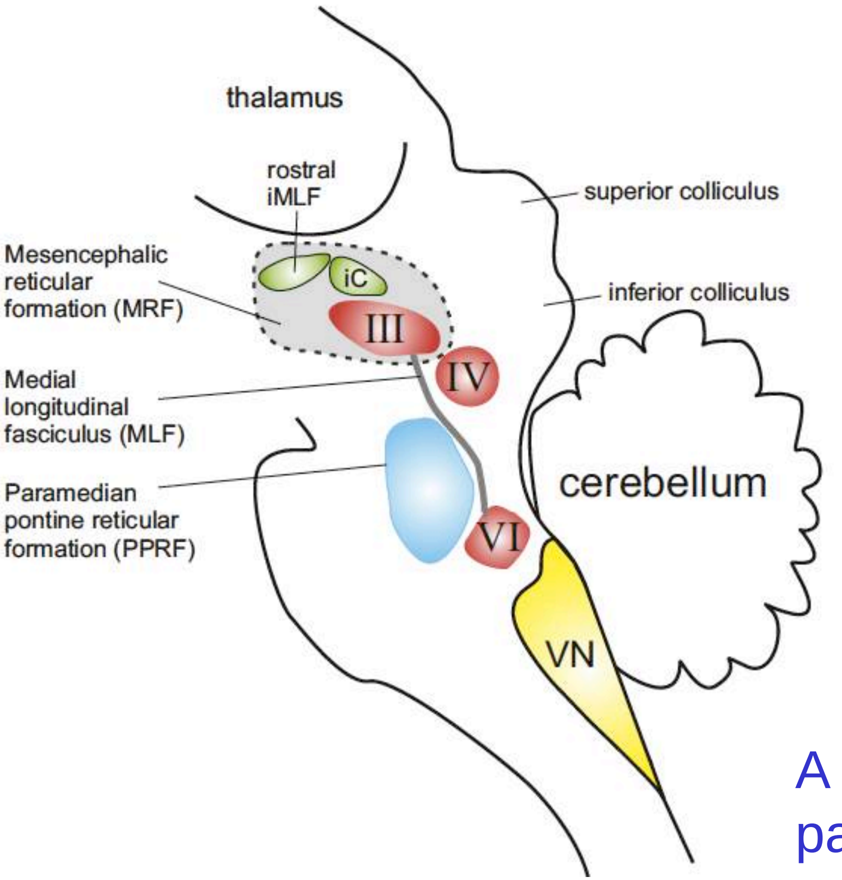
Eye movement classification		Function
Voluntary	Saccade	Fast redirection of gaze between stationary targets
	Pursuit	Slow eye movements used to track moving targets
	Vergence	Rotation of the eyes in opposite directions to fixation targets at different depths
Involuntary	Vestibulo-ocular	Uses vestibular inputs to hold images stationary on the retina as the head moves
	Optokinetic	Uses visual inputs to stabilize gaze in response to low frequency head movements

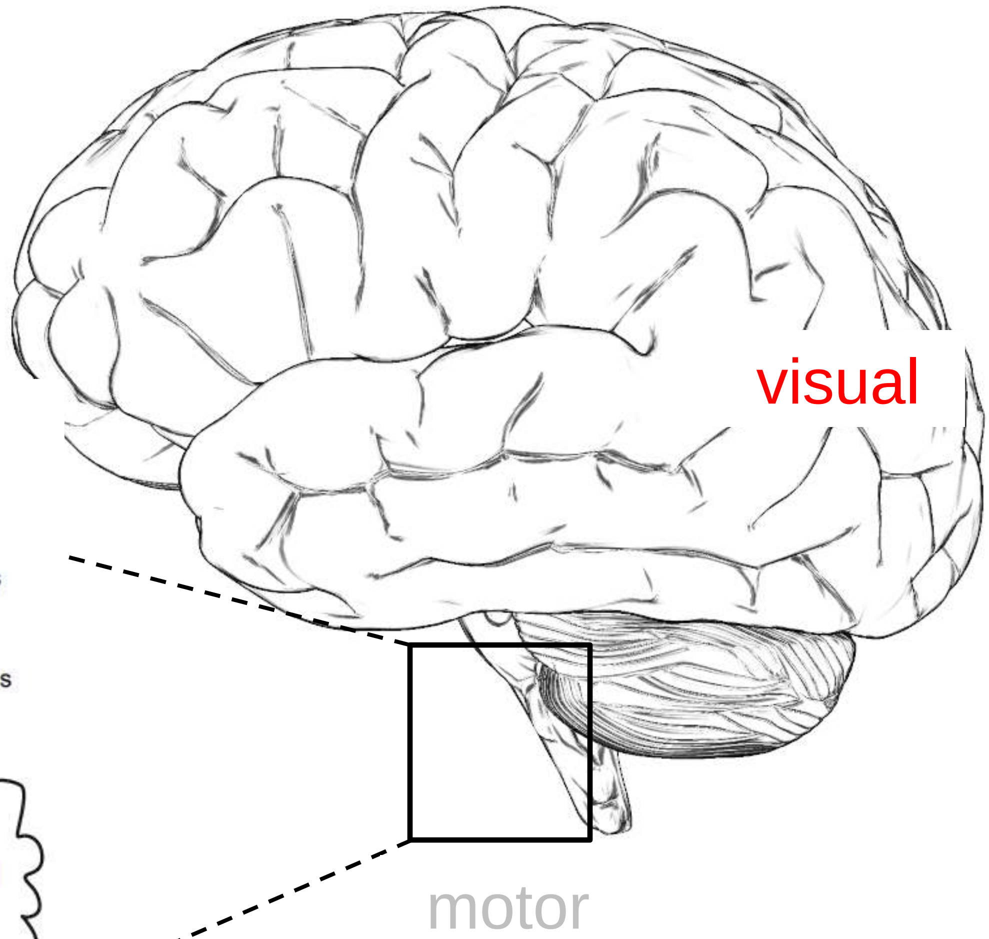
Classically eye movements grouped into 5 types

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.

The Brainstem

motor

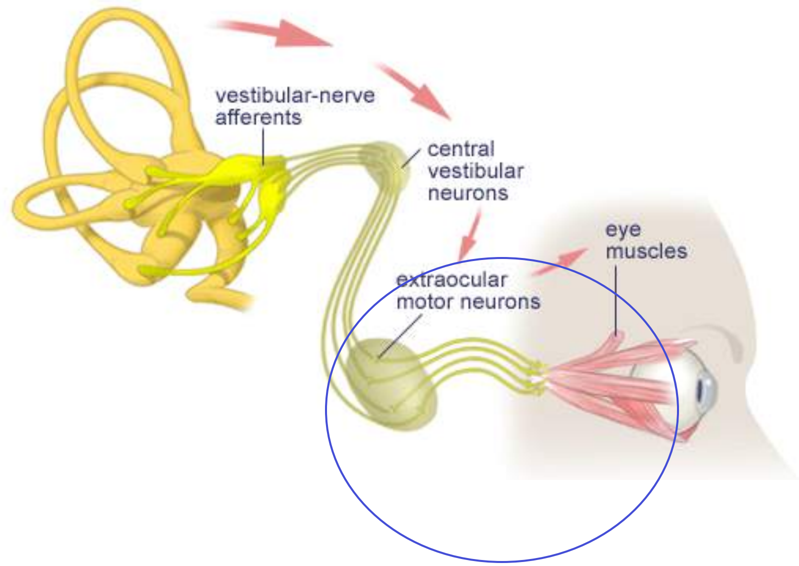


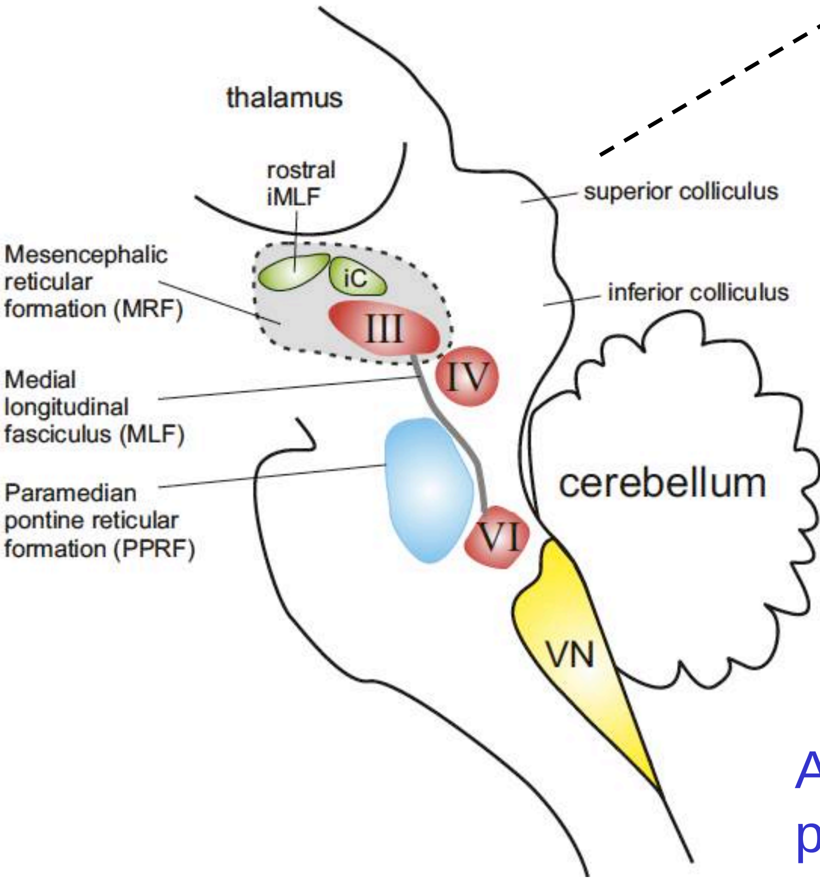


A given extraocular motoneuron participates in all classes of eye movements
.

The Vestibulo-ocular reflex

motor





motor

A given extraocular motoneuron participates in all classes of eye movements .

Description of MN discharge rate

Recall:

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

↓

In the Laplace domain:

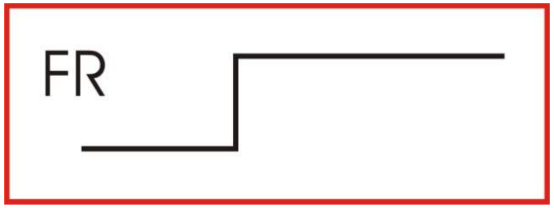
Derivative: $\ell[\frac{df}{dt}] = sF(s) - f(0^+)$

↓

2) $Fr(s) = KE(s) + r\,s\,E(s)$

$H(s) = E(s)/Fr(s) = (1/K)/\,[(\mathbf{r/K})s + 1]$

The time constant: $\boldsymbol{\tau_e = {}^{r}/_{k}}$



Description of MN discharge rate

3) $Fr - Ro = KE + r\dot{E}$ if $\tau_e = {}^{r}/_{k}$

$E(t) = R(1- e^{-t/\tau e})$

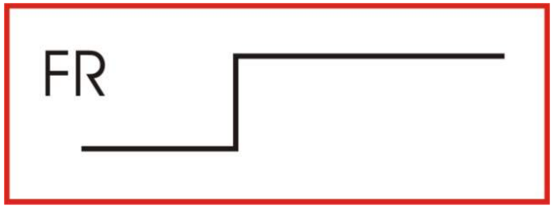
$E(t) = R(1- e^{-1})$ if $t = \tau_e$

$= R(1 - {}^{1}/_{e})$

$= R(1 - {}^{1}/2.7)$

$= R \times .63$

If : r =1, K =5, then $\tau_e = 250$ ms



Consider, eye dynamics if muscles received a step command of FR – they would be too slow. Saccades can be on target in less than 100ms.

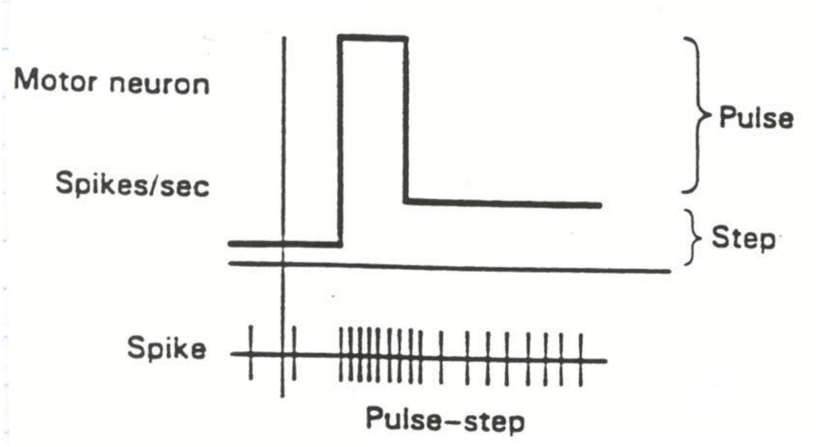
Analysis of Motoneuron Signals

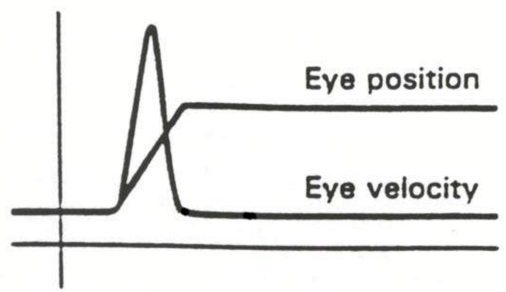
Pulse

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).

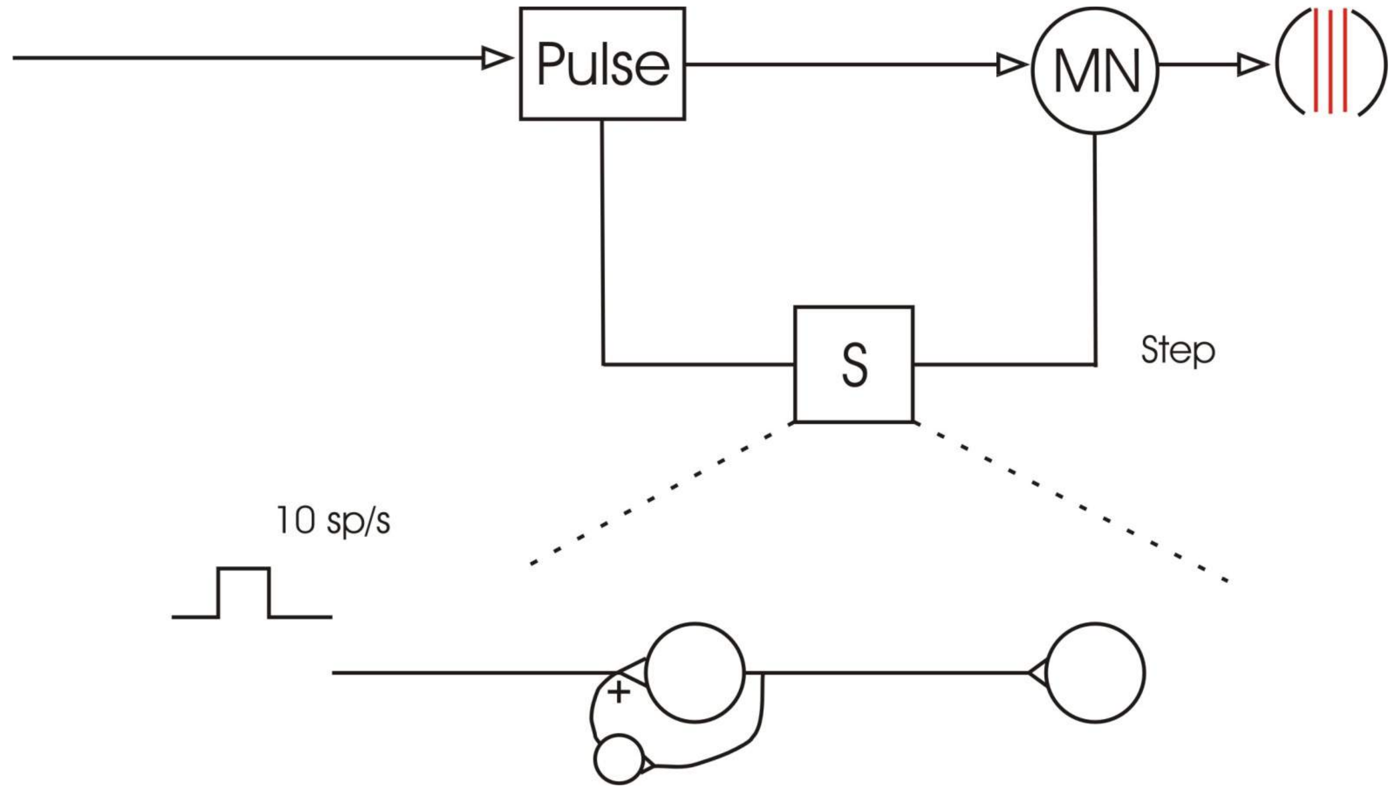




Note, The pulse resembles velocity + The step resembles position

Neural Circuit: A simple form of memory

Tonic activity after saccade (step) generated by the oculomotor neural integrator

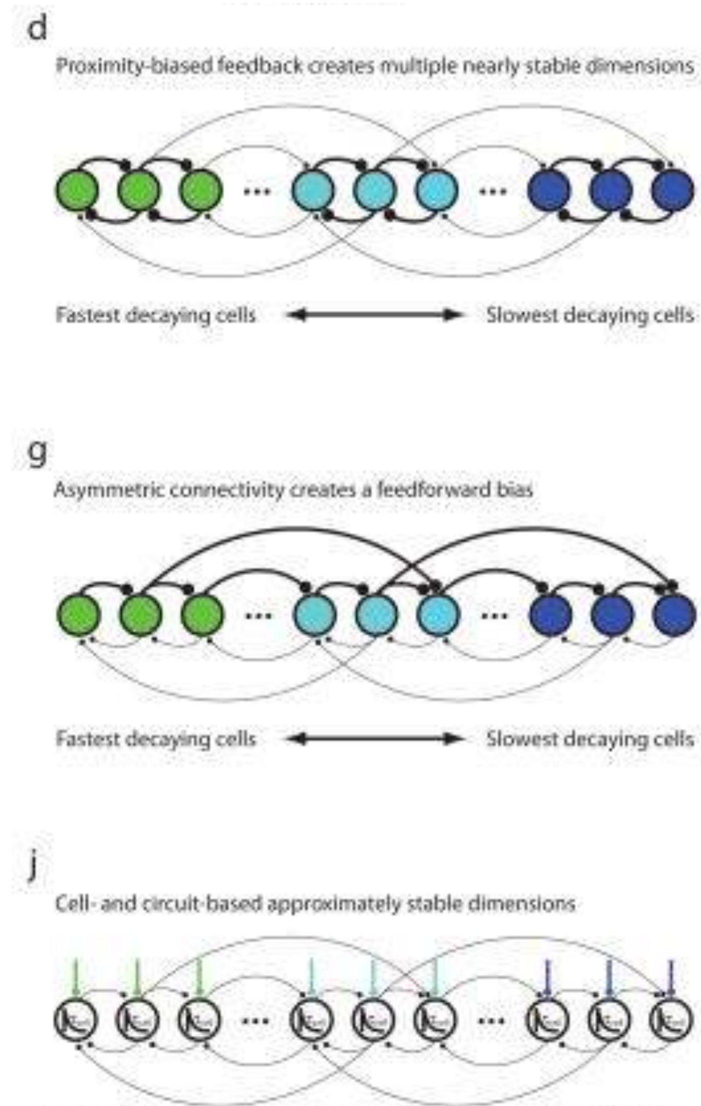


Similar integration is also performed in the VOR pathway, but the mechanism is somewhat different

