Internal models and neural integration in the control of eye movements

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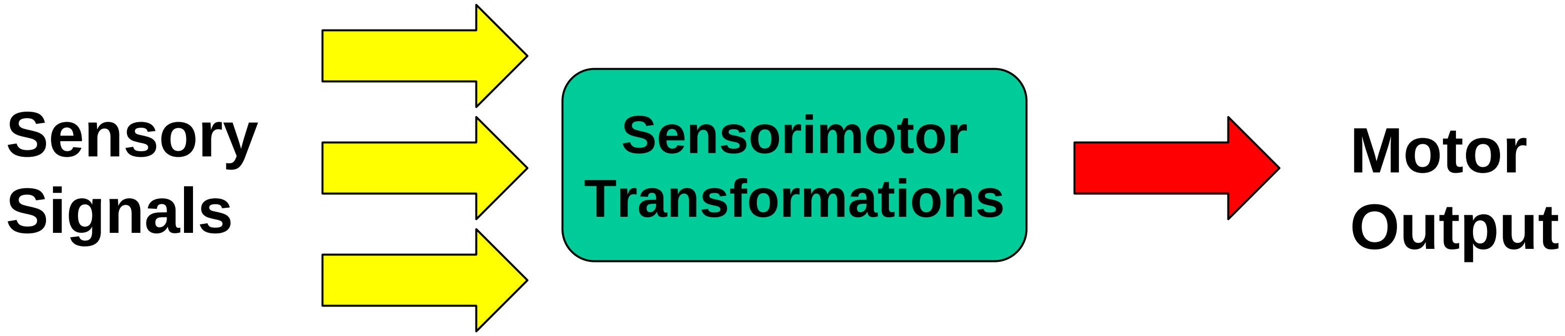
Overview

- Overview of different types of eye movements
- Introduction to the theory of control systems
- Contribution of computational approaches to our understanding of the sensorimotor transformations that take place in the oculomotor system

Why study the oculomotor system?

- Eye movements play an essential functional role in vision
- Excellent model system for investigating how sensory signals are transformed into motor commands



Sensory Signals

Sensorimotor Transformations

Motor Output

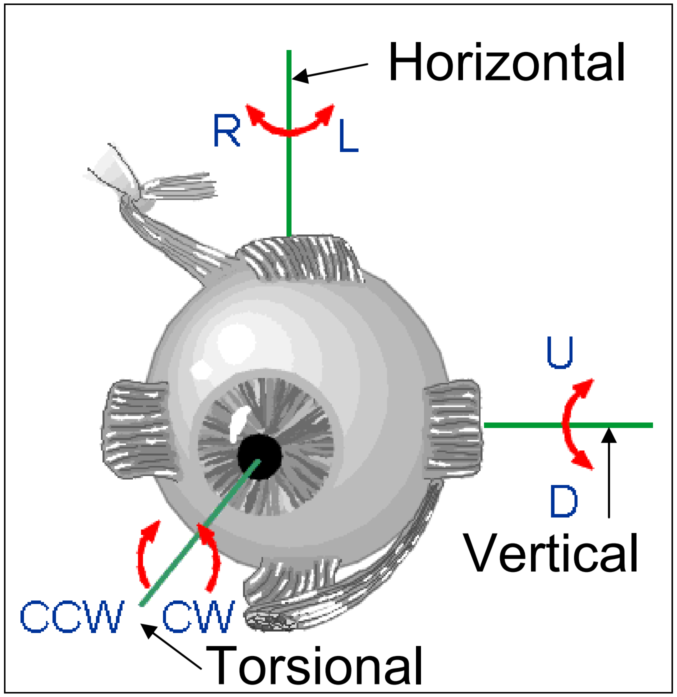
Motor Output: Eye movements
Sensory Signals: Visual and Vestibular systems

<u>Advantages of studying this system include</u>:

- The eye is a relatively simple single-joint system and does not carry a load → computations easier to identify and understand than for limb control
- Neurons involved in the transformations are easily accessible for neural recording

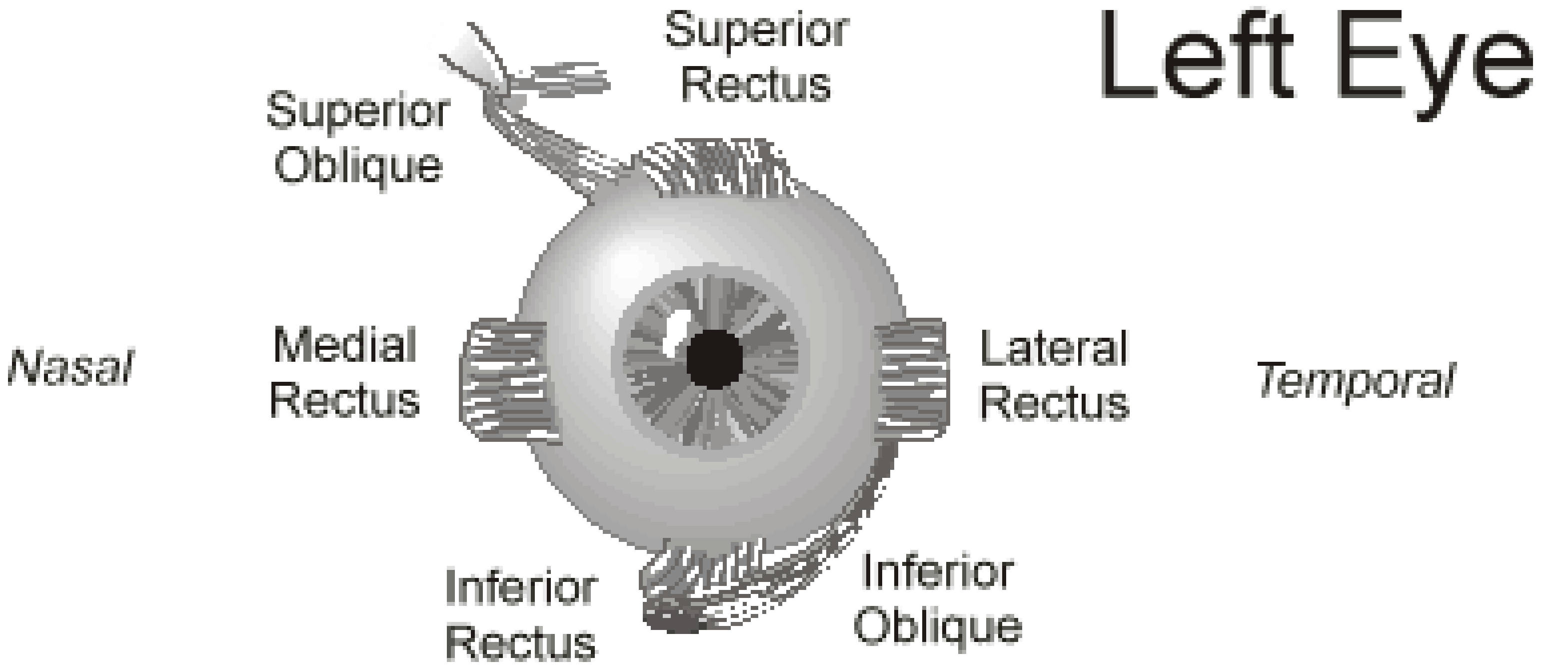
Why do we move the eyes?