Neural Circuit: Controlling Saccades

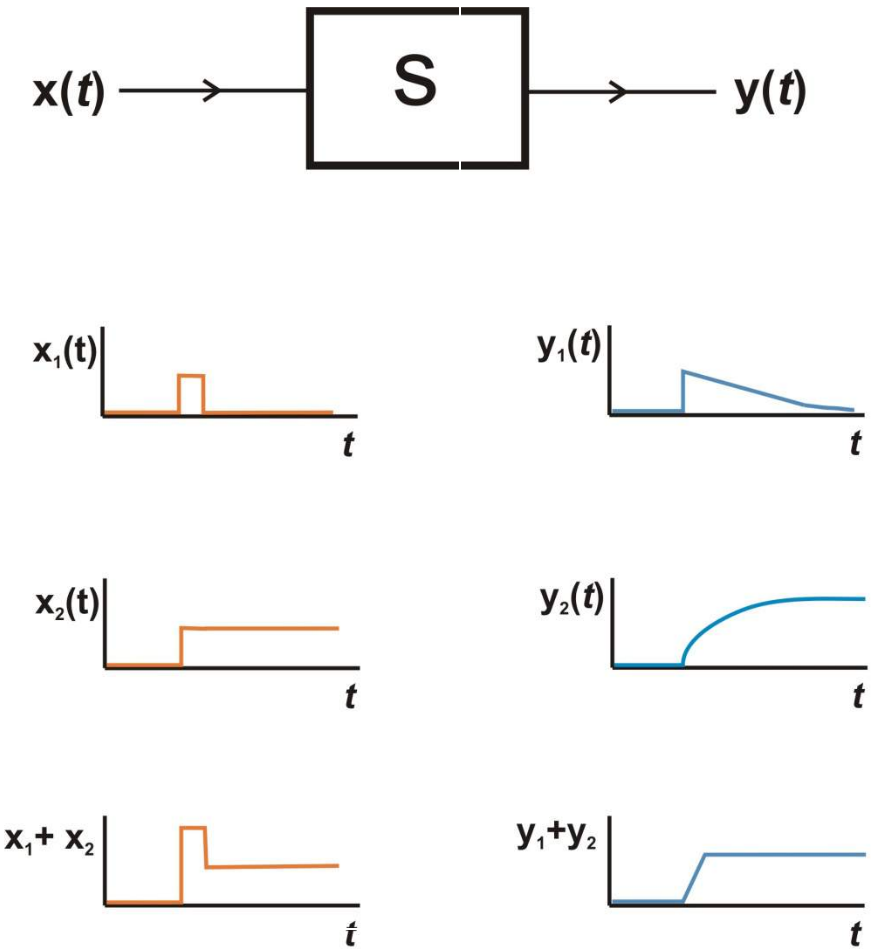
Tonic activity after saccade (step) generated by the oculomotor neural integrator

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



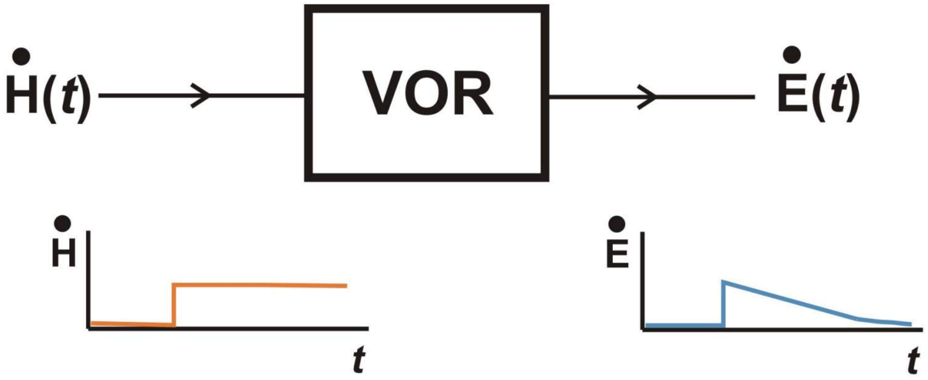
Miri et al,
Nature NS., 2011

Linearity and Superposition:

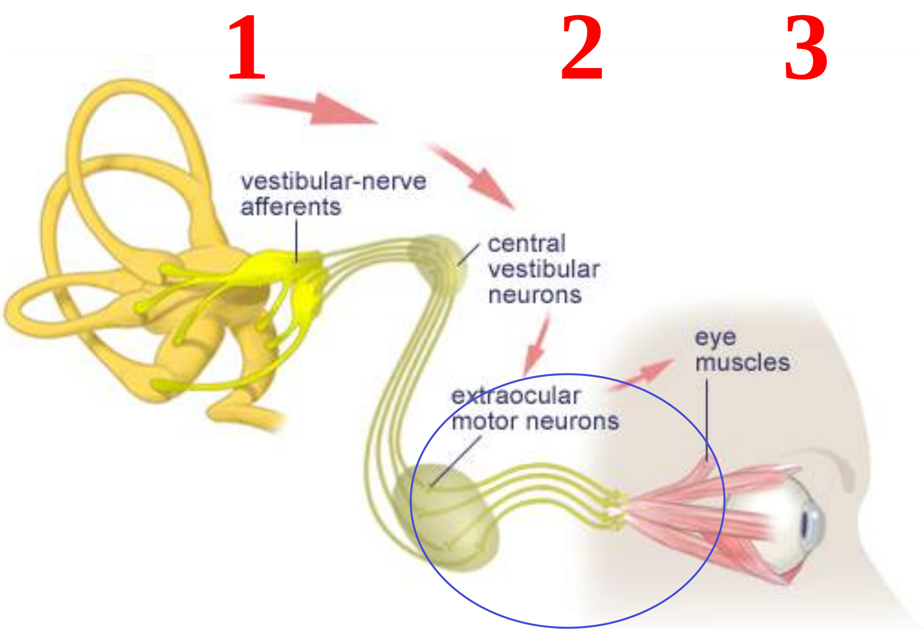


For example, the MN equation added the results from 3 experiments, together. *Assumption: The system is linear*. If we put in 2 signals, the output is the same as as the sum of the response of each alone.

The most direct VOR is a 3 neuron pathway – Example System

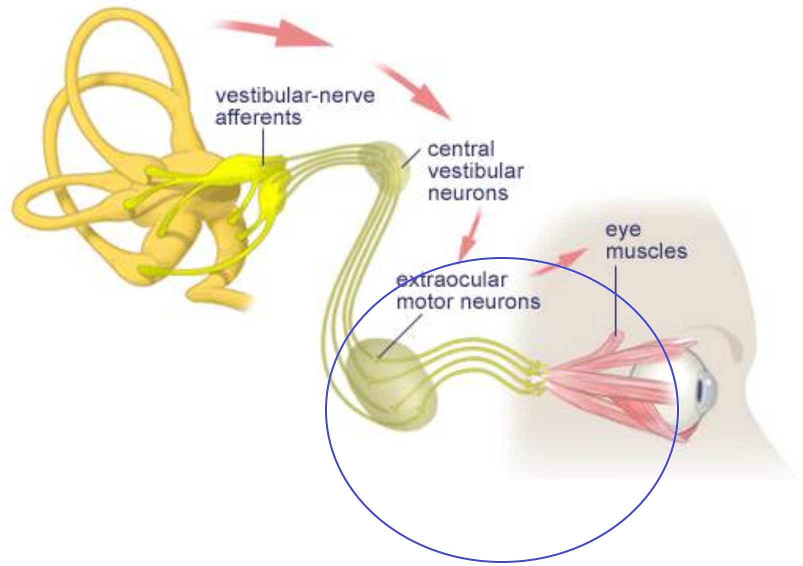


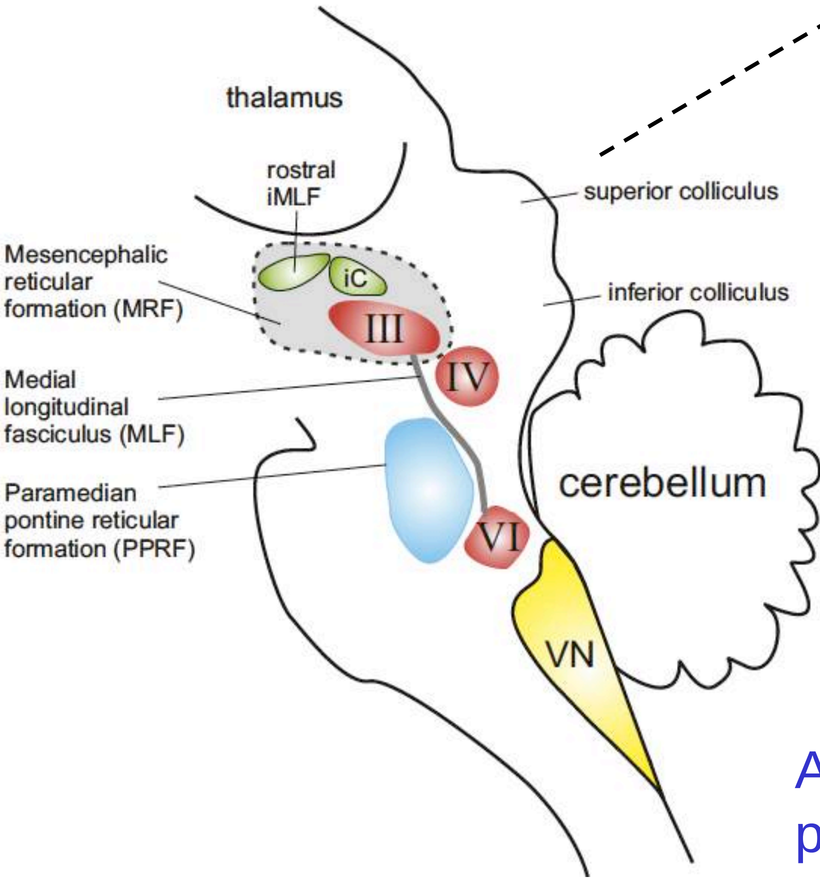
The problem is to now find S for the VOR



The Vestibulo-ocular reflex

motor





motor

A given extraocular motoneuron participates in all classes of eye movements
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Sensorimotor transformations: VOR

So, far we have considered

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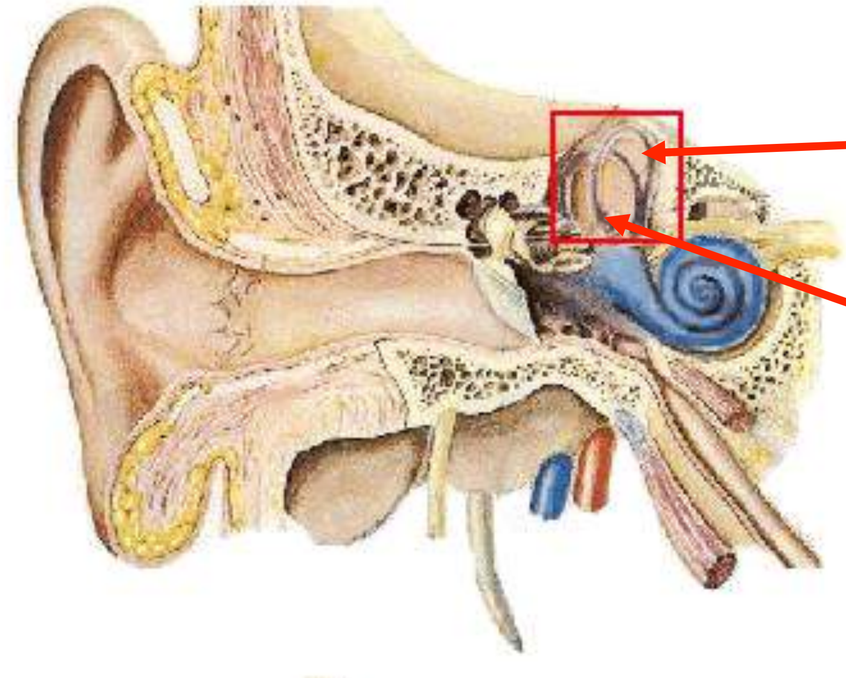
Function of the Vestibular System



Semicircular canals
 - sense angular rotation

Otoliths
 - sense linear acceleration

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

Organization of the Vestibular System

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

1) Otoliths (linear acceleration)

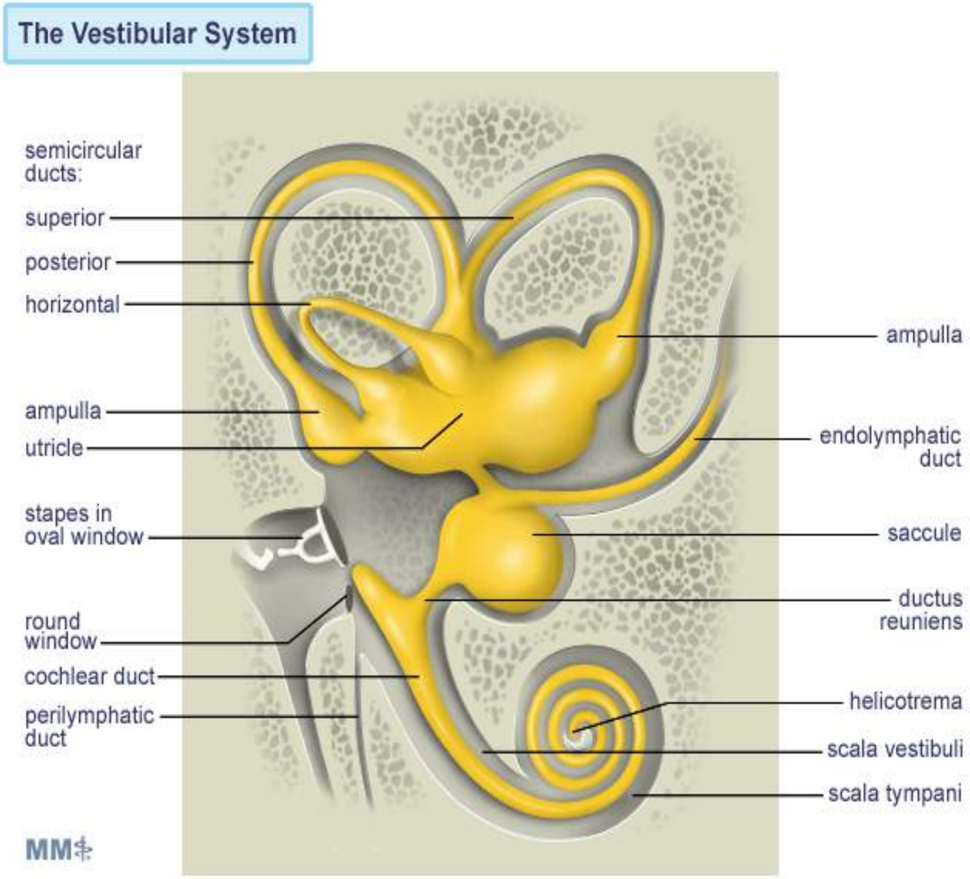
→ saccule
→ utricle

Macula

2) Semicircular canals
(angular acceleration)

→ horizontal
→ superior
→ posterior

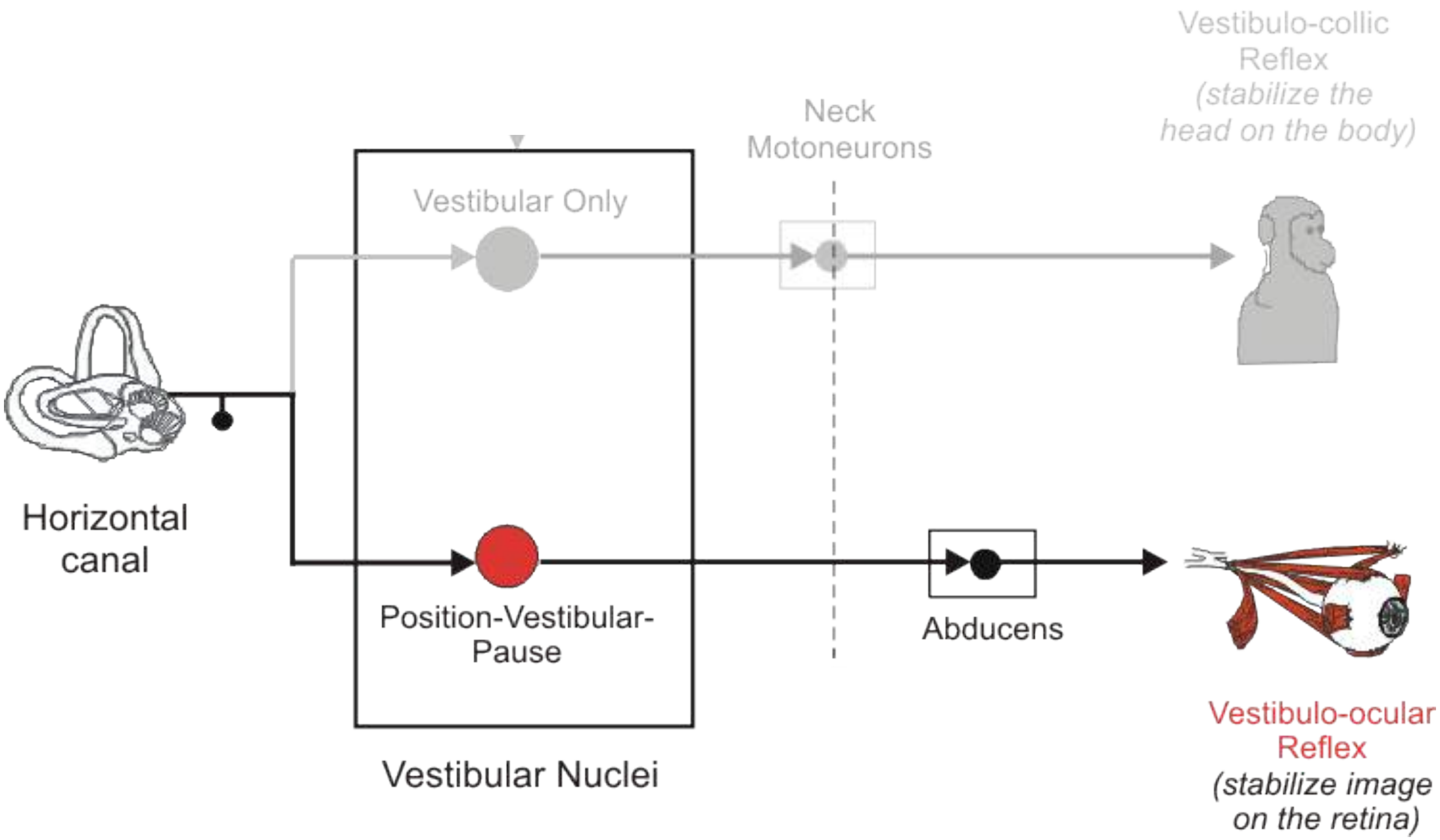
Ampula
(crista)



Note: Entire system is continuous with scala media of the cochlea via the ductus reunions.

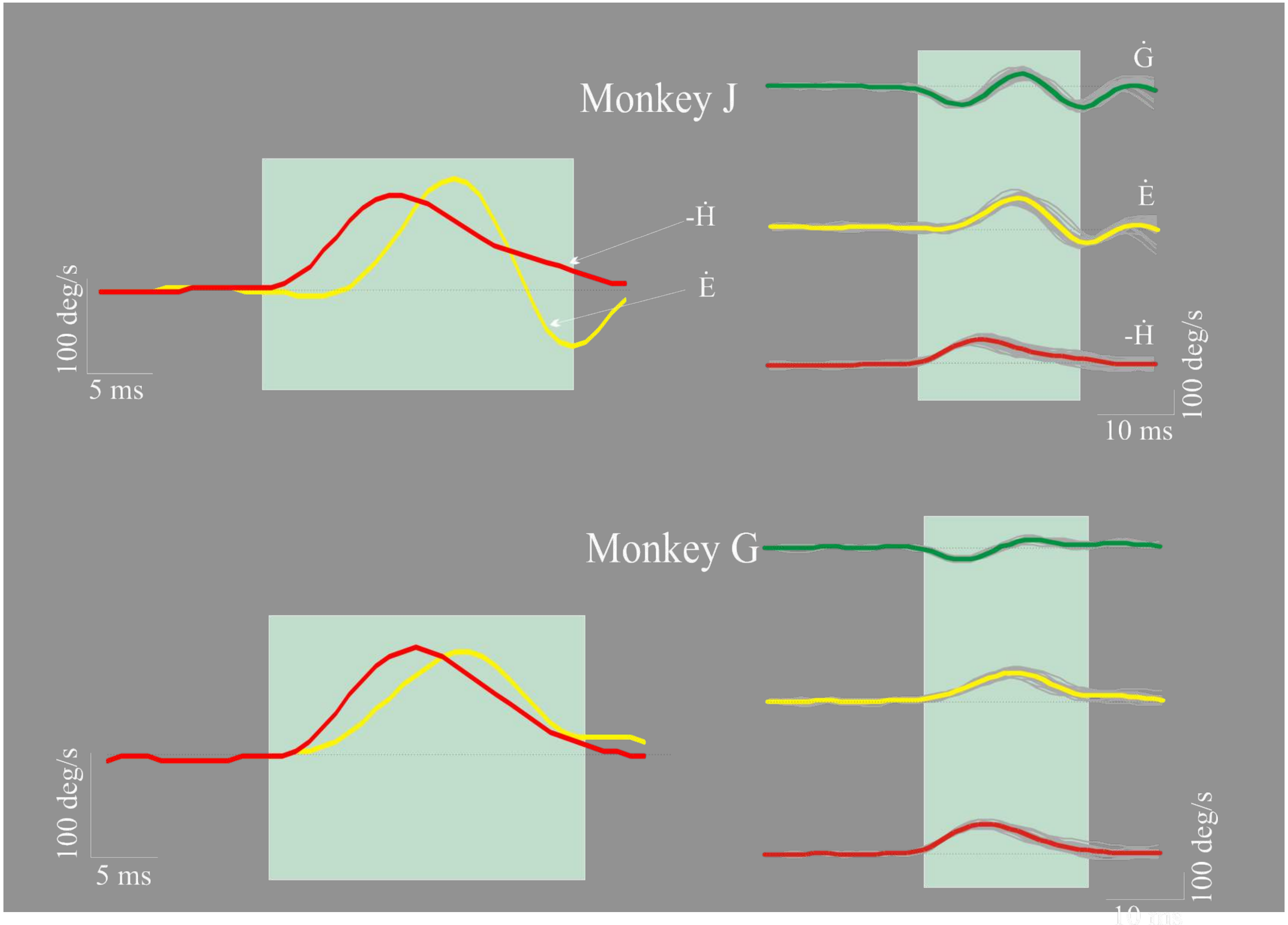
Function of the Vestibular System

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



Function of the VOR

Gaze Stabilization via the Vestibulo-ocular Reflex



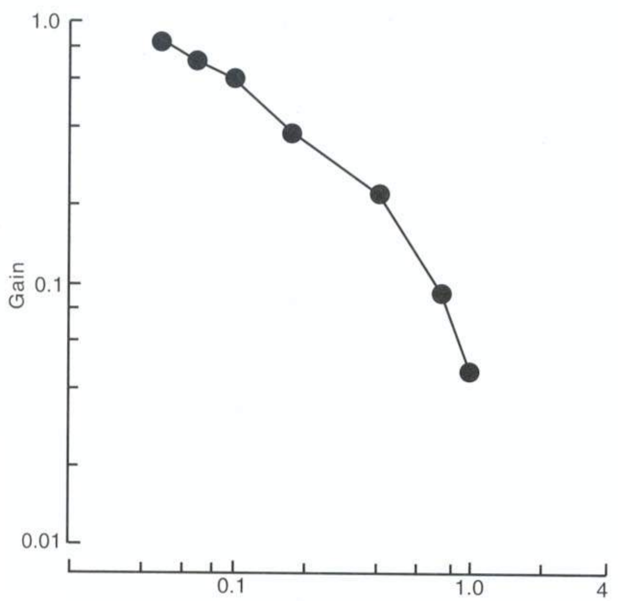
More effective than vision since response latency is very short!

Huterer and Cullen, *J. Neurophys.*, 2002

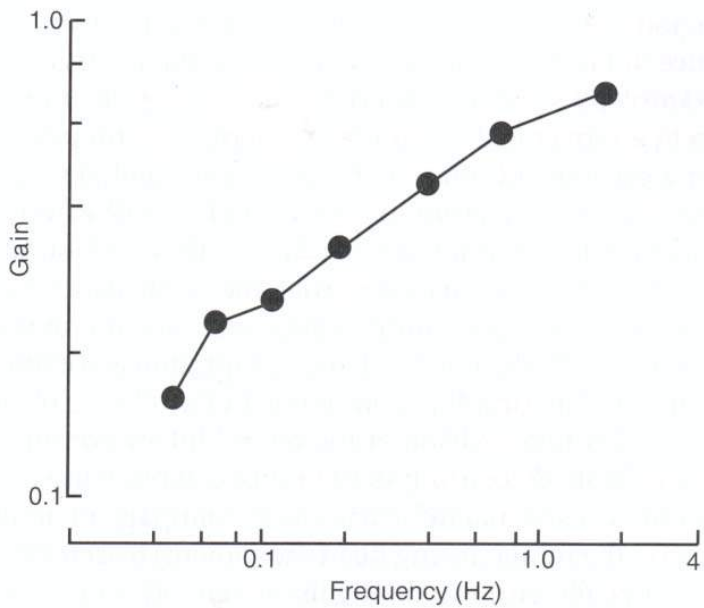
Function of the VOR

Gaze Stabilization via the Vestibulo-ocular Reflex

OKN Gain



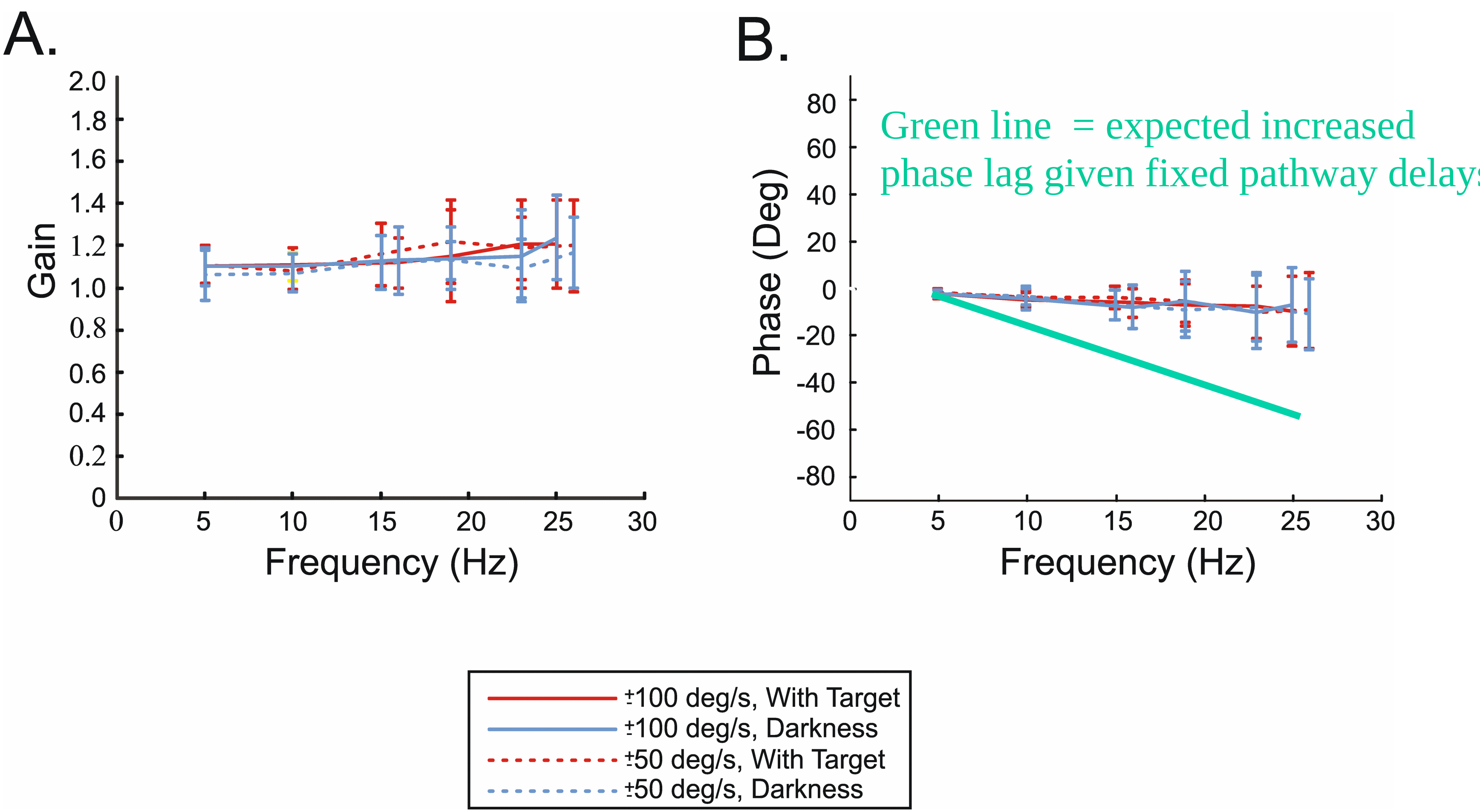
VOR Gain



Accordingly, VOR is more effective than visually driven OKN at higher frequenceis

Vestibulo-ocular reflex (VOR) Dynamics:

The VOR is compensatory over a wide frequency range



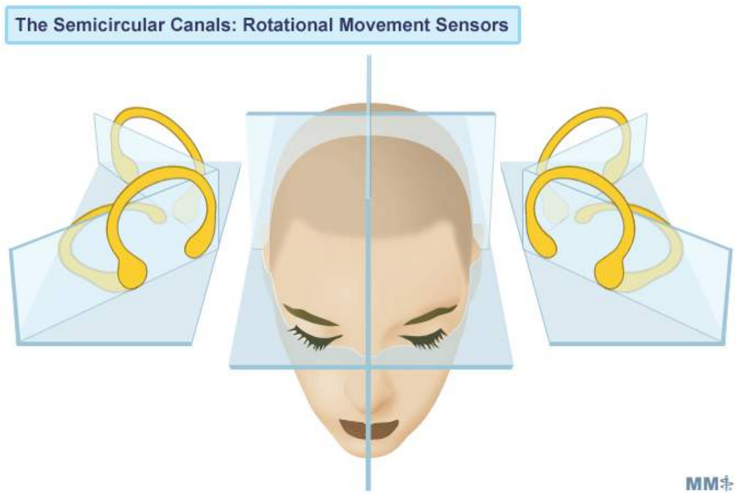
Huterer and Cullen, JNP 2000

The Vestibulo-Ocular Reflex

(video)

http://www.nejm.org/doi/full/10.1056/NEJMicm031134

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.

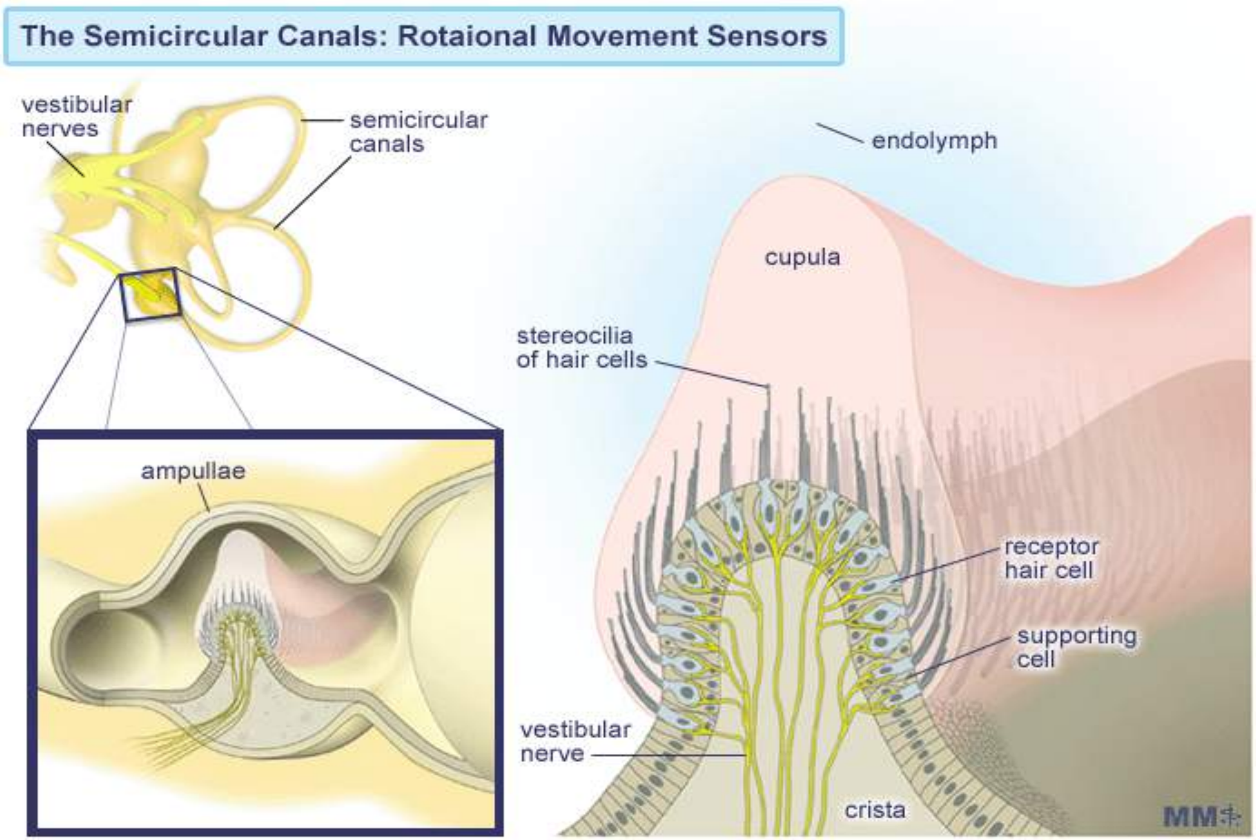
Superior
Posterior → subtend 45° relative to the sagittal and frontal plane.

Each canal consists of

1) A circular fluid path

2) Ampulla → crista – hair cells
→ cupula – elastic membrane (water tight)

Mechanical Analysis of the Semicircular Canals



Receptor Cells

All hair cells are oriented in the same direction for each canal.

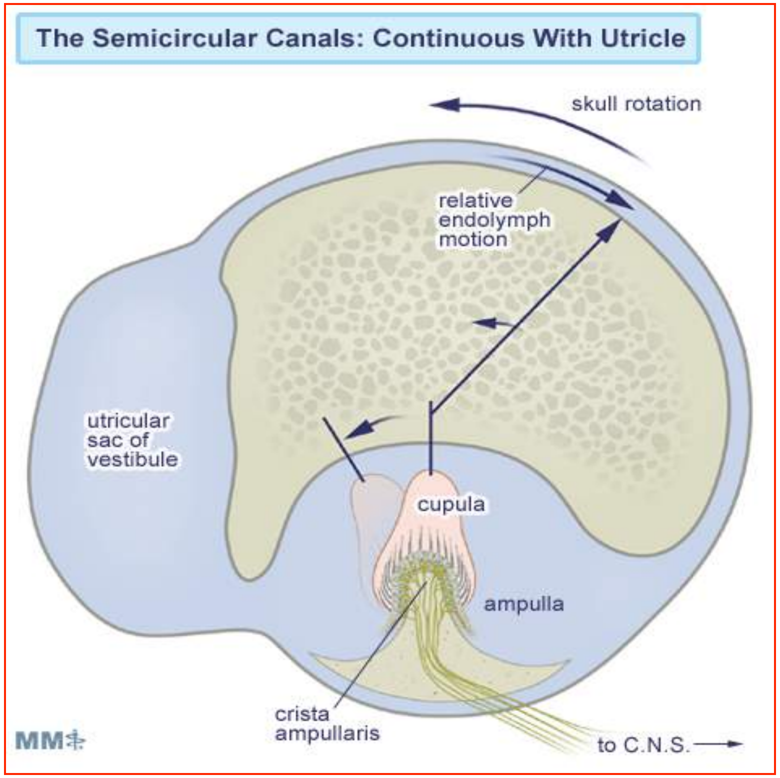
Mechanism: Head rotates

→ fluid is left behind

→ ampulla pushes against it

→ bends cilia.

Mechanical Analysis of the Semicircular Canals



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 ∫ (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:

$$\theta d\, \varepsilon^2/dt^2 + \Pi\, d\, \varepsilon(t)/dt + \Delta\, \varepsilon(t) = \theta\alpha(t)$$

Where: θ is the effective moment of inertia of the endolymph.

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

Δ Is a elastic restoring factor related

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

1) a long one ($\tau 1= \Pi / \Delta = 5s$) and
2) a short one ($\tau 2= \theta / \Pi = .004s$).

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:

$\theta d\, \varepsilon^2/dt^2 + \Pi\, d\, \varepsilon(t)/dt + \Delta\, \varepsilon(t) = \theta\alpha(t)$

In the Laplace domain:

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

$$\ell[\frac{d^2 f}{dt^2}] = s^2 F(s) - s\ f^1(0^+) - f^0(0^+)$$

$H(s) = E(s)/\alpha(s)$

$H(s) = 1/ [(\Pi / \Delta)\, s+1]\, [(\theta / \Pi)\, s+1]$

Where: θ is the effective moment of inertia of the endolymph.

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

Δ Is a elastic restoring factor related

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

1) a long one ($\tau 1 = \Pi / \Delta = 5s$) and
2) a short one ($\tau 2 = \theta / \Pi = .004s$).

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.

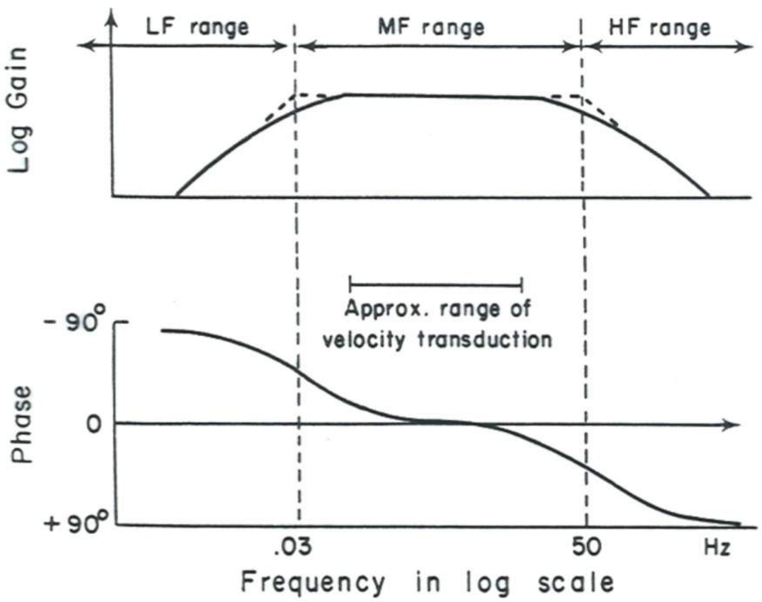
These opposing forces cause the movement of the endolymph (relative to the cupula) to *lag* head acceleration
(as would be the case if the only the inertia of the endolymph were significant). • •

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

So, far we have considered

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Hair Cells and Afferent Responses