- To orient the fovea to an object we want to look at (i.e., redirection of gaze or target tracking)
- To maintain visual acuity by stabilizing gaze during head movement

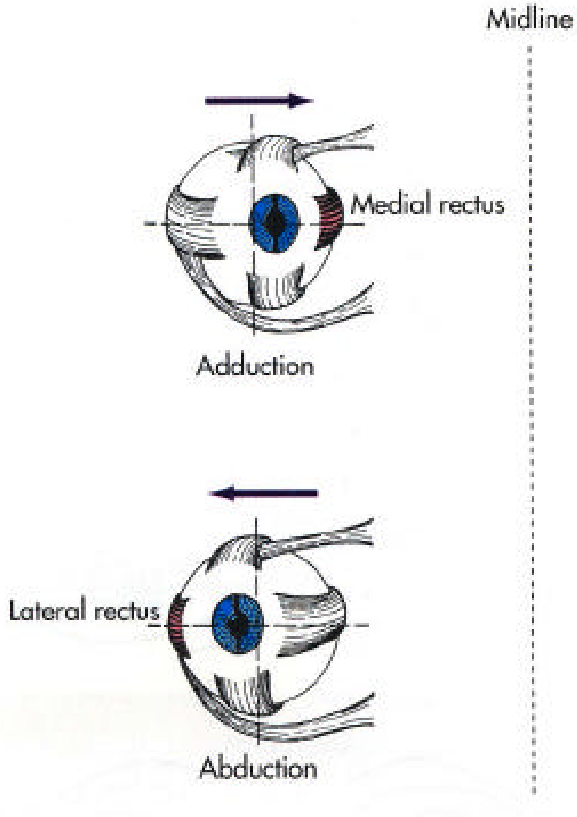


- Eye rotates in 3D
  - Horizontal
  - Vertical
  - Torsional

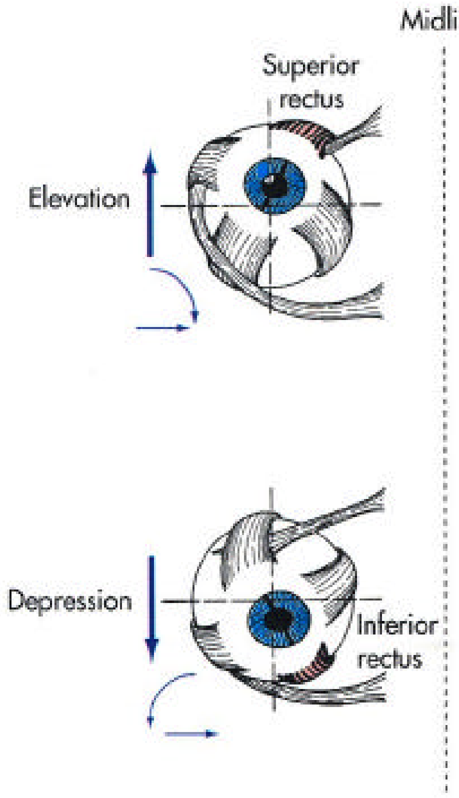
The eyes are rotated by 6 extraocular muscles