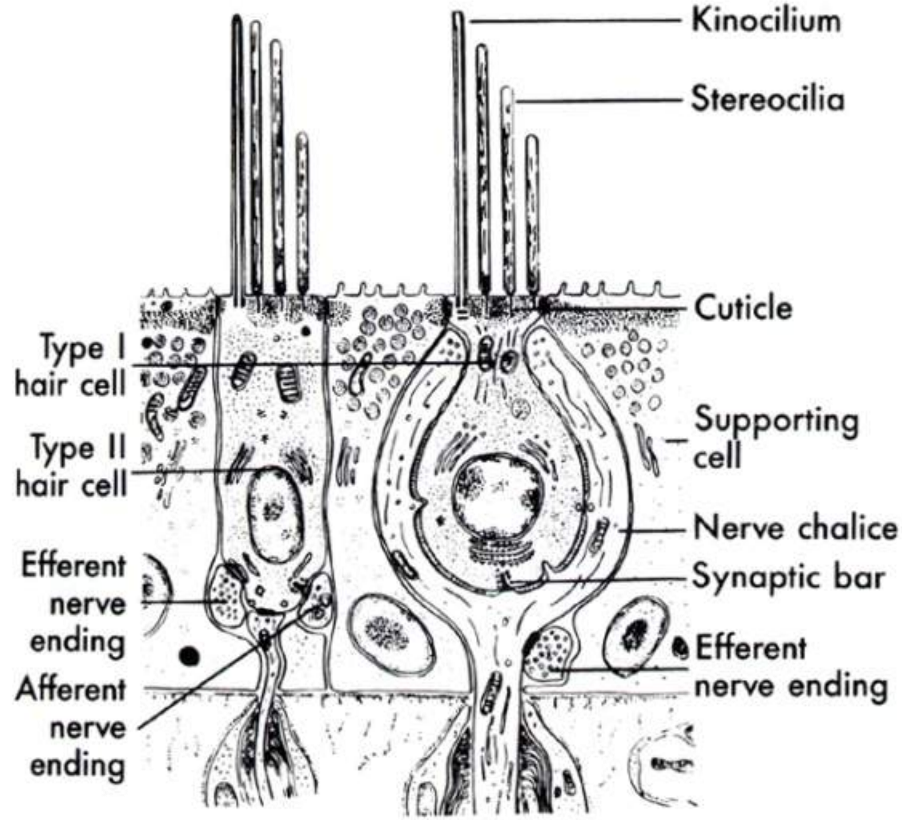
Two types of Hair cells

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

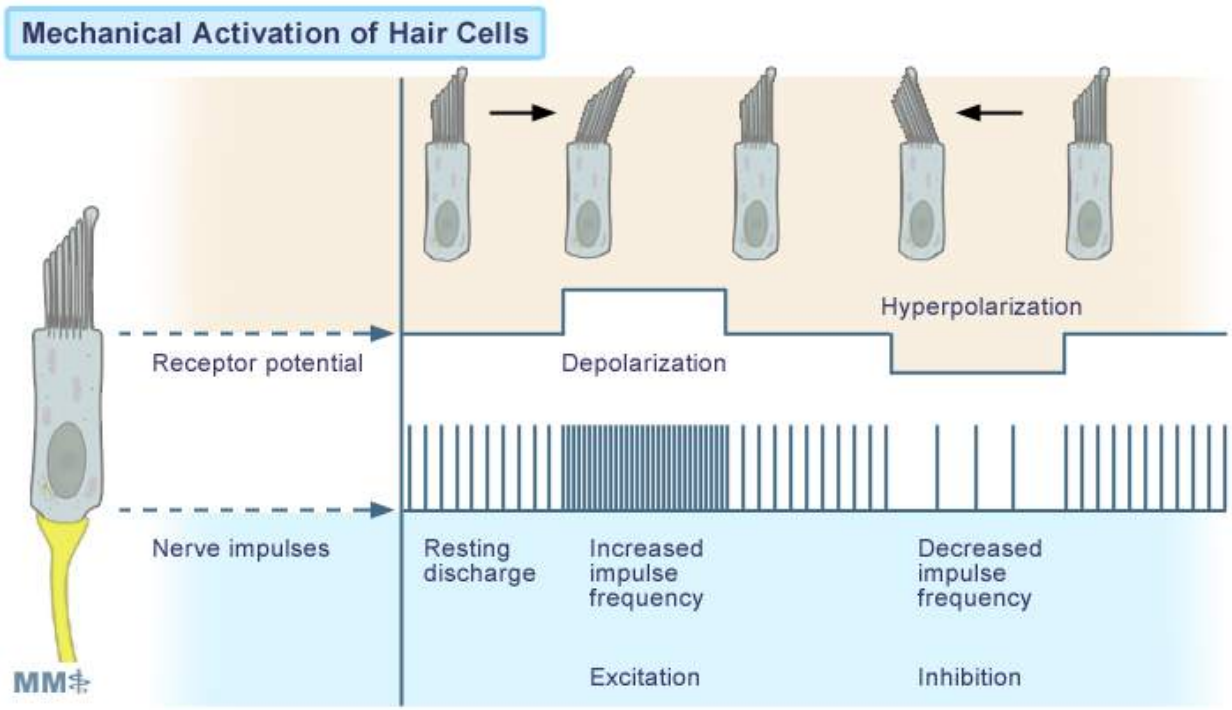
Exhibit a constant resting discharge when not stimulated

1) Bending cilia <u>towards</u> kinocilia

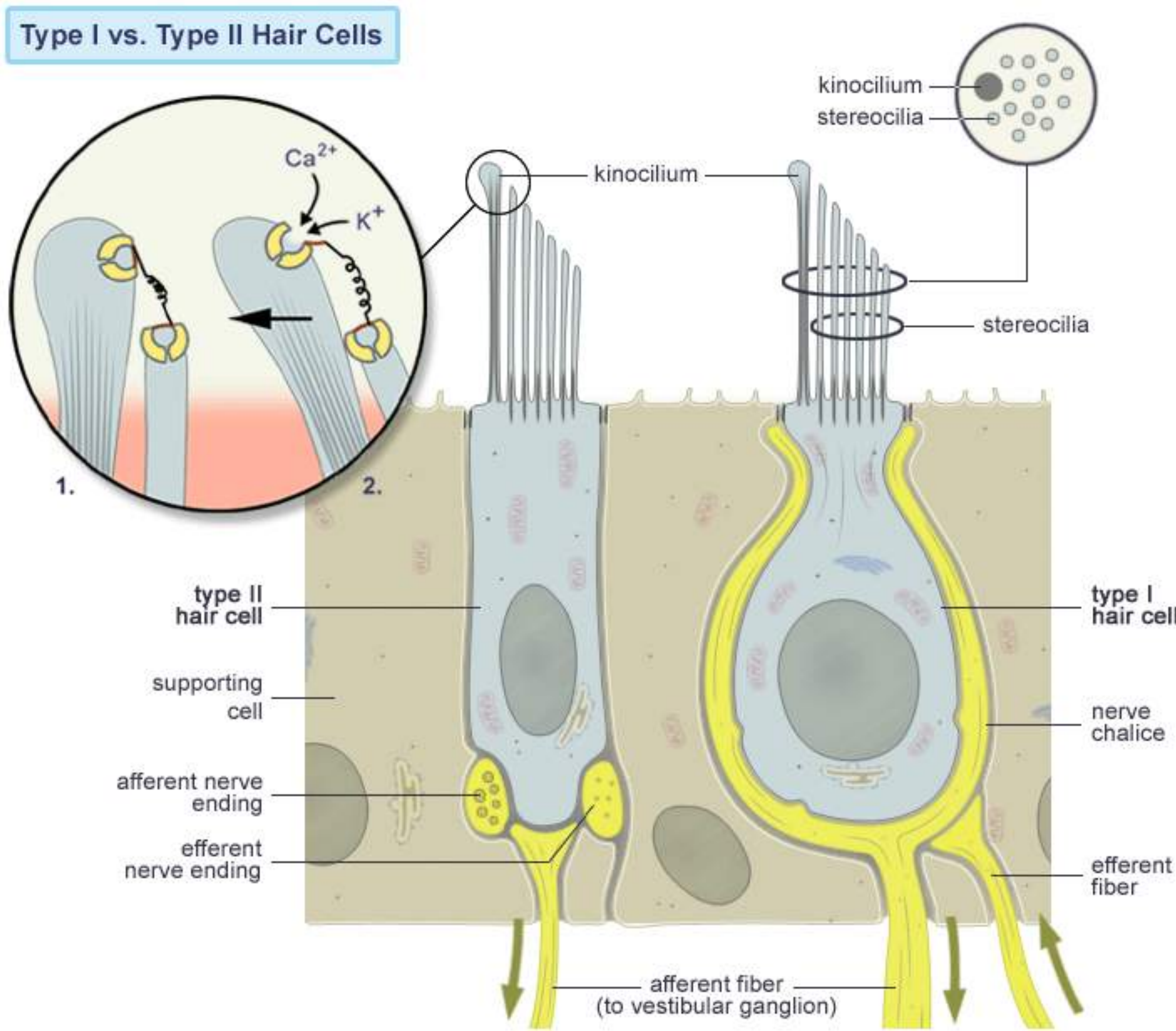
excites hair cell: ↑ action potential, VIII nerve.

2) Bending cilia <u>away from</u> kinocilia

inhibits hair cell: ↓ action potential, VIII nerve.



Thus, the resting discharge (spontaneous discharge) allows the CNS to sense stimulation in 2 directions (opposite via the <u>change</u> in activity).



Mechanism of Mechano-Neural Transduction: similar to auditory system Role of Efferent system: not yet understood

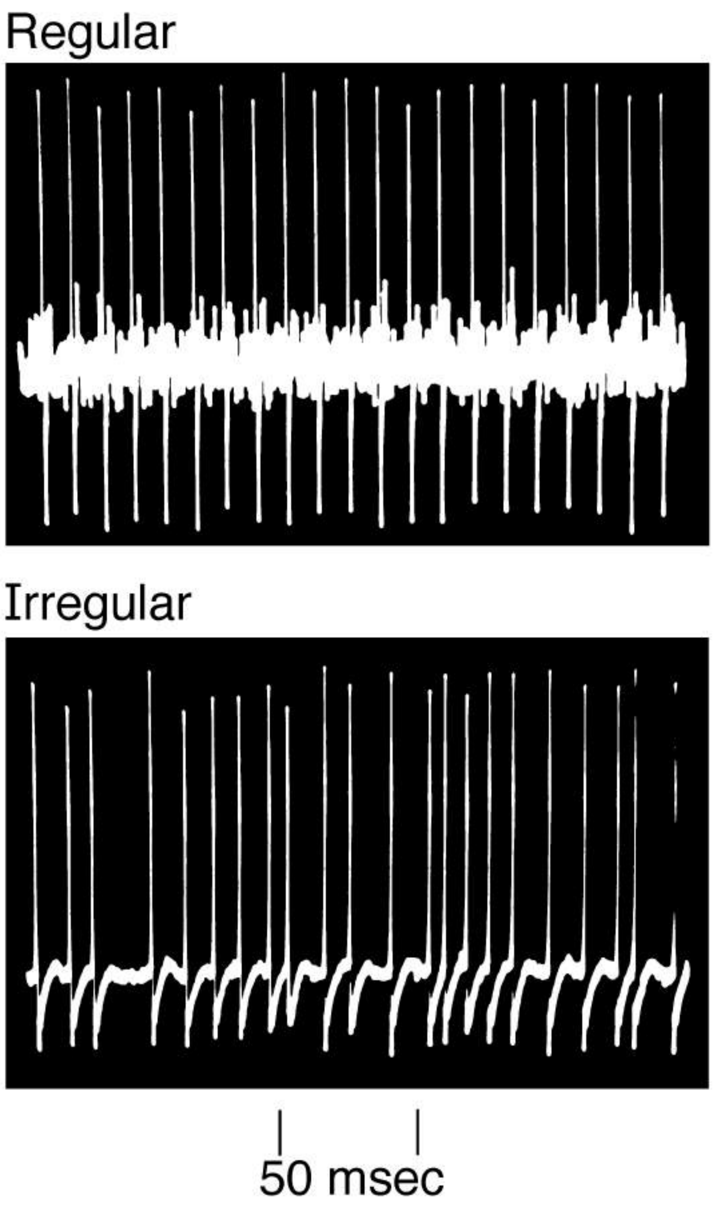
Hair Cells and Afferent Responses

Regular Versus Irregular Afferents

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

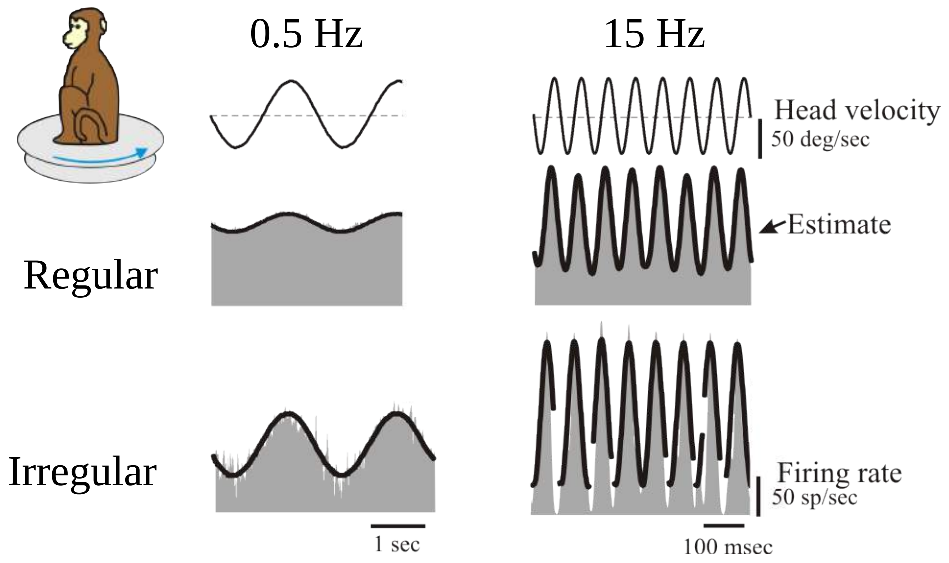
Regulars:

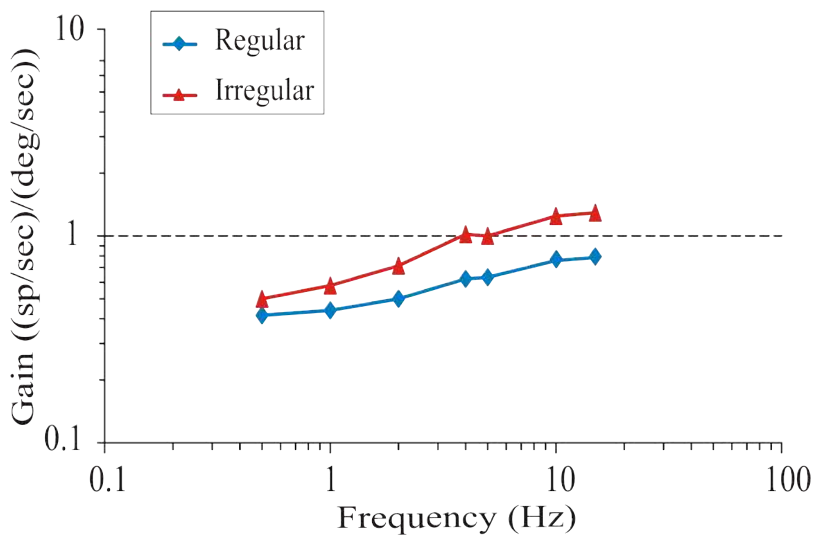
- More regular action potentials spacing
- Lower Afferent gain and phase
- Lower Efferent response magnitude
- Lower Galvanic sensitivity



Vestibular afferent Dynamics:

Afferents show a response gain increase with frequency

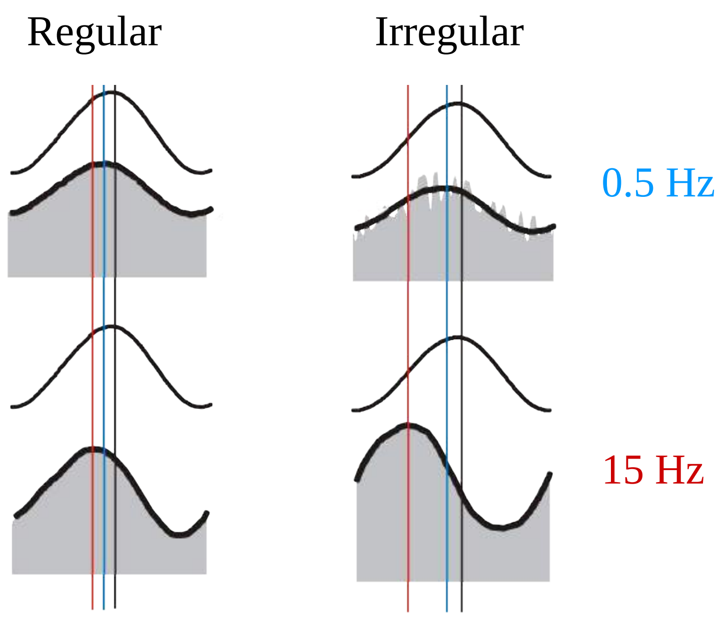


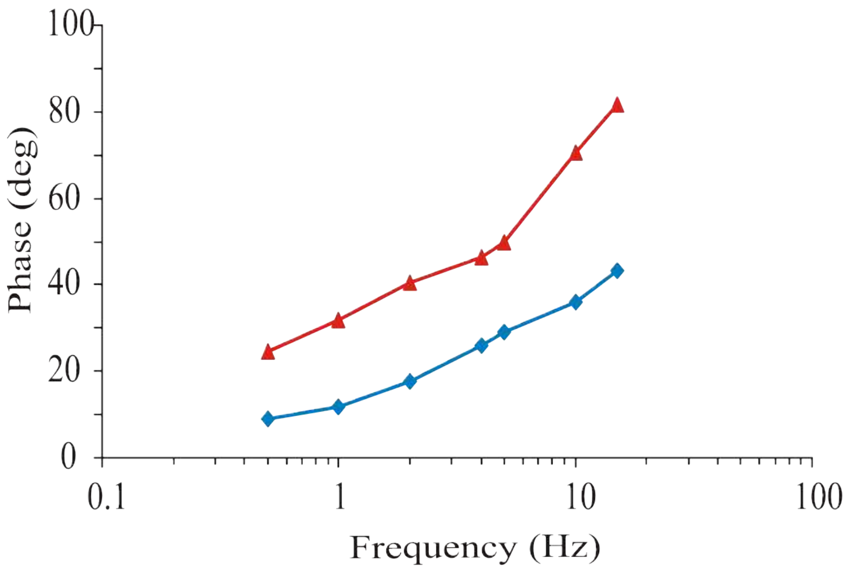


Sadeghi, Minor, and Cullen;
J Neurophys, 2007

Vestibular afferent Dynamics:

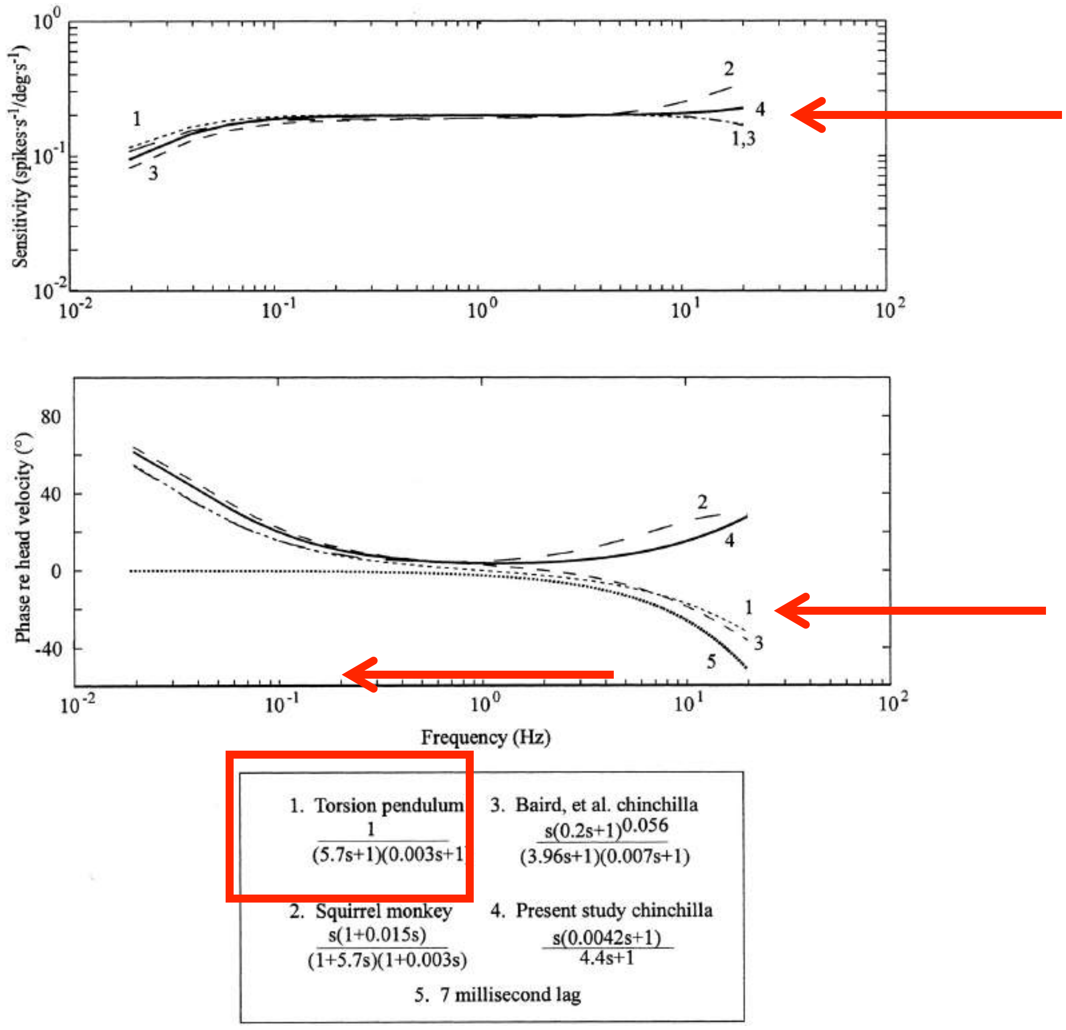
Afferents (particularly irregular afferents) also show a response phase increase with frequency





Sadeghi, Minor, and Cullen; J Neurophys, 2007

Vestibular-Nerve Afferents:
Response to Sinusoidal Rotation



Hullar, T. E. et al. J Neurophysiol 82: 2000-2005 1999

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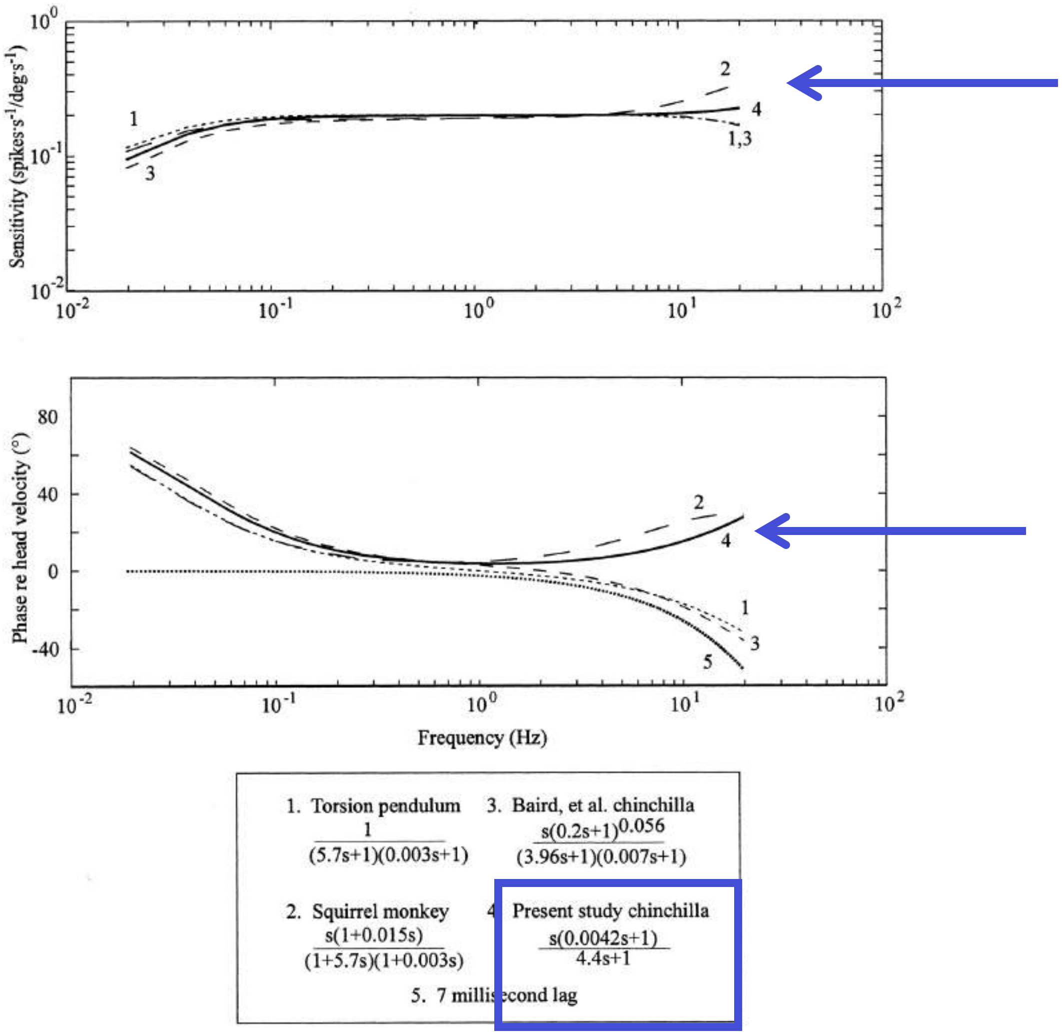
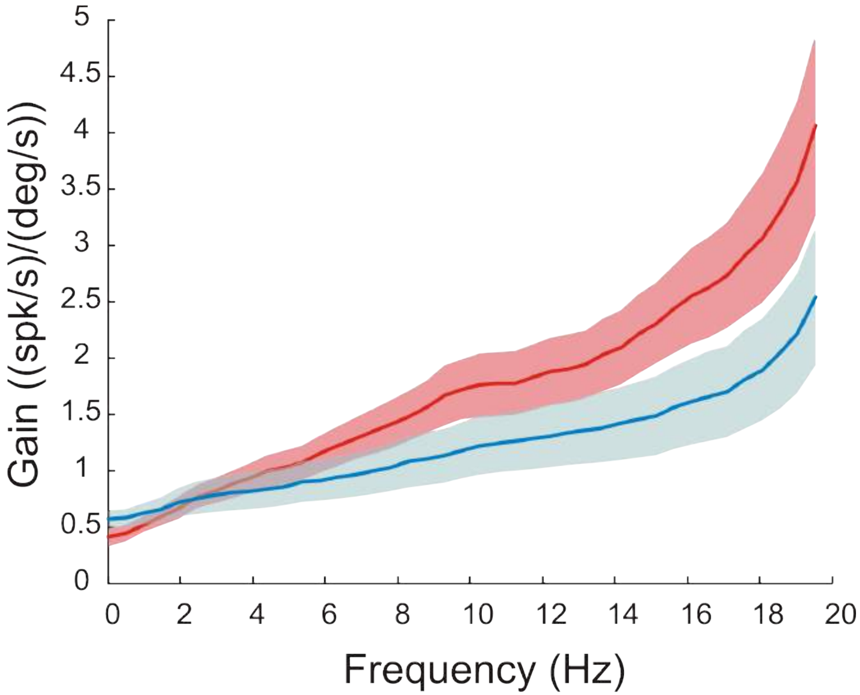


Hullar, T. E. et al. J Neurophysiol 82: 2000-2005 1999

Vestibular-Nerve Afferents:
Response to broadband stimulus



$G(f)=|P_{rs}(f)/P_{ss}(f)|$

Sadeghi, Chacron, Taylor, and Cullen, *J. Neurosci*, *2007*
Massot, Schneider, Chacron, Cullen, *Plos Biology*, *2012*

Vestibular-Nerve Afferents:

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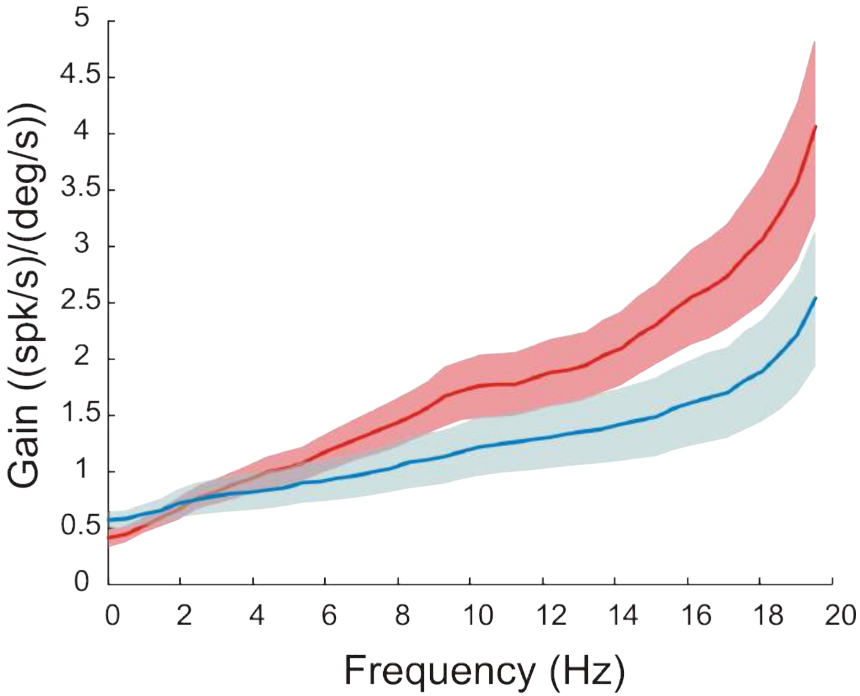
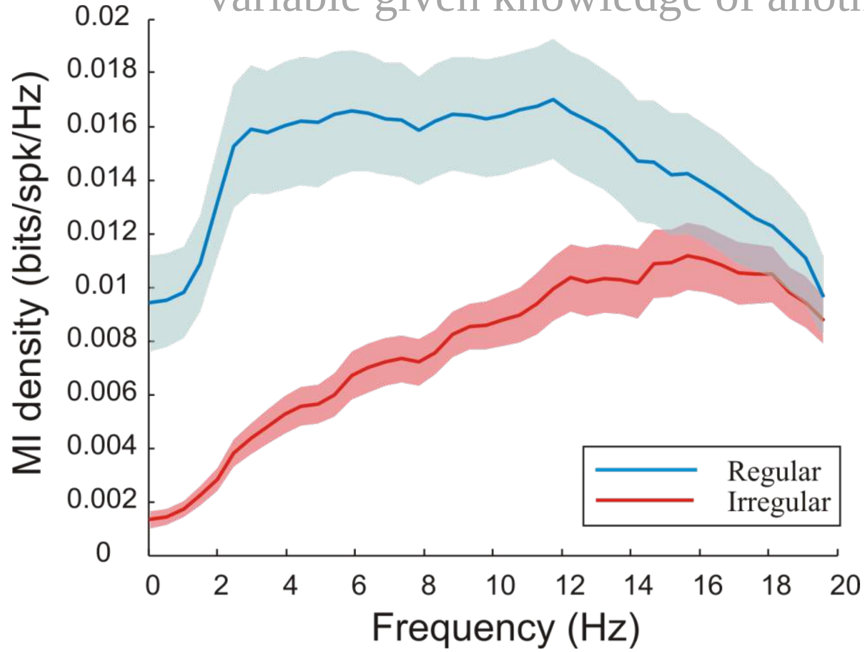


Mutual Information: reduction in uncertainty about one random variable given knowledge of another



$G(f)=|P_{rs}(f)/P_{ss}(f)|$

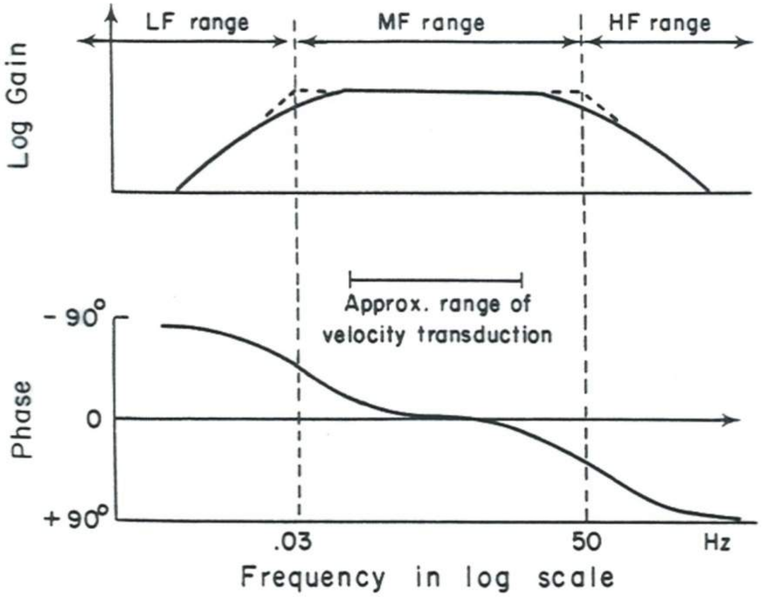
$MI=[-\log_2(1-C(f)]$

$C(f)=|P_{rs}(f)|^2/[P_{ss}(f)P_{rr}(f)]$

Sadeghi, Chacron, Taylor, and Cullen, *J. Neurosci*, *2007*
Massot, Schneider, Chacron, Cullen, *Plos Biology*, *2012*

Mechanical Analysis of the Semicircular Canals

Frequency Response



Prediction:

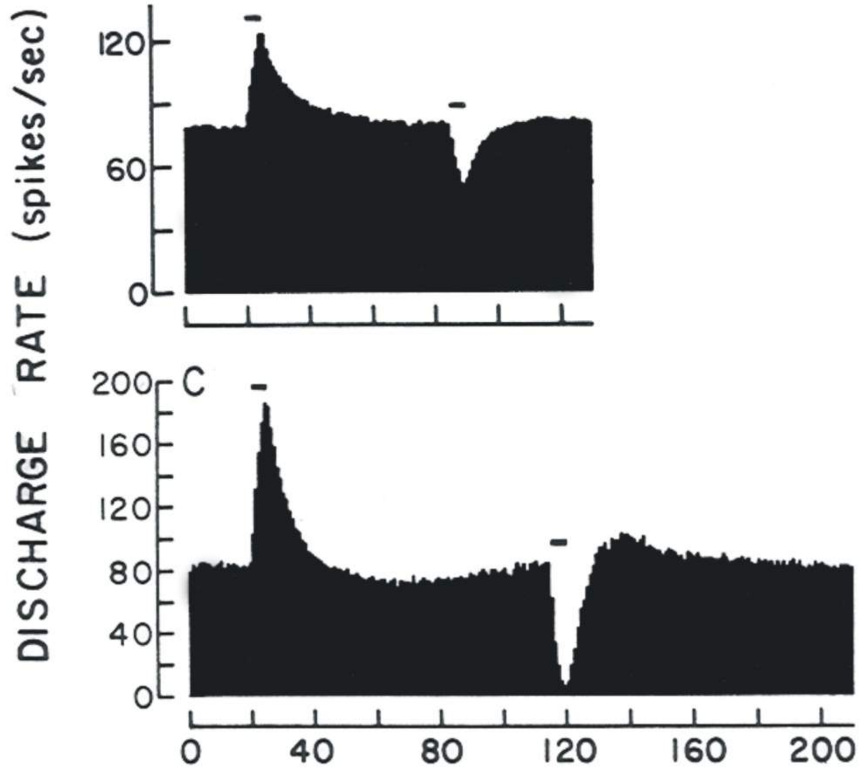
What should the VOR response to a step input look like?

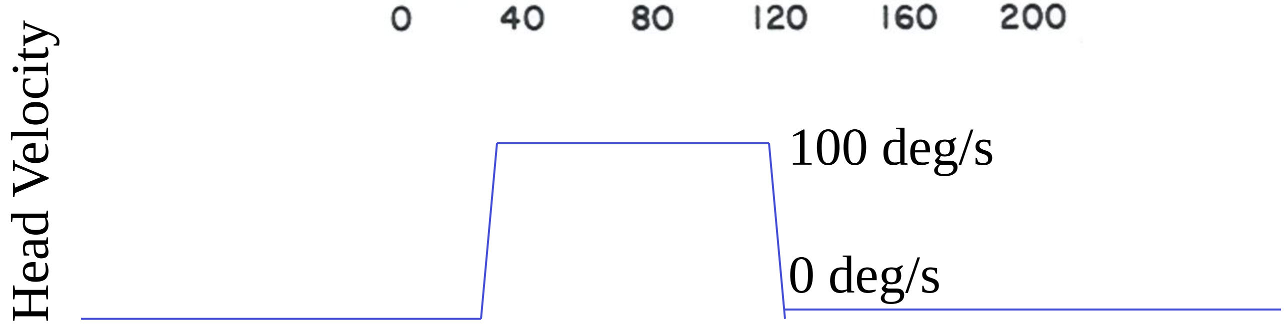
Vestibular afferents response to “velocity trapezoid” inputs as predicted by the torsion-pendulum model

$$\theta d\, \varepsilon 2/dt2 + \Pi\, d\, \varepsilon(t)/dt + \Delta\, \varepsilon(t) = \theta\alpha(t)$$

Dominant time constant is 5 sec

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





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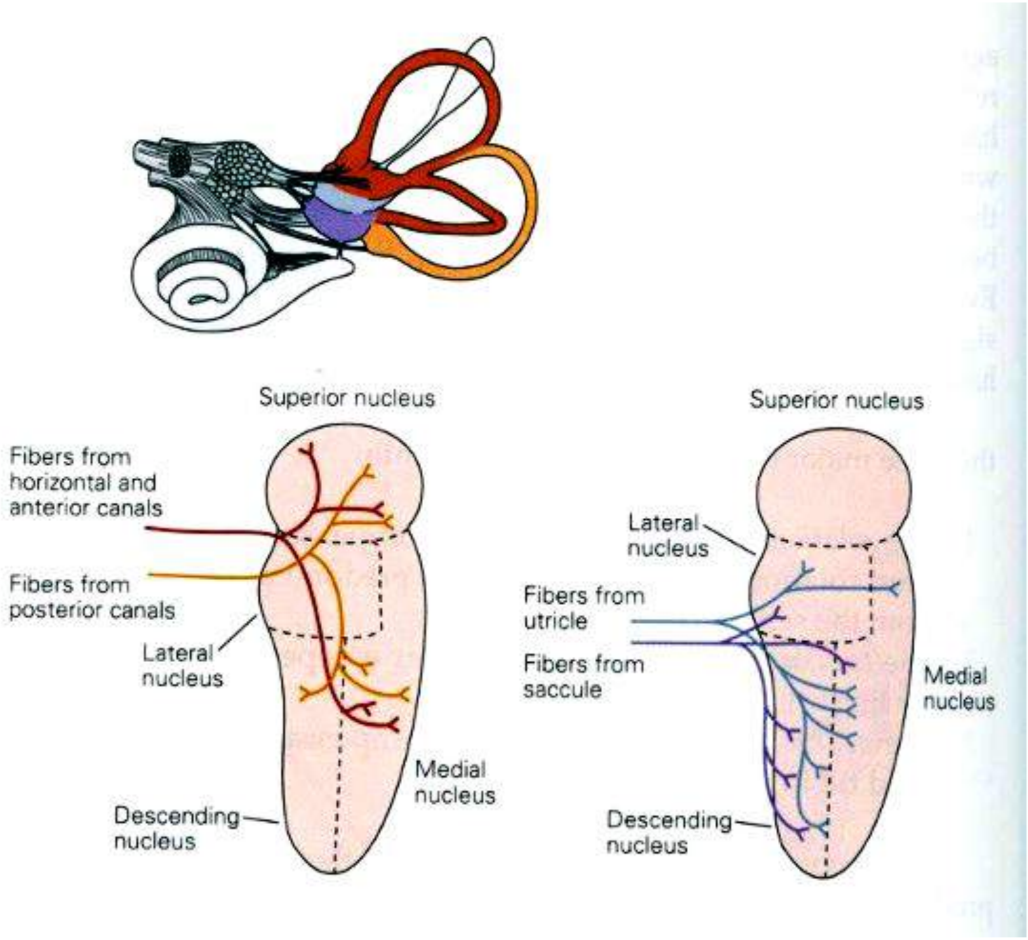
Central Vestibular Processing for the VOR

Central Pathways: Vestibular Nuclei



4 subdivisions:

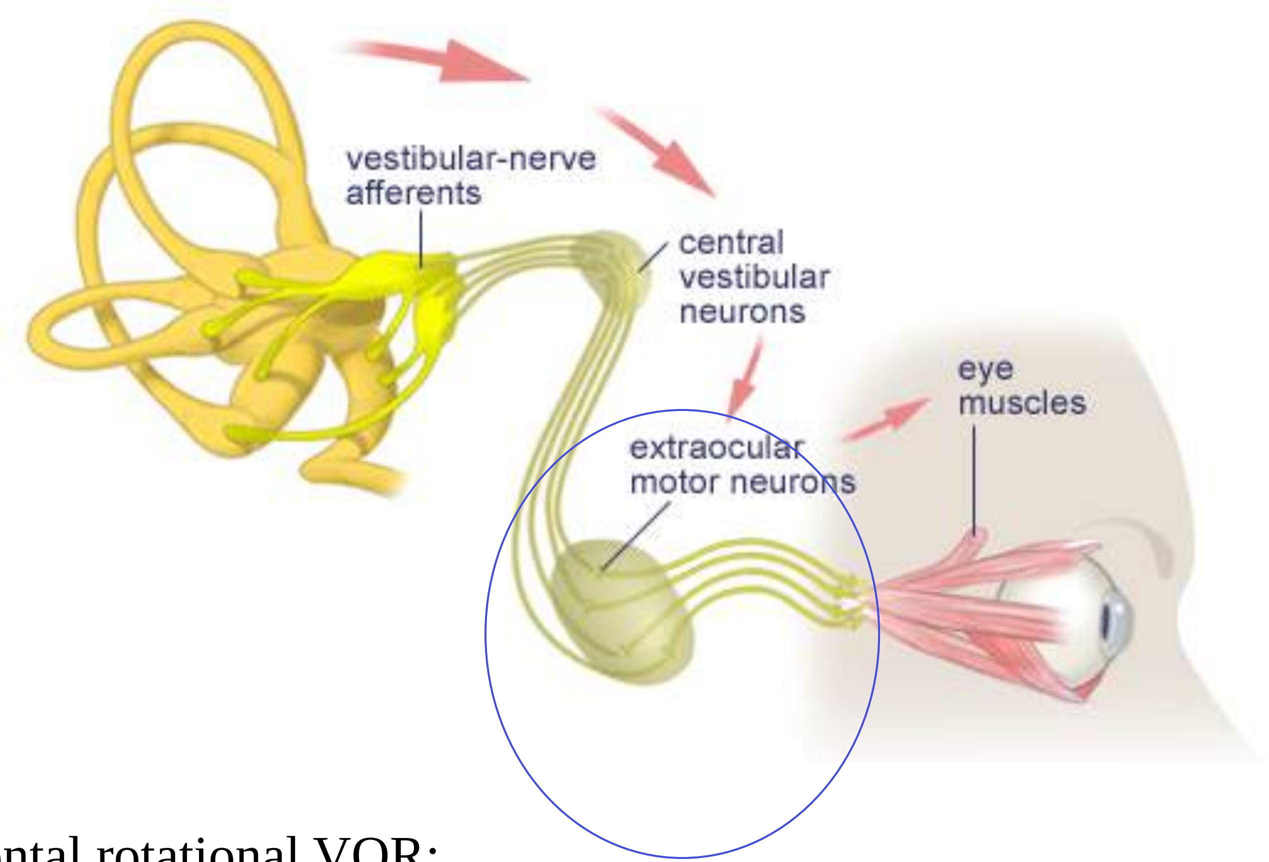
Superior/Medial
predominantly canal

Lateral
canal and otolith

Descending
predominantly otolith

Central Vestibular Processing for the VOR

Central Pathways: Vestibular Nuclei



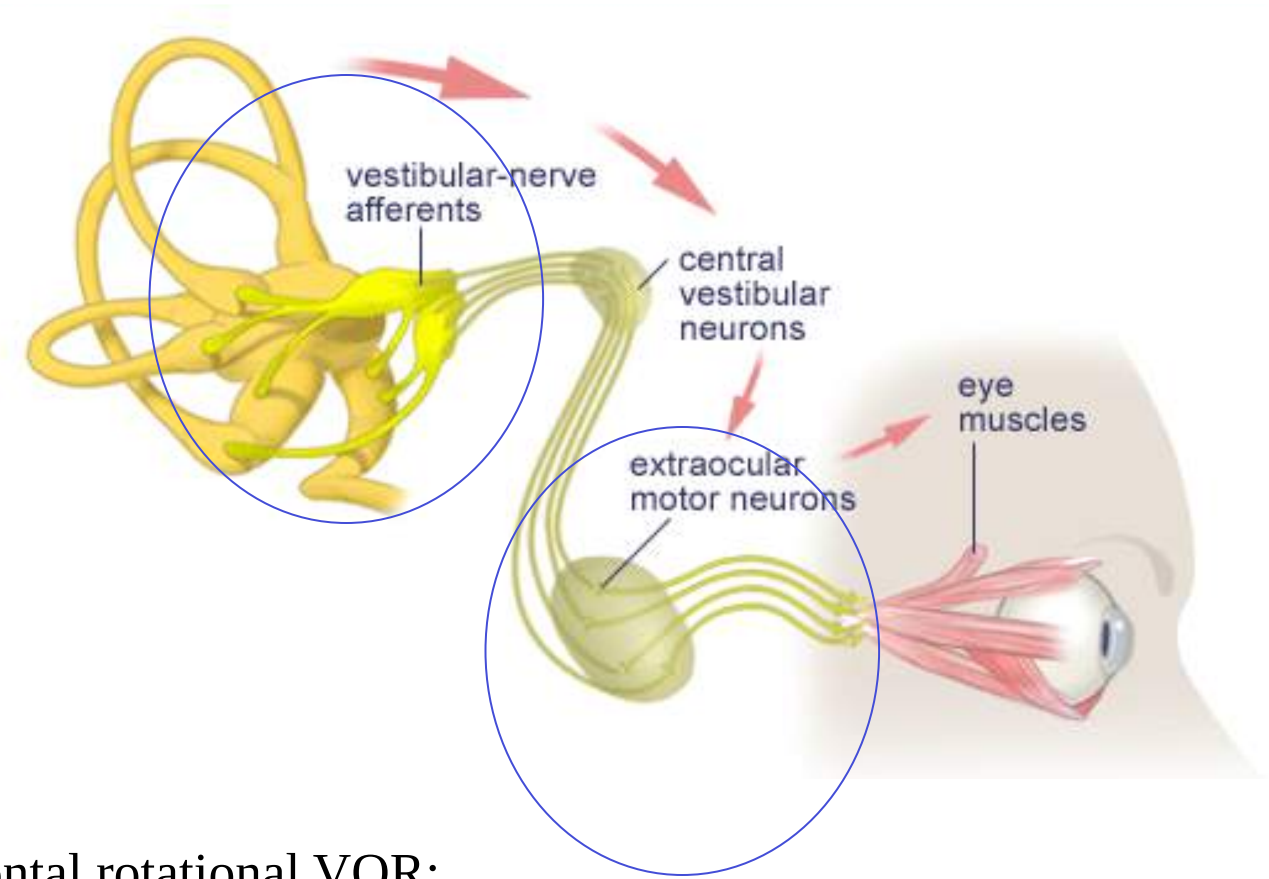
For the Horizontal rotational VOR:

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



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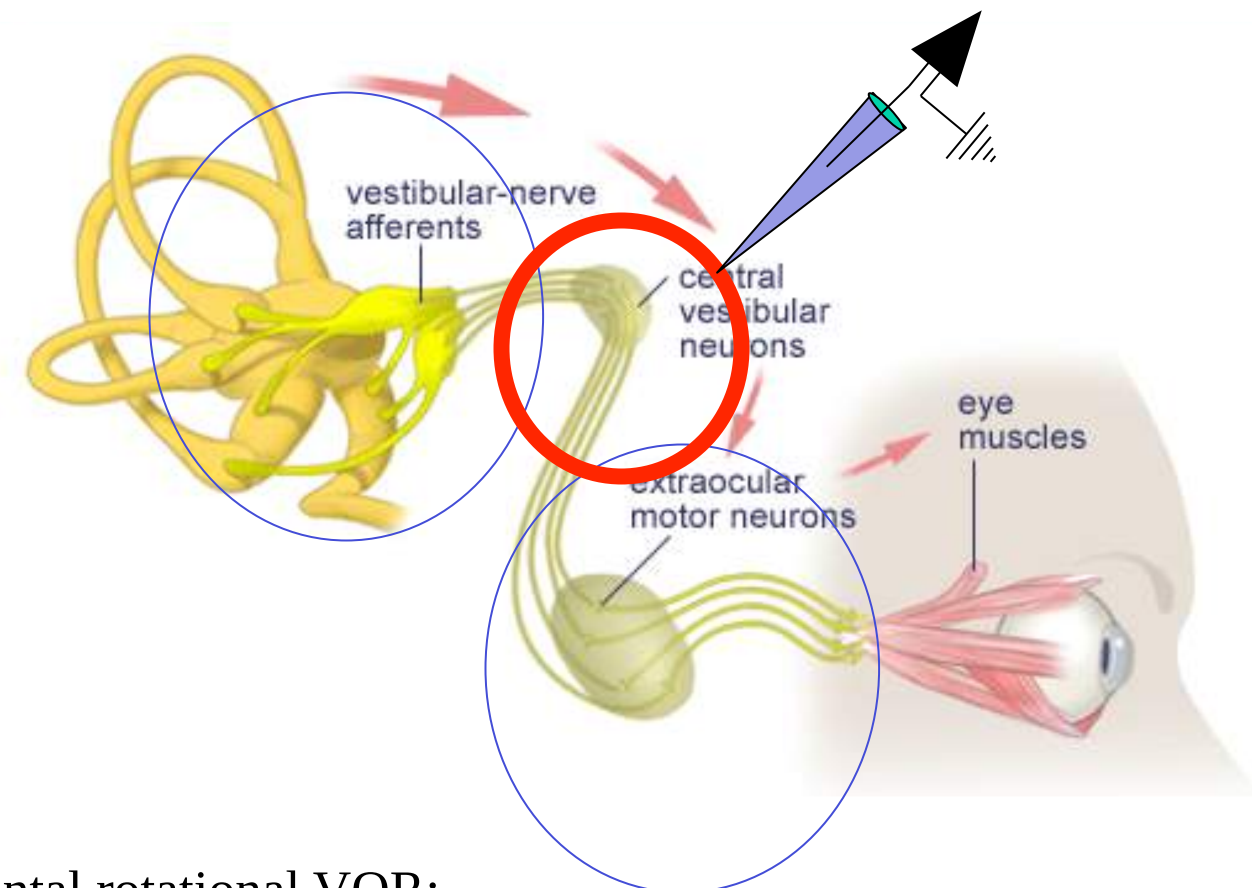

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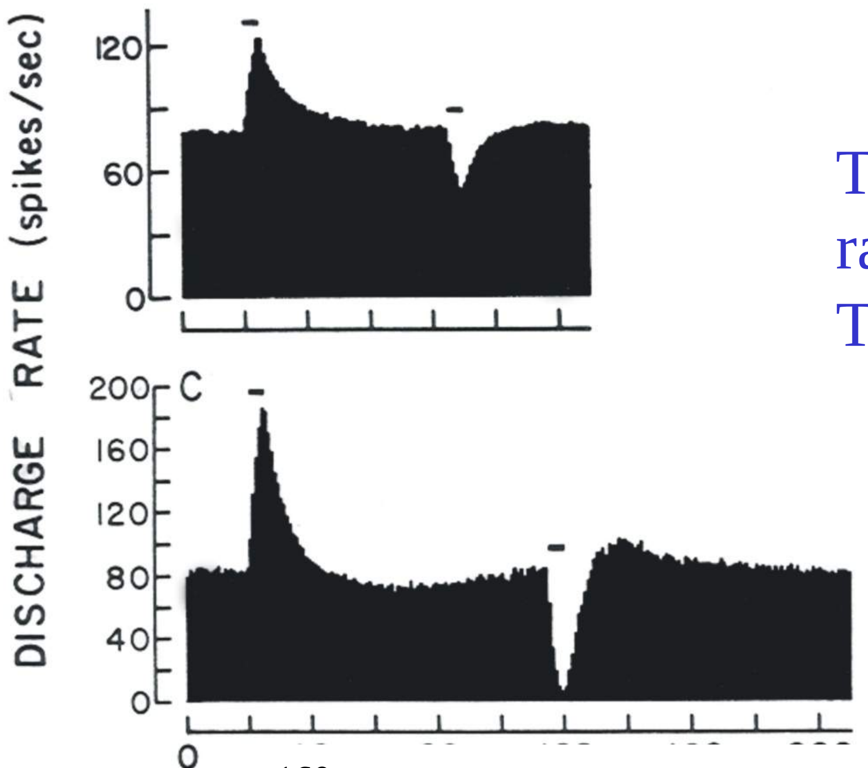
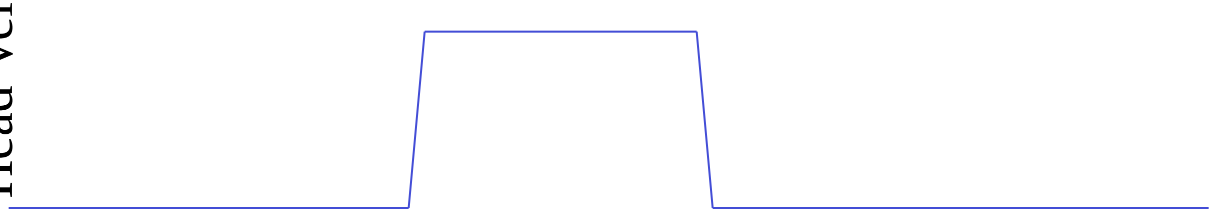
Central Pathways: Vestibular Nuclei



160

Time constant is ~20 sec rather than 5 sec as for The Vestibular Afferents.

Head Velocity



100 deg/s

0 deg/s

Central Vestibular Processing for the VOR

Central Pathways: Vestibular Nuclei and Velocity Storage

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.

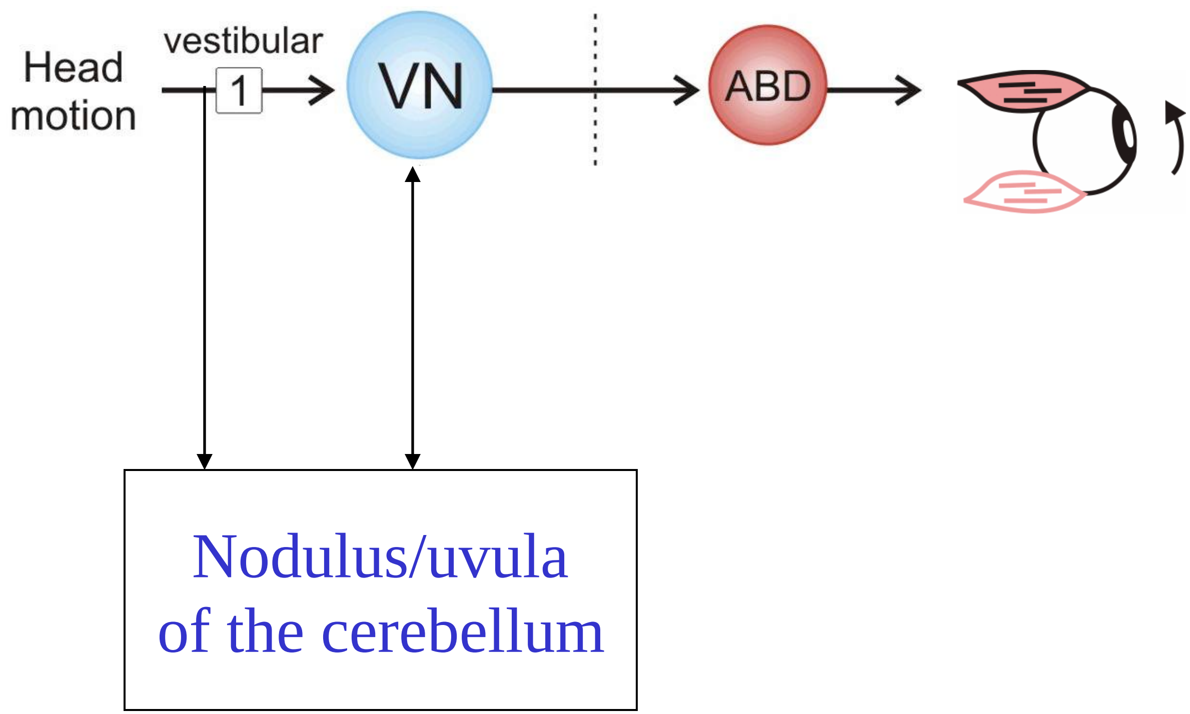
1) The central mechanism responsible for lengthening the afferent time course is referred to as "velocity storage".

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

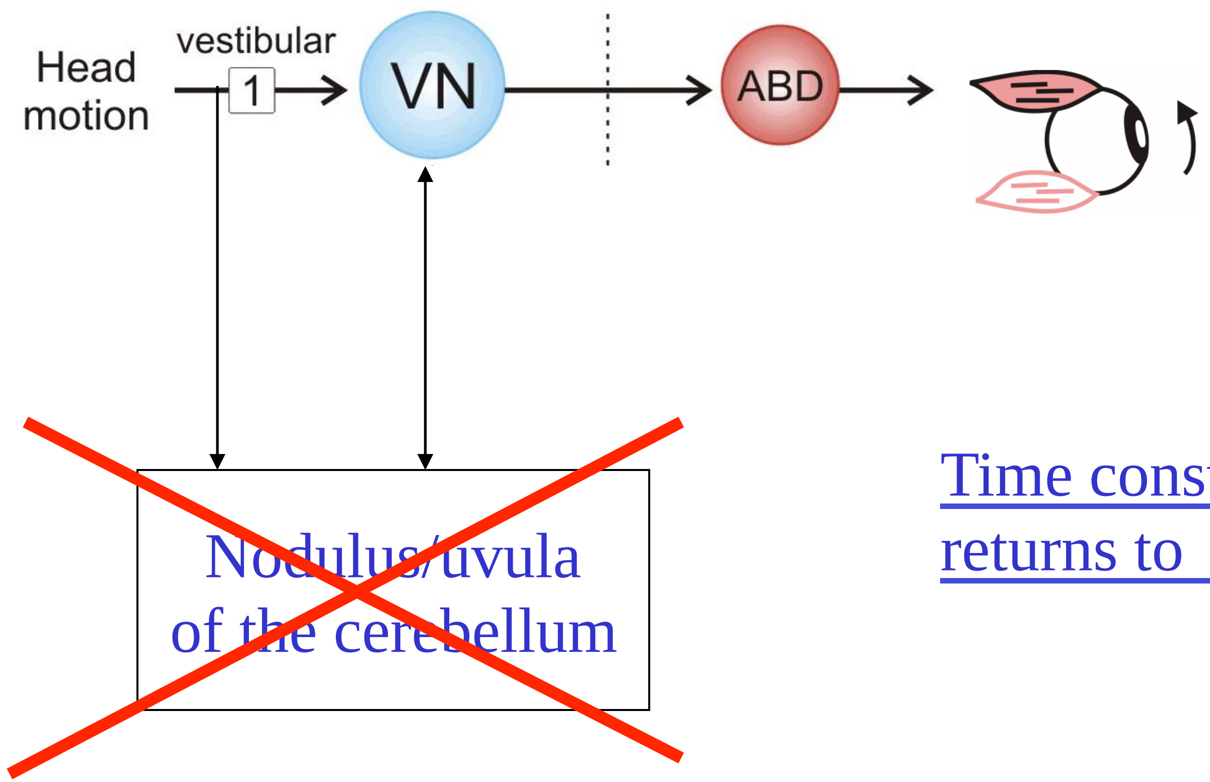
1 ms 1 ms 1 ms 4 ms



Central Vestibular Processing for the VOR

Central Pathways: Vestibular Nuclei and Velocity Storage

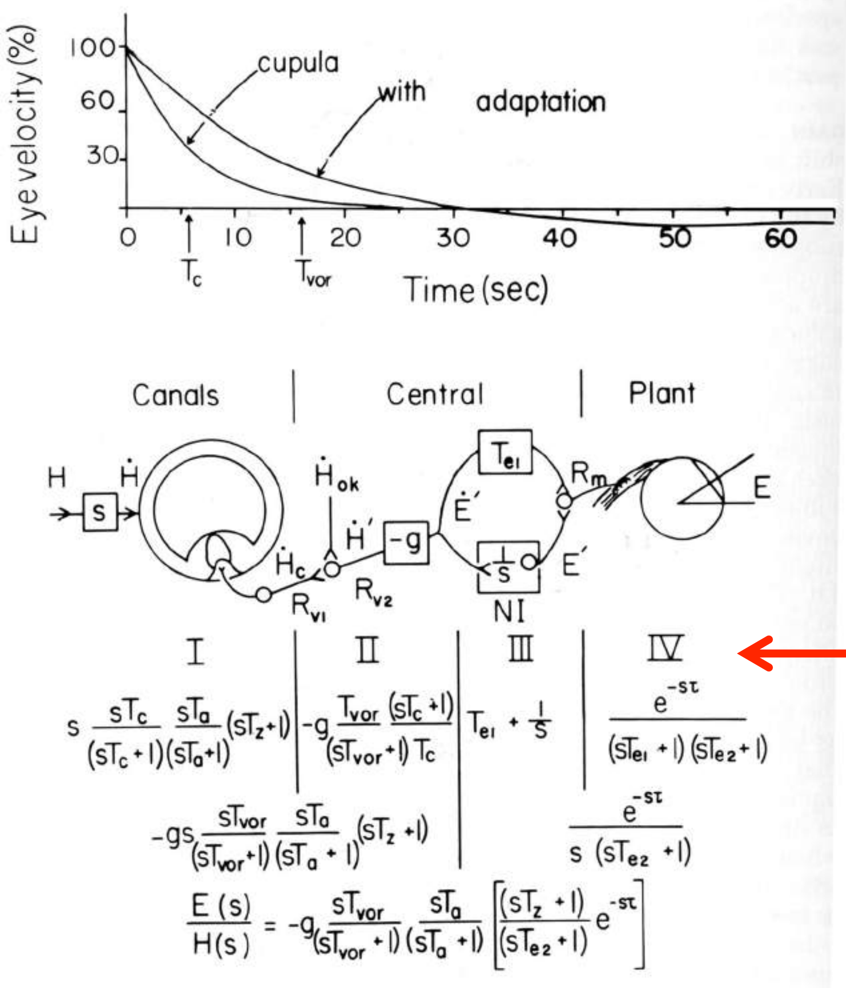
1 ms　1 ms　1 ms　4 ms　= 7 ms delay



Time constant returns to ~5 s.