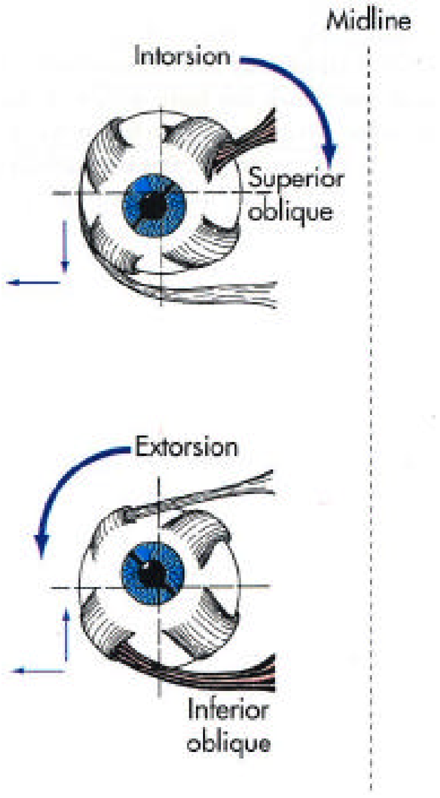
Actions of the extraocular muscles



Horizontal eye movements

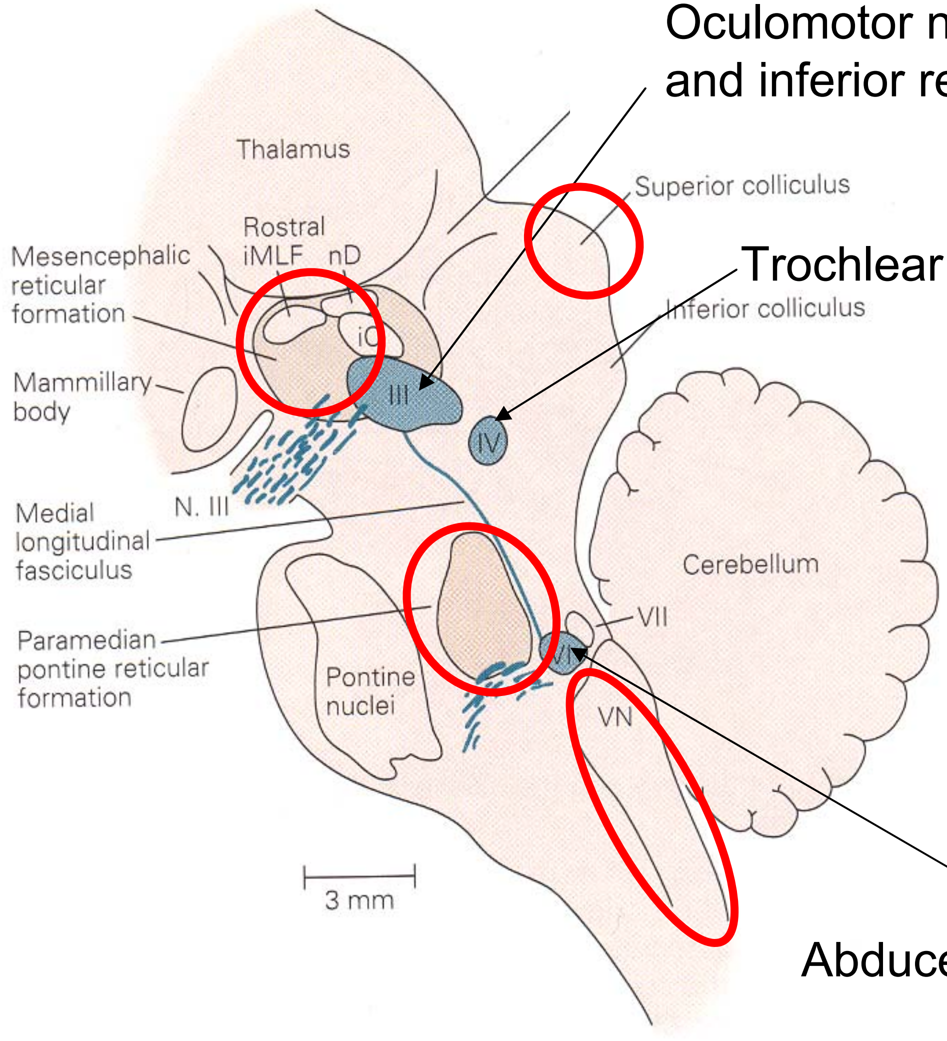


Vertical/torsional eye movements



Torsional/vertical eye movements

Extraocular motor nuclei



Oculomotor nucleus (III): medial, superior and inferior rectii and inferior oblique

Trochlear nucleus (IV): superior oblique

Abducens nucleus (VI): lateral rectus

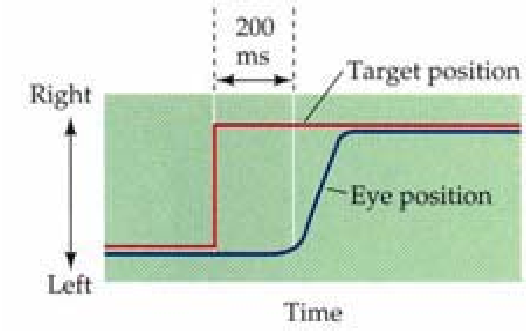
Different types of eye movements

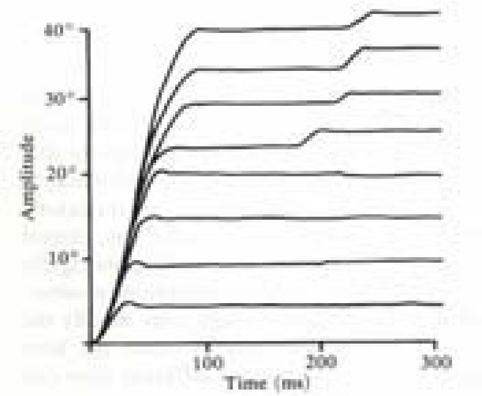
Orienting Eye Movements

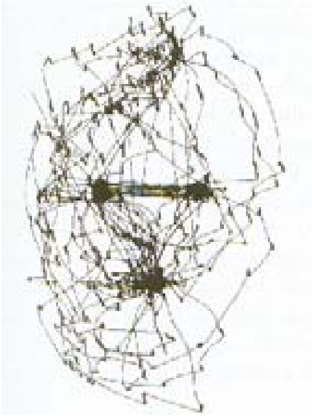
- Saccades
  - Goal: Redirect gaze to a target of interest
  - Input: Position error relative to fovea
- Smooth Pursuit
  - Goal: Foveal tracking of small targets
  - Input: Velocity error relative to fovea (visual motion)
- Vergence
  - Goal: Maintain binocular fusion
  - Input: Retinal disparity

Saccades

- Rapid movements of the eyes that abruptly reorient gaze
- Amplitude ranges from miniature eye movements (0.1°) to movements of ≈ 45° in amplitude
- Velocities as high as 900 °/s

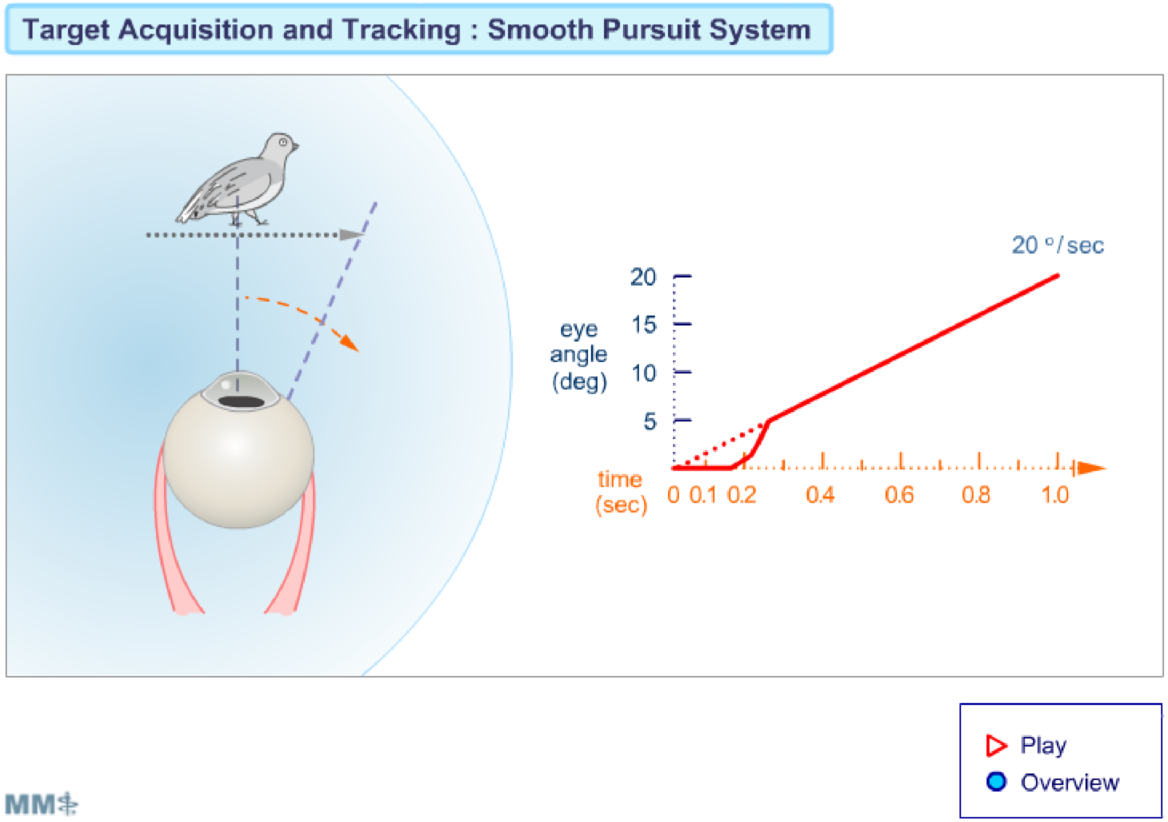






Smooth Pursuit

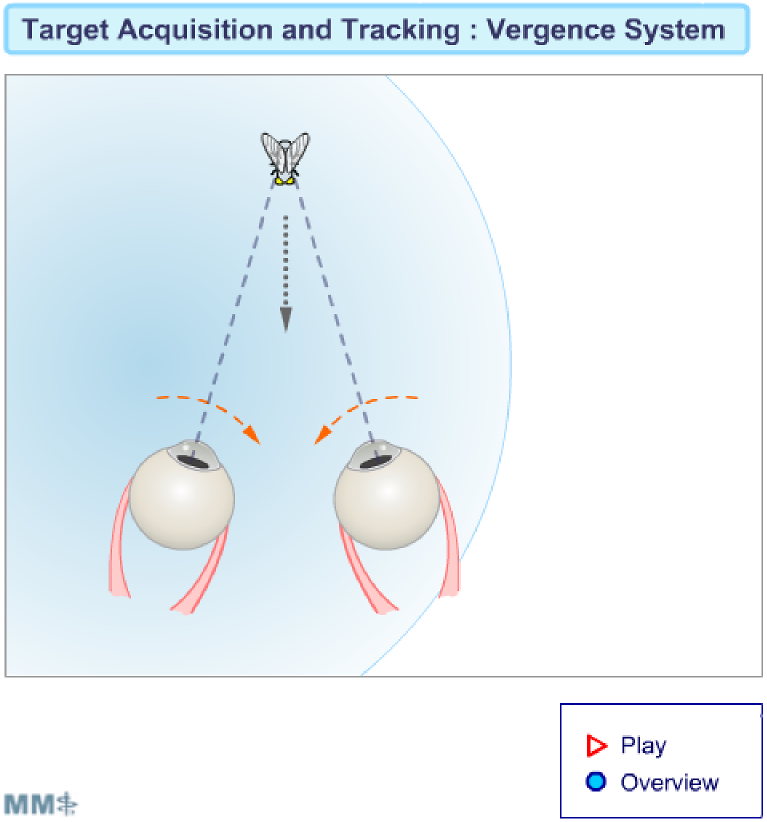
- Smooth pursuit movements are slow movements of the two eyes designed to track a moving visual stimulus
- If a stimulus is moving too fast these smooth movements are interspersed with fast saccadic movements (“catch-up” saccades)



Target Acquisition and Tracking : Smooth Pursuit System

Vergence

- Vergence eye movements align the fovea with targets located at a different distances (near or far from the observer)
- These are *disconjugate* movements (they move the eyes in opposite directions)



Different types of eye movements

Orienting Eye Movements

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- Vergence
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    - Input: Retinal disparity

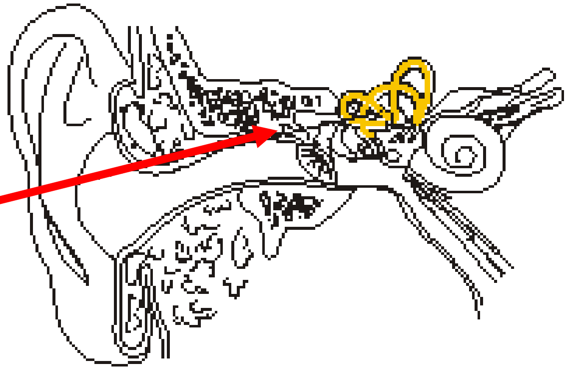
Stabilizing Eye Movements

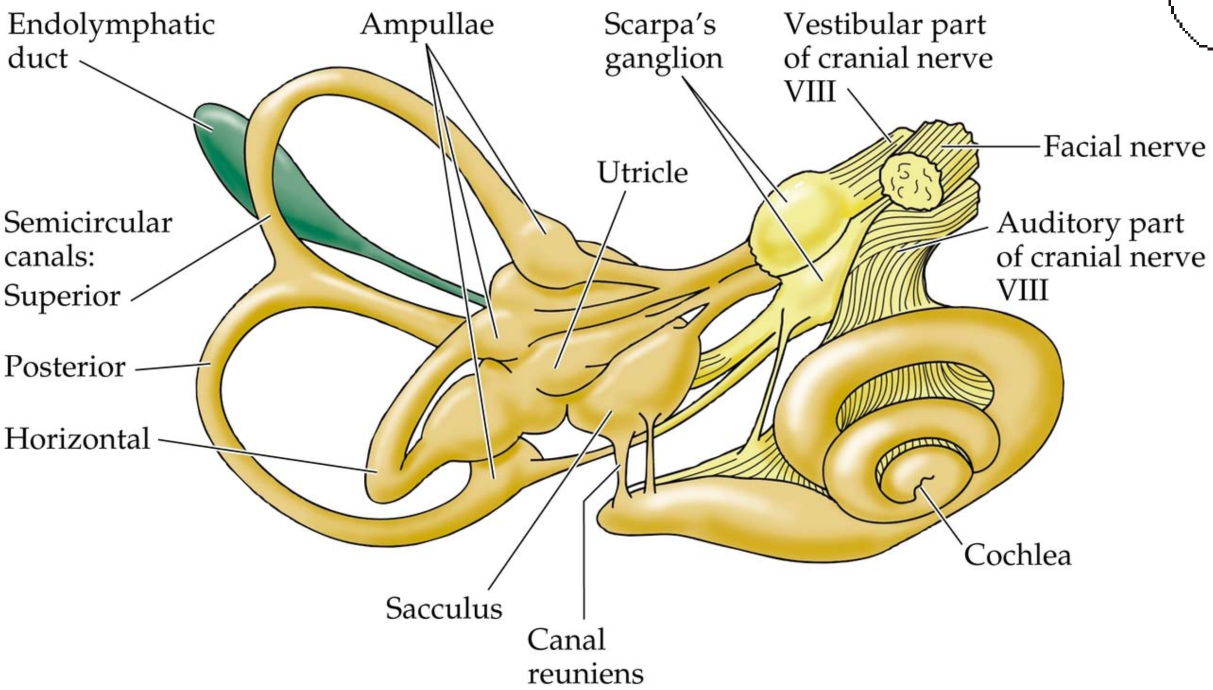
- Vestibulo-ocular Reflex (VOR)
    - Goal: Stabilize gaze during head movement
    - Input: Head motion
- Optokinetic Reflex (OKN)
    - Goal: Stabilize gaze during head movement
    - Input: Optic flow (visual motion across a large field)