Central Vestibular Processing for the VOR

Neuronal Pathway: Model of the VOR



IV (plant transfer function)

$Fr = Ro + kE + r\dot{E}$

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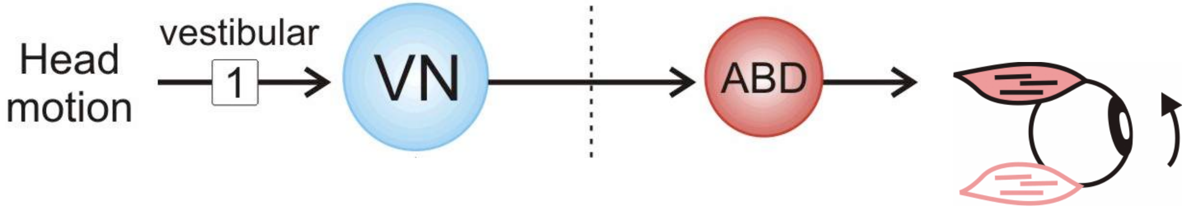
            - System Dynamics and Levels of Analysis
            - 1) Behavior, 2) Neural Circuits, 3) Neurons.

Neuronal Processing for the VOR

Central Pathways: Intrinsic Cellular Properties

1 ms 1 ms 1 ms 4 ms



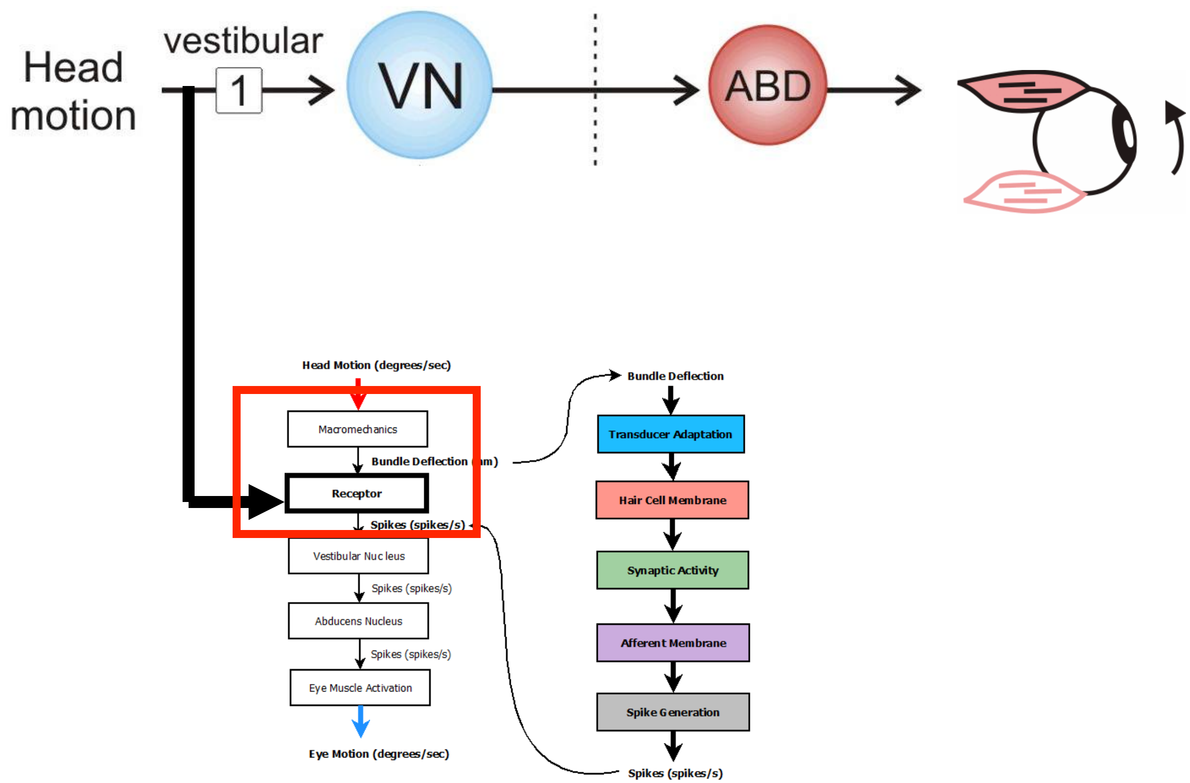
Considerations:

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

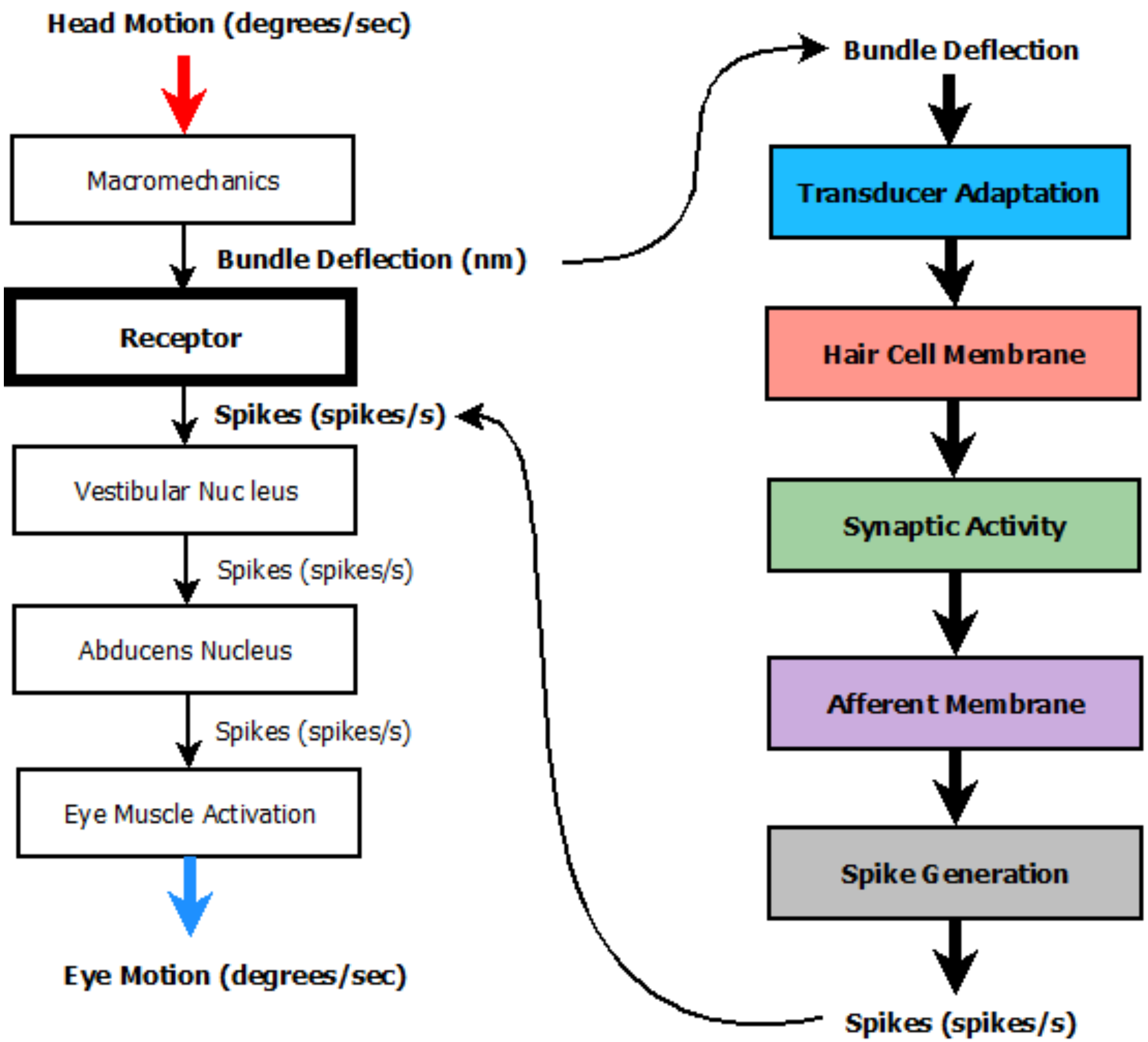
Central Pathways: Intrinsic Processing and Membrane Properties

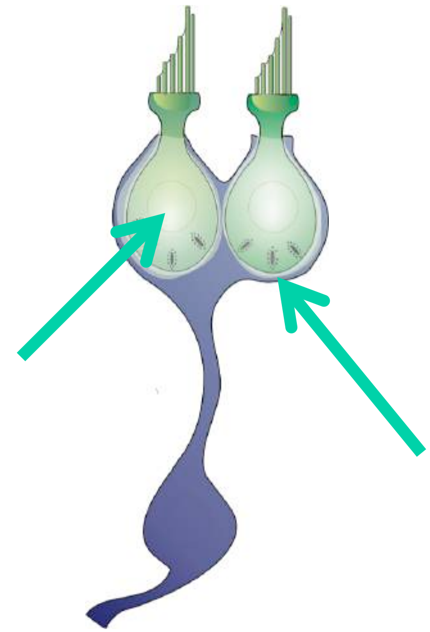
1 ms 1 ms 1 ms 4 ms



Neuronal Processing for the VOR

Central Pathways: Intrinsic Processing and Membrane Properties





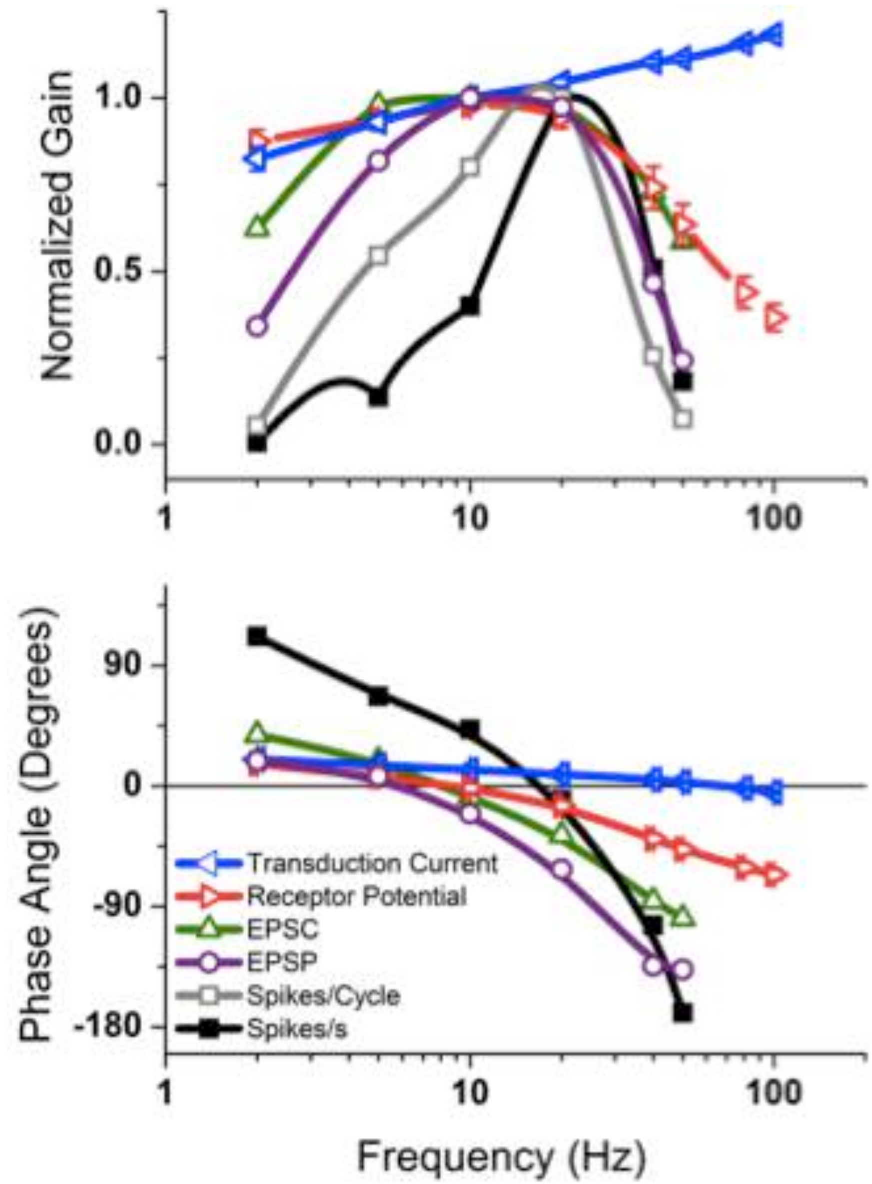
Neuronal Processing for the VOR

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

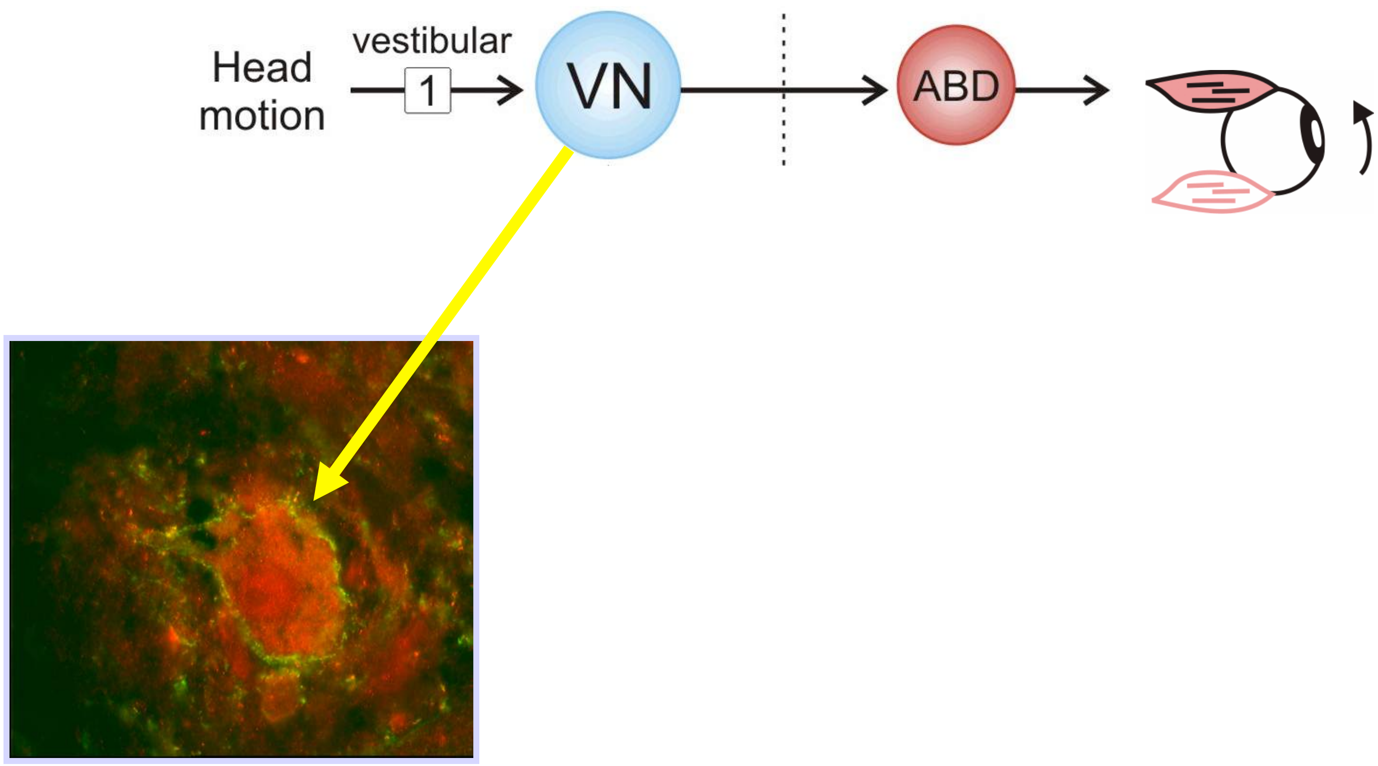


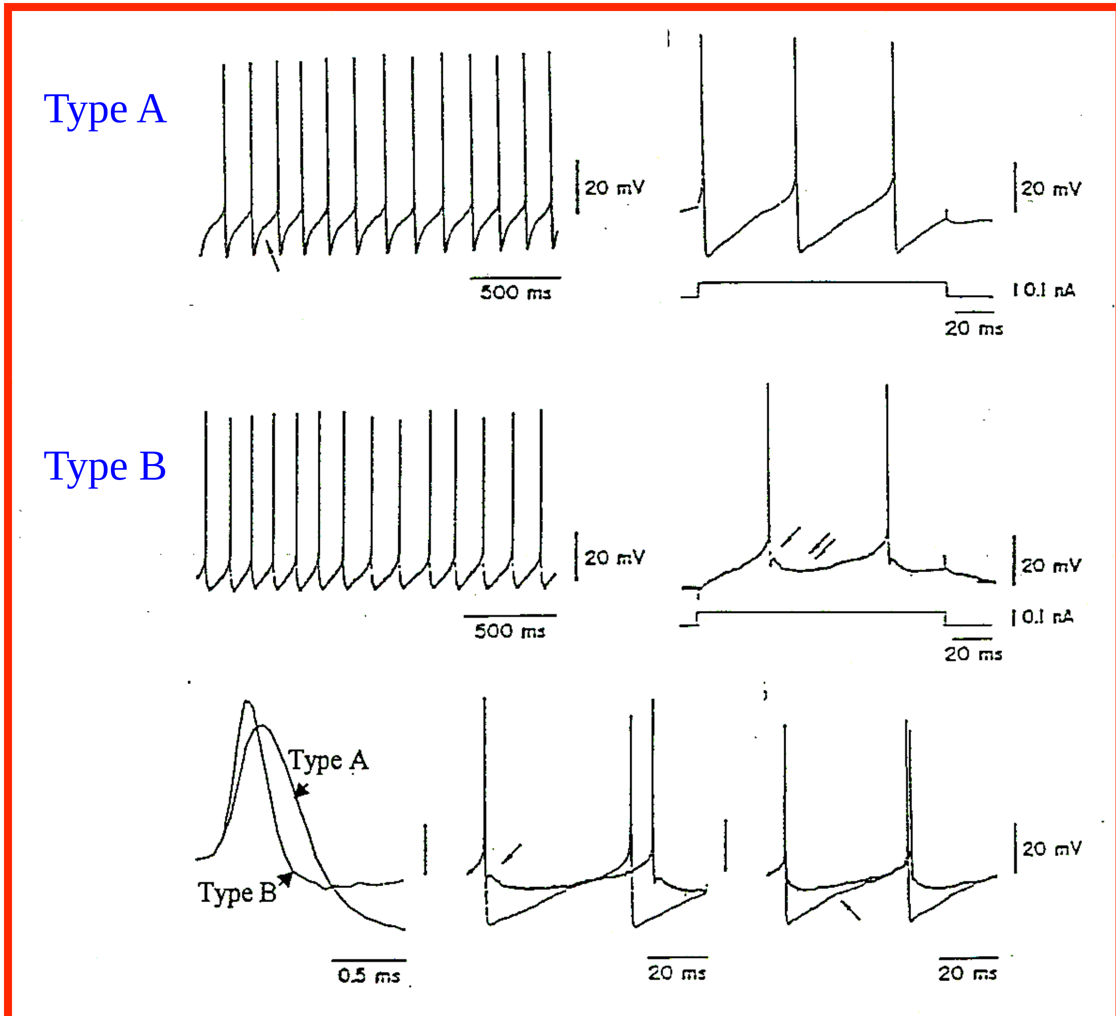
Songer and Eatock, JNS 2013

Central Vestibular Processing for the VOR

Central Pathways: Intrinsic Cellular Properties

1 ms 1 ms 1 ms 4 ms





Serafin et al. 1991a,b

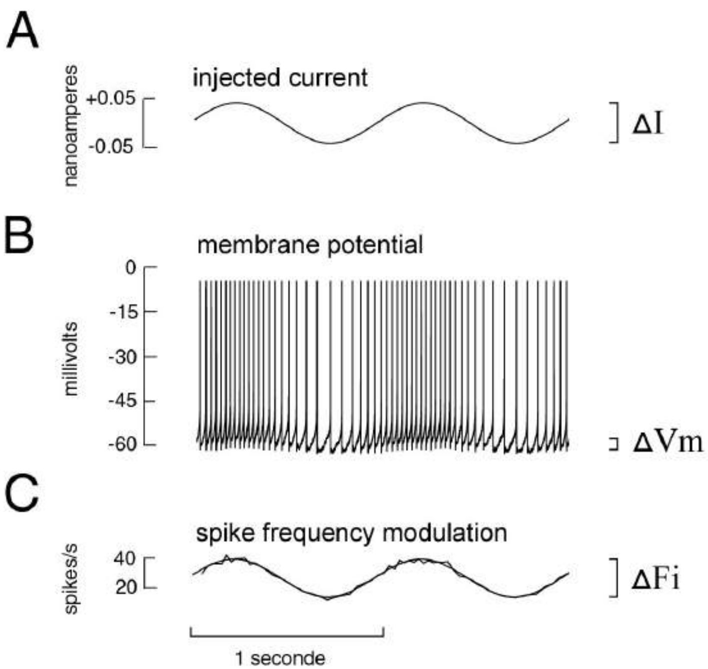
Summarized properties of 170 MVN neurones

Type A neurones 32.3%	• Wide action potential • Large single AHP • Single range firing • A-type rectification • Small high threshold calcium ($HT-Ca^{2+}$) spikes
Type B neurones 47.1%	• Thin action potential • 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%	

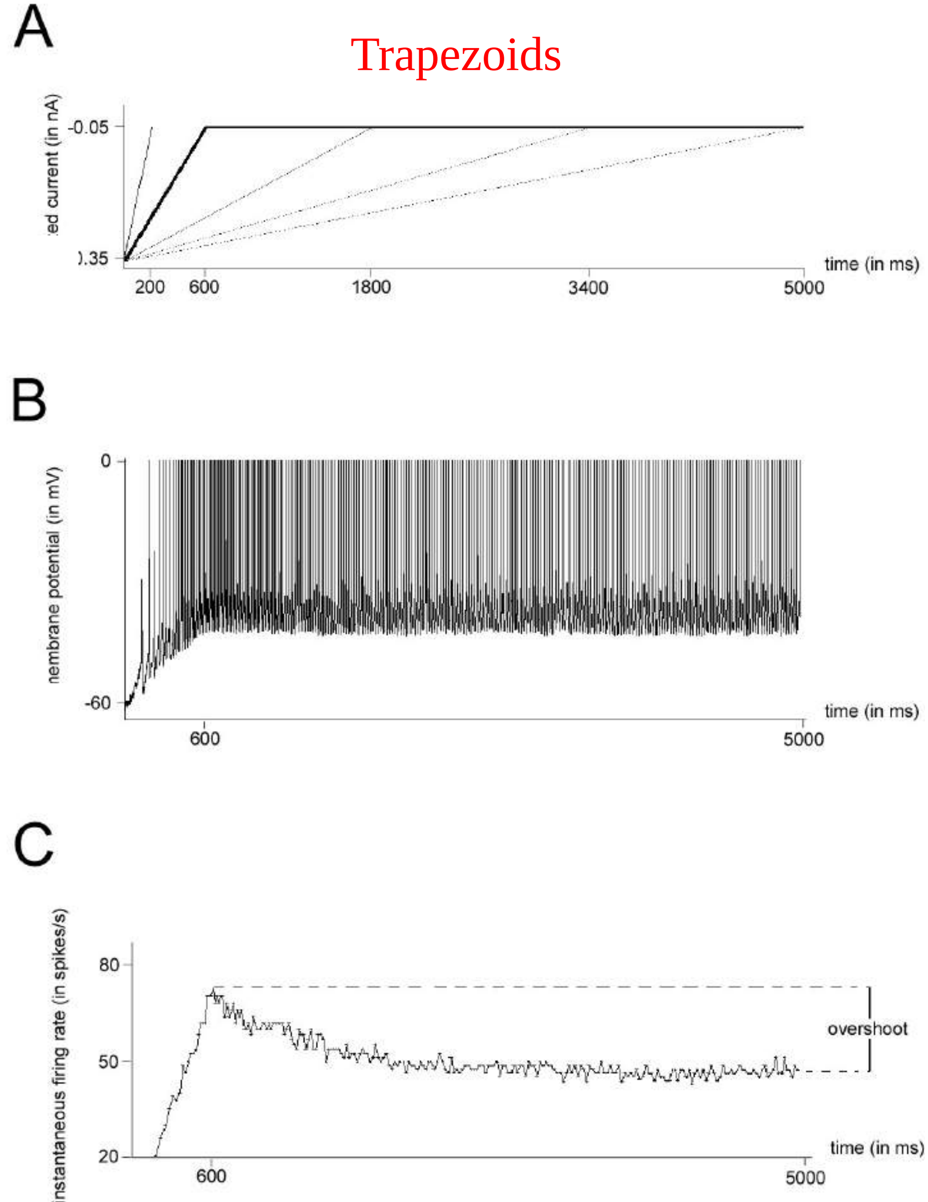
Central Vestibular Processing for the VOR

Intrinsic Cellular Properties: Input-Output Analysis

Sinusoids



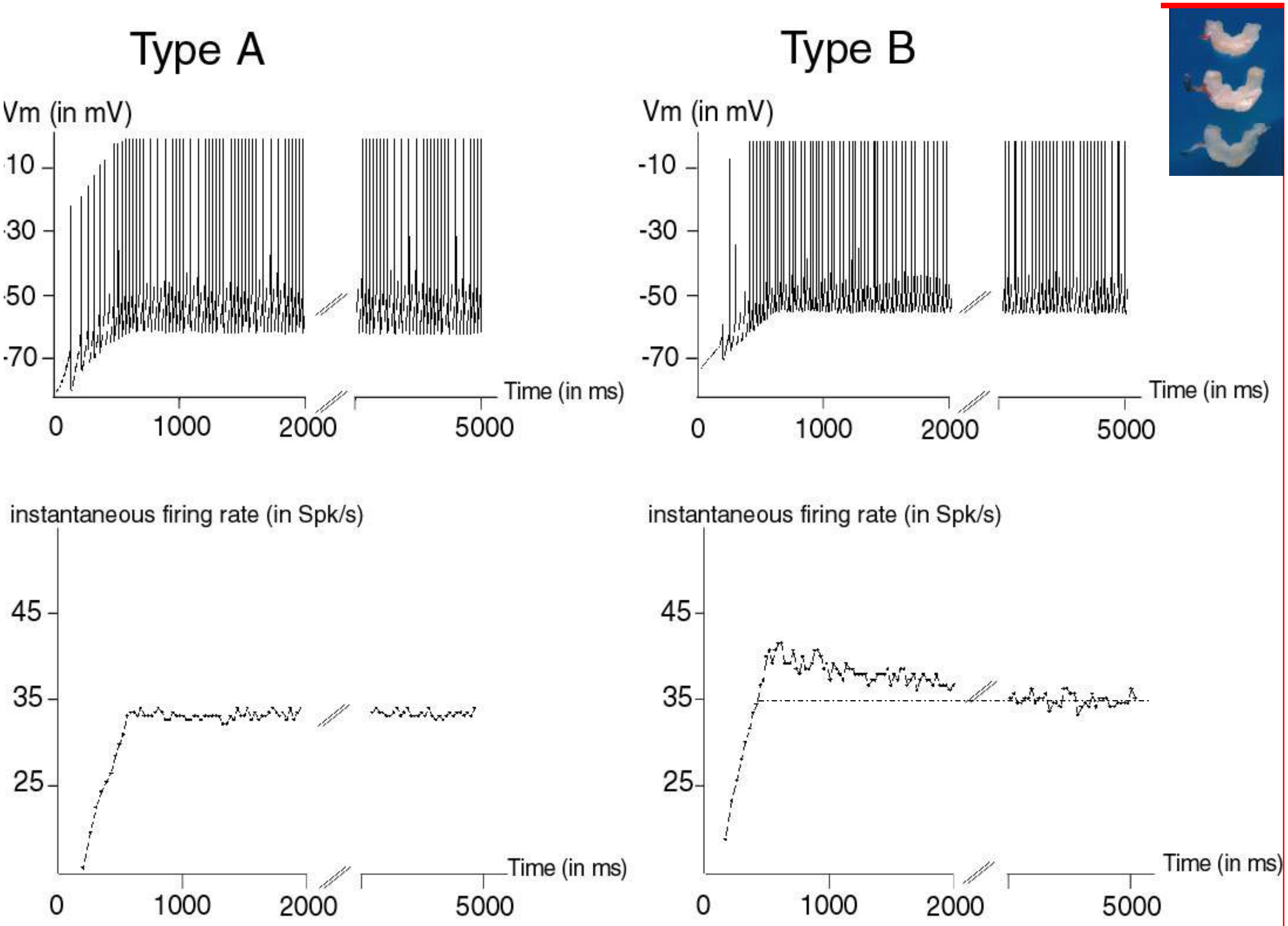
Trapezoids



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

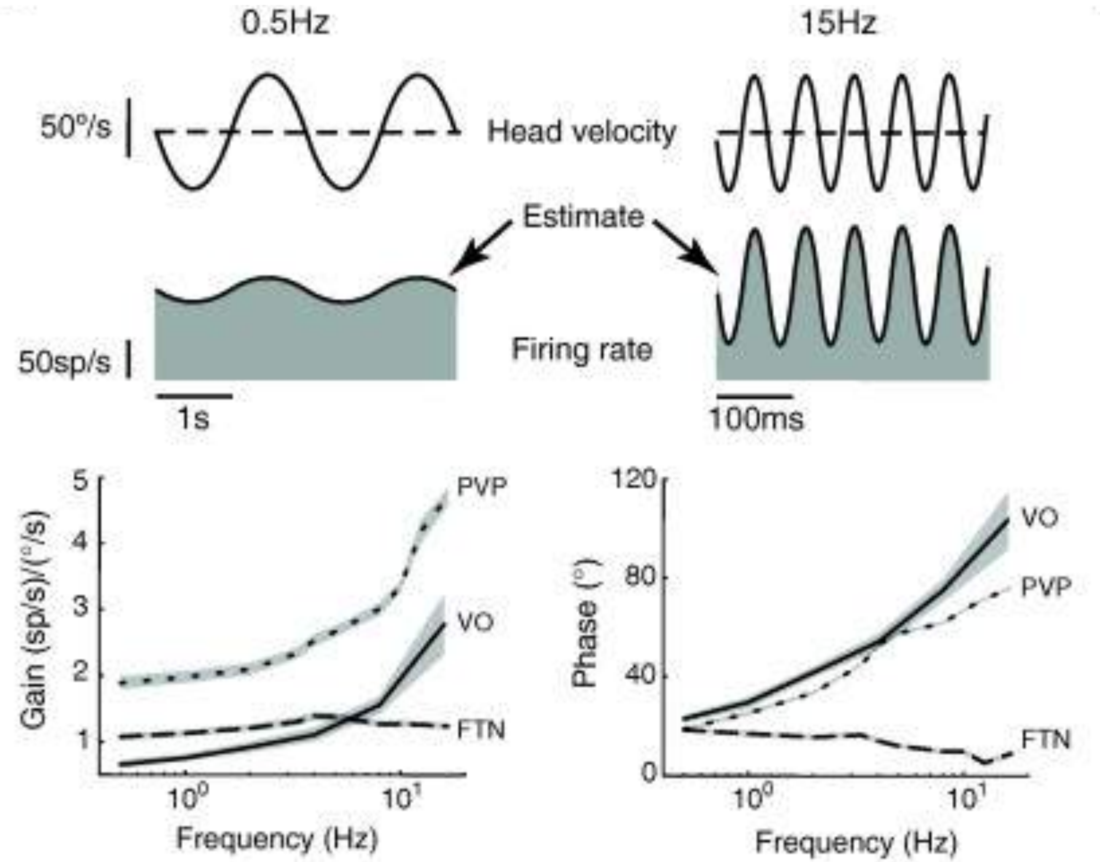
- More linear
- Less sensitive to current
- Less phase lead, regular
- follow up mode

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

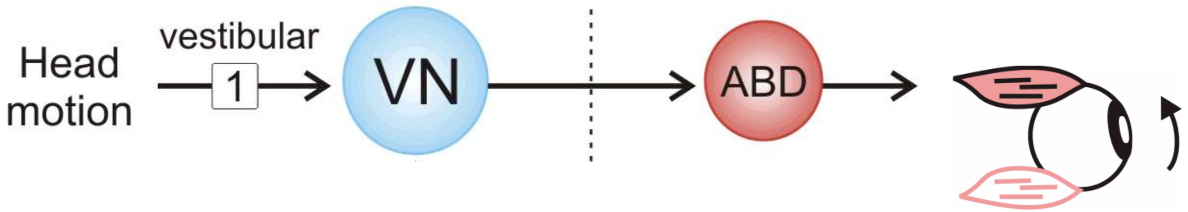
Type A

Cullen, TINs 2012

Central Vestibular Processing for the VOR

Central Pathways: Pathway Delays – Phase compensation

1 ms 1 ms 1 ms 4 ms

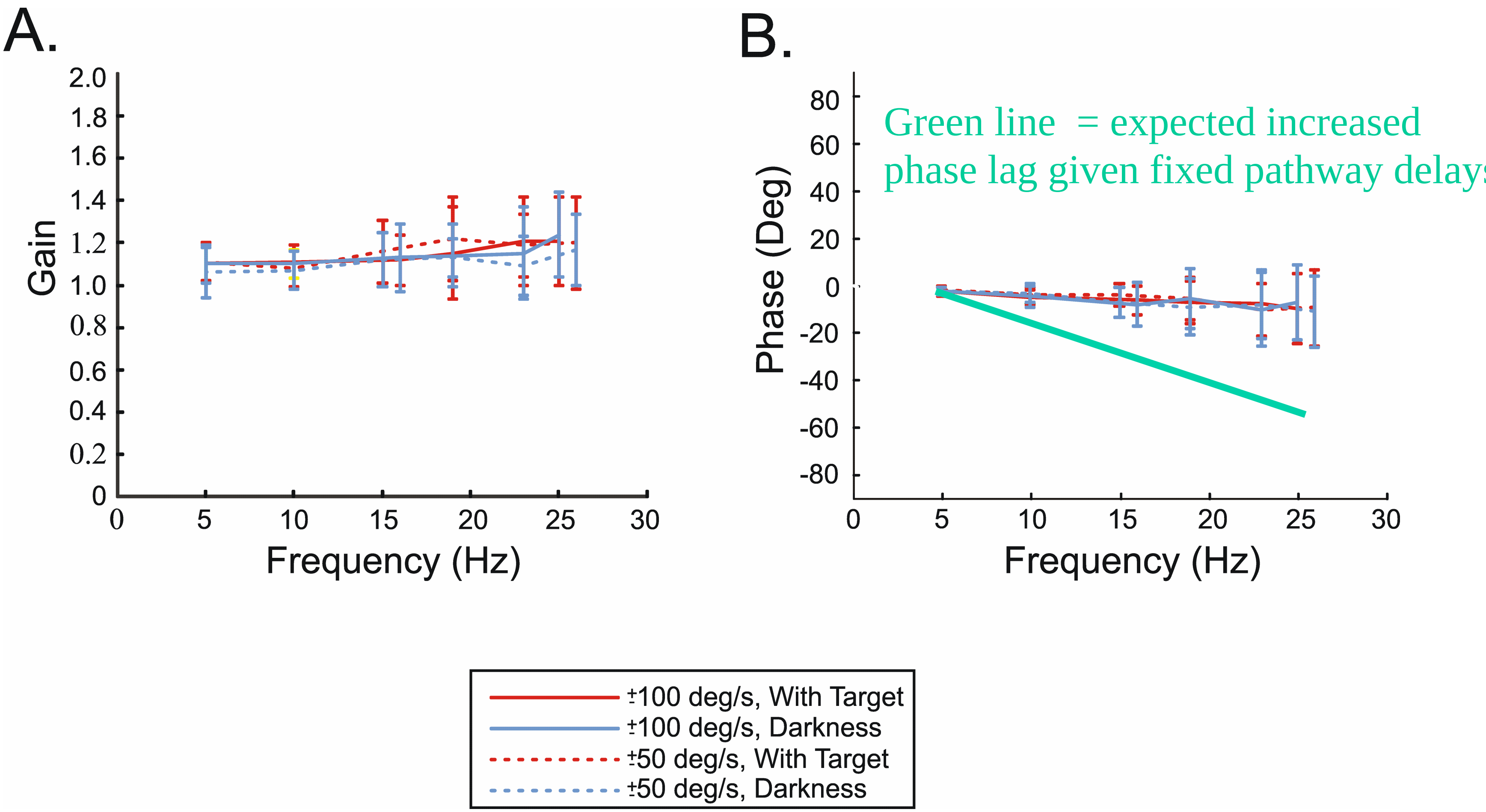


Considerations:

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



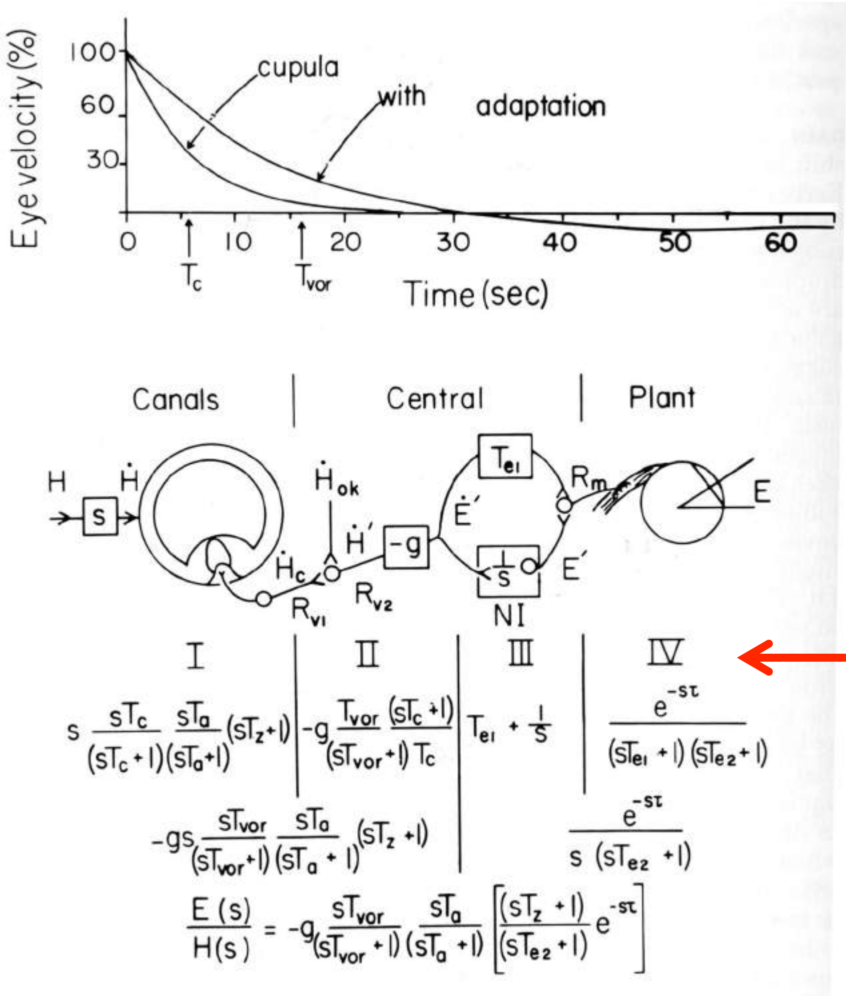
Huterer and Cullen, JNP 2000

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
            - 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)

$Fr = Ro + kE + r\dot{E}$