Vestibular sensors

Semicircular canals → angular velocity

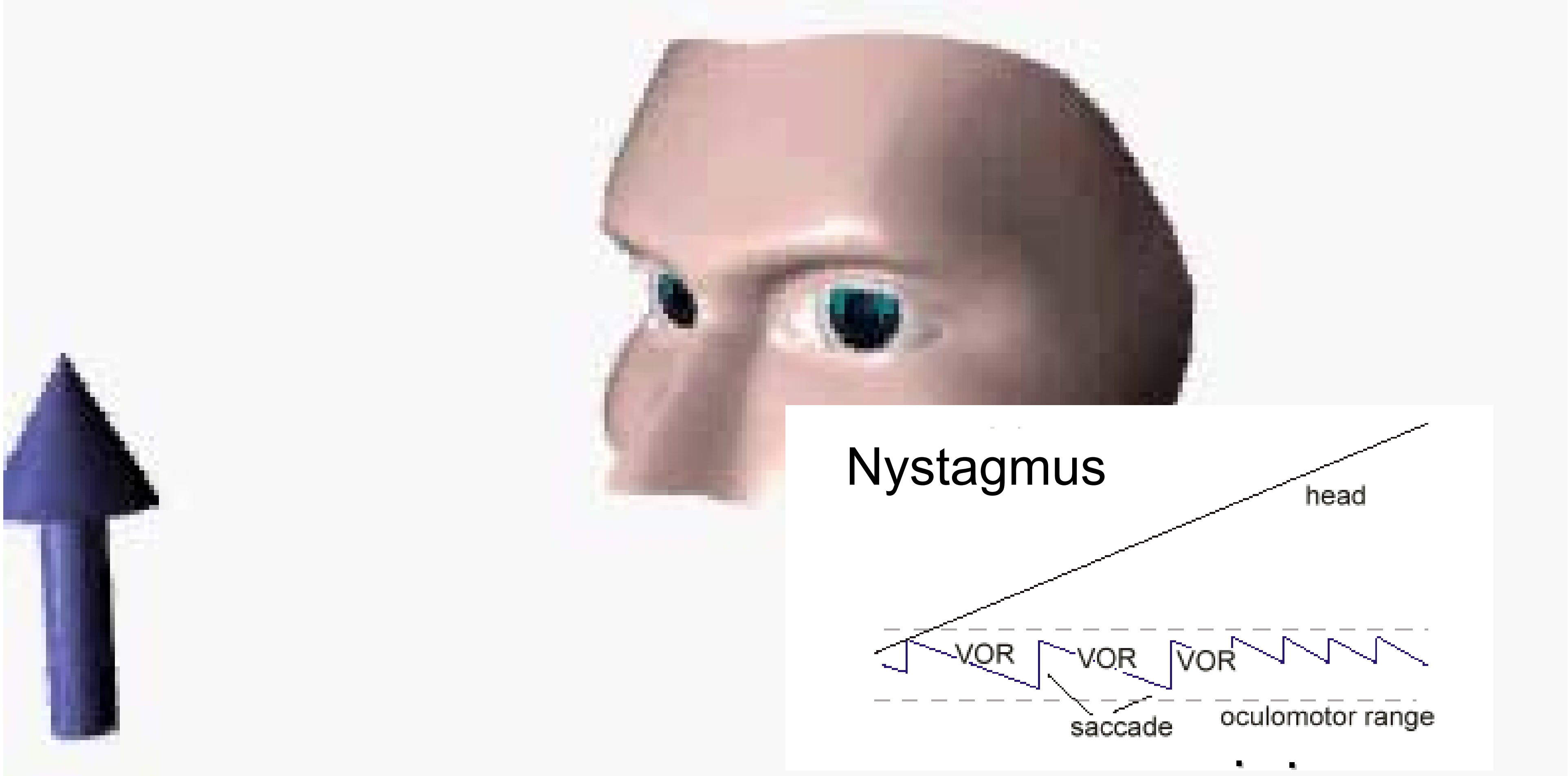
Otolith organs → linear acceleration





Vestibulo-Ocular Reflex (VOR)

Vestibulo-Ocular Reflex (VOR)



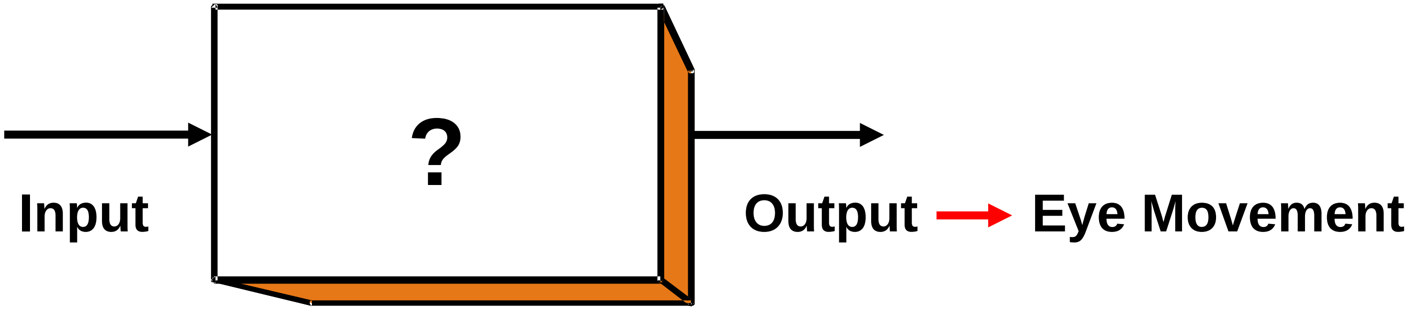
VOR Gain = eye velocity/head velocity ($\dot{E}/\dot{H}$)

Optokinetic reflex

- The optokinetic reflex is a reflexive response to a full – field optic flow stimulus
- This reflex aids the vestibular system in stabilizing gaze particularly at low frequencies

How have computational approaches aided in studying eye movements?

- Signal processing to quantify neural and motor responses
- Control systems approach to understanding what sensorimotor transformations must be taking place

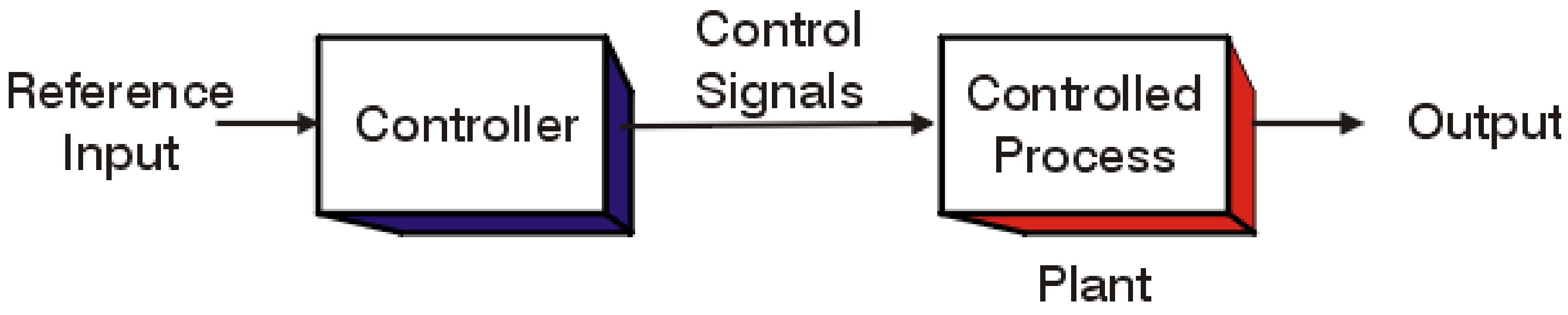


What is a control system?

Inputs

Control System

Outputs



Reference Input

Controller

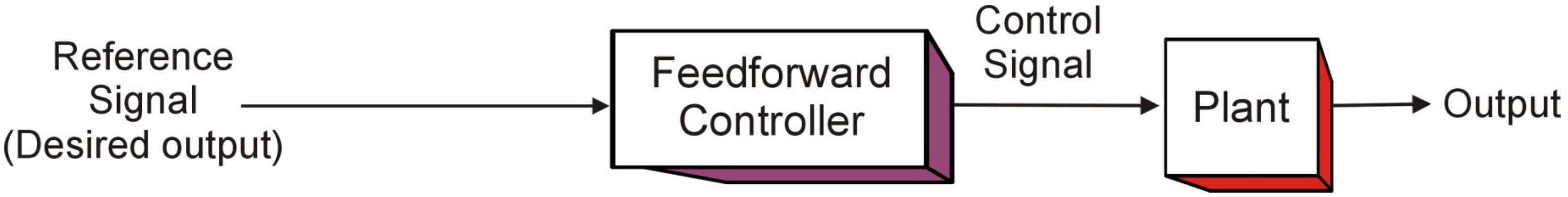
Control Signals

Controlled Process

Plant

Output

Feedforward control



Reference Signal (Desired output)

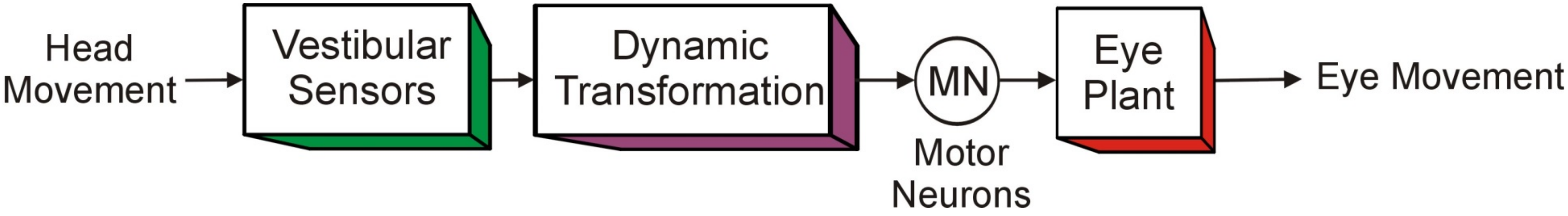
Feedforward Controller

Control Signal

Plant

Output

e.g., Vestibulo-ocular reflex (VOR)



Head Movement

Vestibular Sensors

Dynamic Transformation

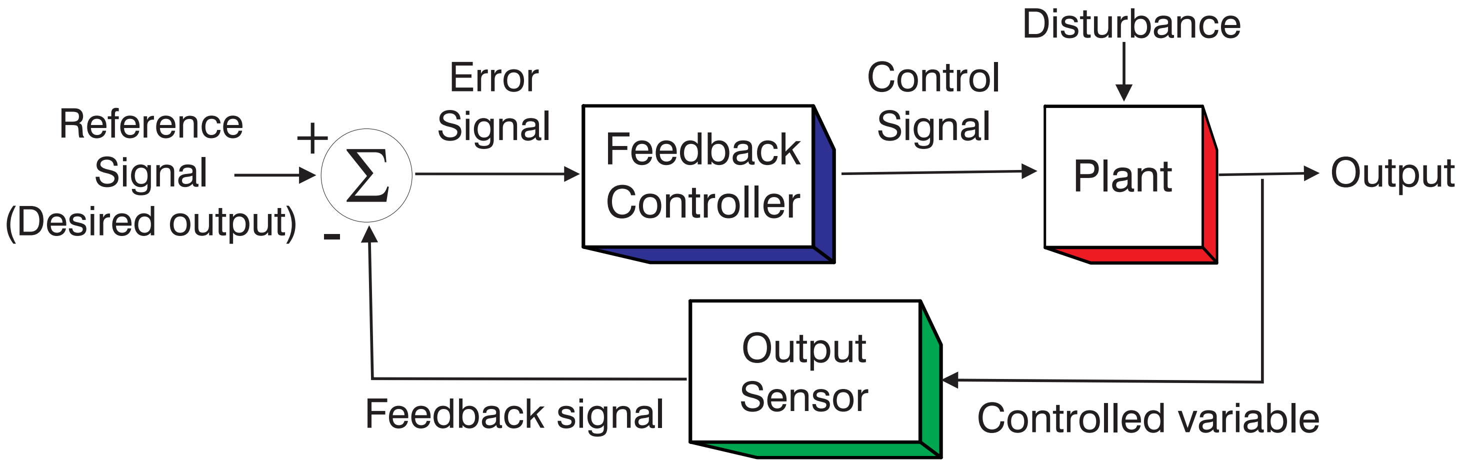
MN

Motor Neurons

Eye Plant

Eye Movement

Feedback control



Disturbance

Error Signal

Control Signal

Reference Signal (Desired output)

+

Σ

-

Feedback Controller

Plant

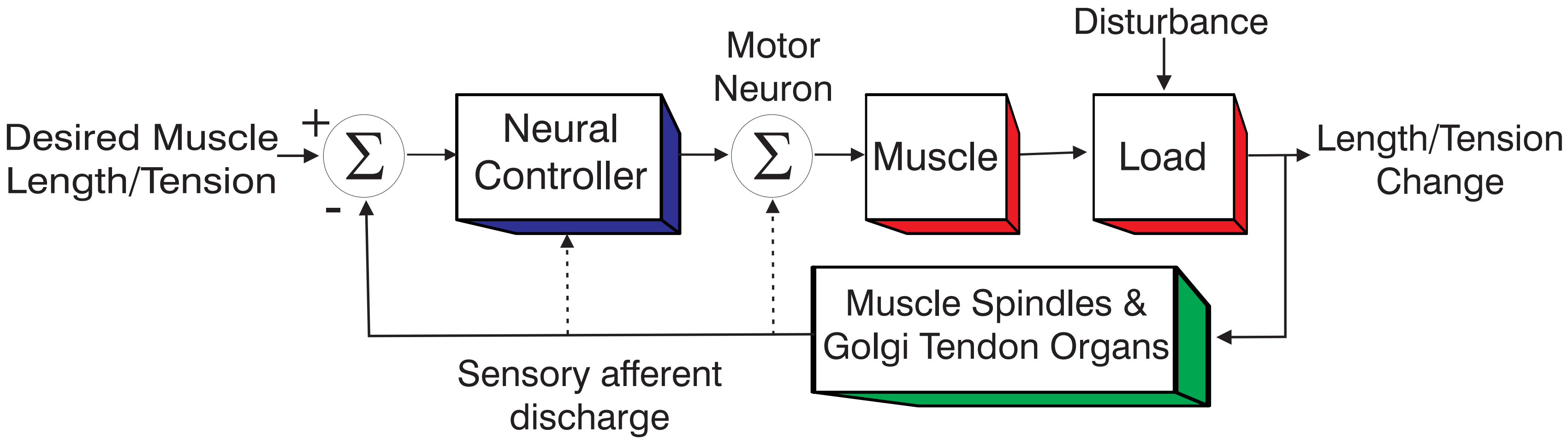
Output

Output Sensor

Feedback signal

Controlled variable

e.g., Muscle Control



Disturbance

Motor Neuron

Desired Muscle Length/Tension

+

Σ

-

Neural Controller

Σ

Muscle

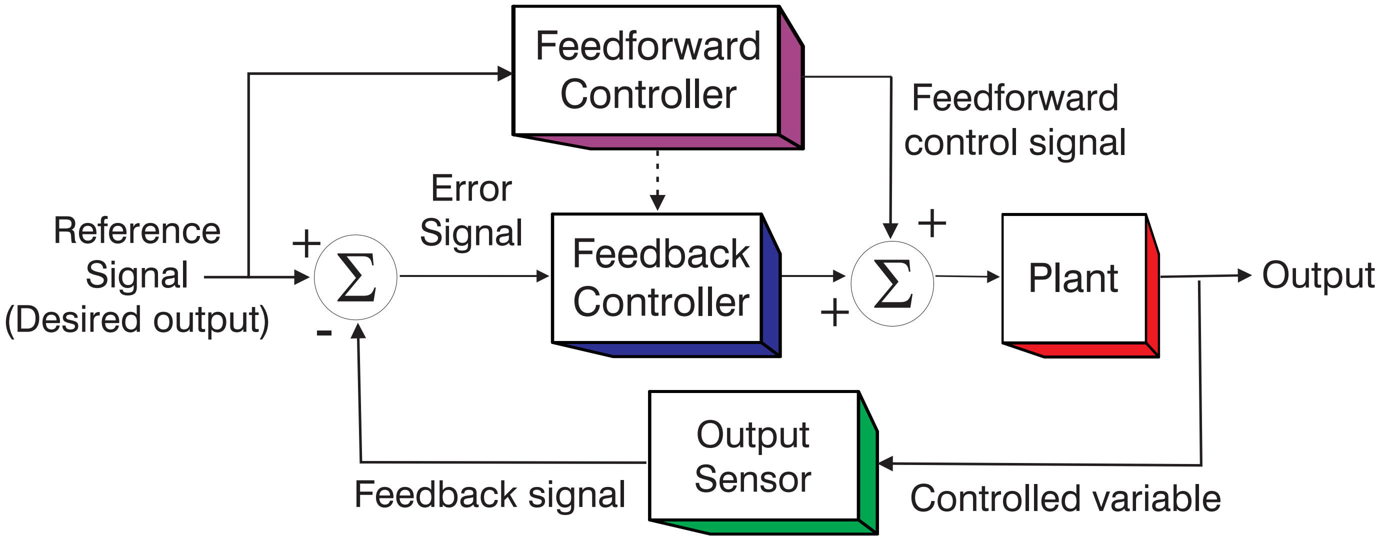
Load

Length/Tension Change

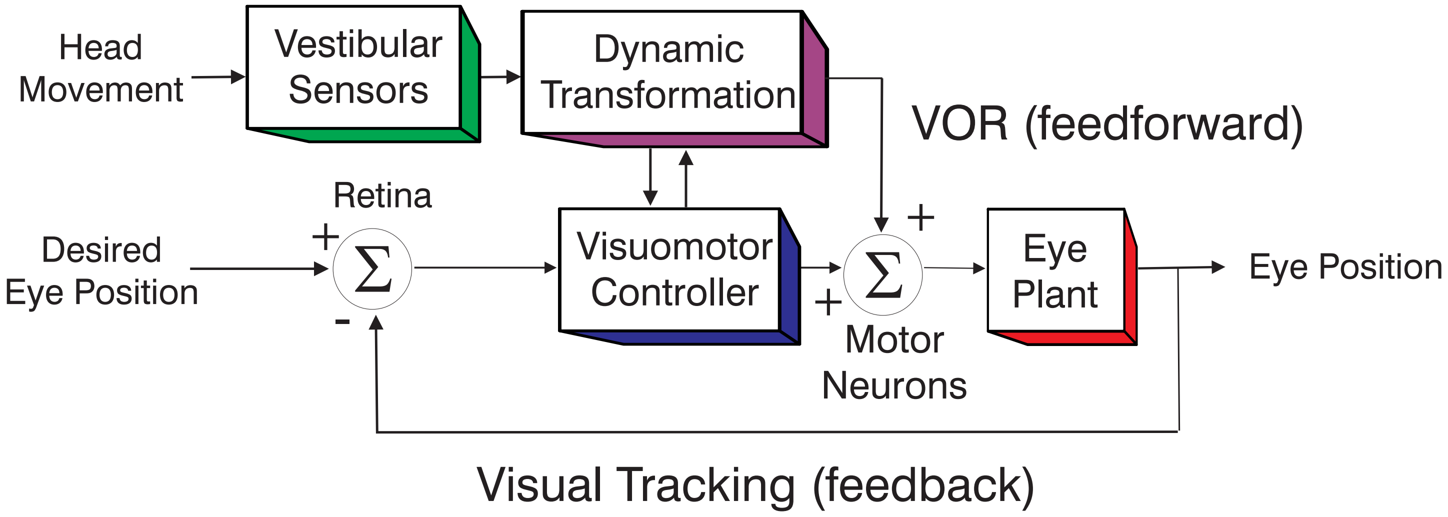
Muscle Spindles & Golgi Tendon Organs

Sensory afferent discharge

Feedforward / feedback control



e.g.,Visual/Vestibular Reflexes



Description of the dynamic characteristics of the control system

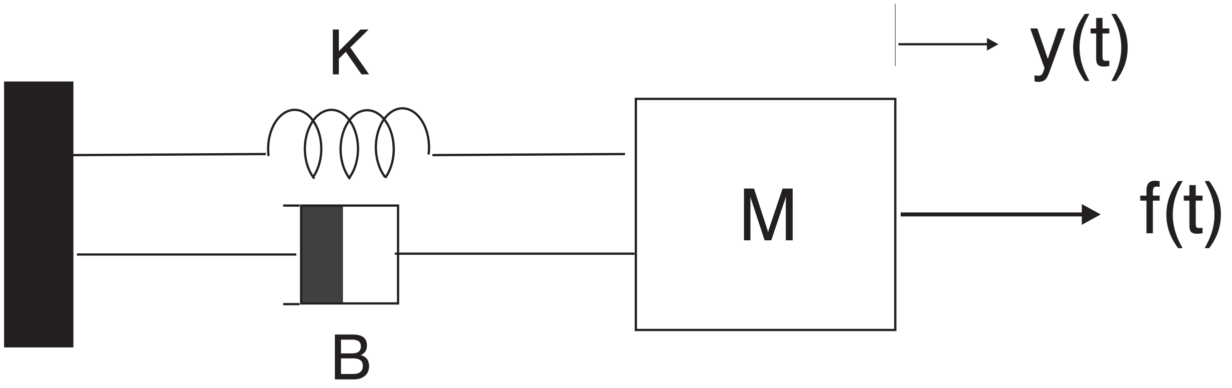
Time domain (state-space) description:

- System described as a set of differential equations in the time domain

Frequency domain description:

- Central concept is the response of the system in terms of magnitude and phase to sinusoidal inputs of different frequencies
- Linear system described using Laplace transforms (closely related to Fourier transforms)

A simple physical model



$$\Sigma F = Ma$$

$$f(t) - Ky(t) - B\frac{dy}{dt} = M\frac{d^2y(t)}{dt^2}$$

applied force
(the input)

mass position
(the output)

To solve:

- solution to homogeneous equation
  (i.e., for zero input, f(t)=0)

$$M\frac{d^2y(t)}{dt^2} + B\frac{dy}{dt} + Ky(t) = 0$$

- particular solution for input f(t)

State-space description

$$\frac{d^2y(t)}{dt^2} = -\frac{K}{M}y(t) - \frac{B}{M}\frac{dy}{dt} + \frac{1}{M}f(t)$$

Simplify by writing as a system of first order differential equations:

$$x_1(t) = y(t) \qquad x_2(t) = \frac{dy}{dt} = \dot{y}(t)$$

$$\dot{x}_1(t) = x_2(t)$$

$$\dot{x}_2(t) = -\frac{K}{M}x_1(t) - \frac{B}{M}x_2(t) + \frac{1}{M}f(t)$$

$$\begin{bmatrix} \dot{x}_1(t) \\ \dot{x}_2(t) \end{bmatrix} = \begin{bmatrix} 0 & 1 \\ -K/M & -B/M \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix} + \begin{bmatrix} 0 \\ 1/M \end{bmatrix} f(t)$$

$$\dot{\mathbf{x}}(\mathrm{t}) = \mathbf{A}\mathbf{x}(\mathrm{t}) + \mathbf{B}\mathrm{f}(\mathrm{t})$$

Solution:

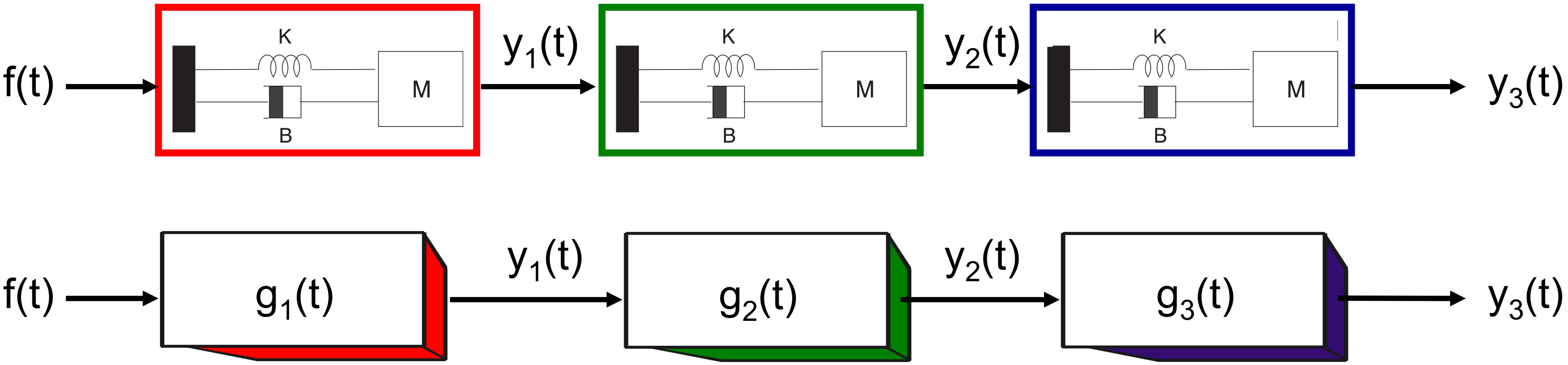
$$\mathbf{x}(\mathrm{t}) = \phi(\mathrm{t})\mathbf{x}(0) + \int_0^{\mathrm{t}} \phi(\mathrm{t} - \tau)\mathbf{B}\mathrm{f}(\tau)d\tau$$

Solution to homogeneous state equation

Convolution integral to obtain solution for particular input f(t)

$$(\phi(\mathrm{t}) * \mathbf{B}\mathrm{f}(\mathrm{t}))$$

Cascade of several dynamic systems



$g(t)$: impulse response function

- describes response of dynamic system to a unit impulse (delta function, $\delta(t)$)
- closely related to the solution to the homogeneous differential equation (i.e. zero input)

Solution:

$$y_1(t) = f(t) * g_1(t)$$

$$y_3(t)=[(f(t)*g_1(t))*g_2(t)]*g_3(t)$$

* Represents convolution

$$f(t) * g_1(t) = \int_{-\infty}^{\infty} f(\tau) g_1(t-\tau) d\tau$$

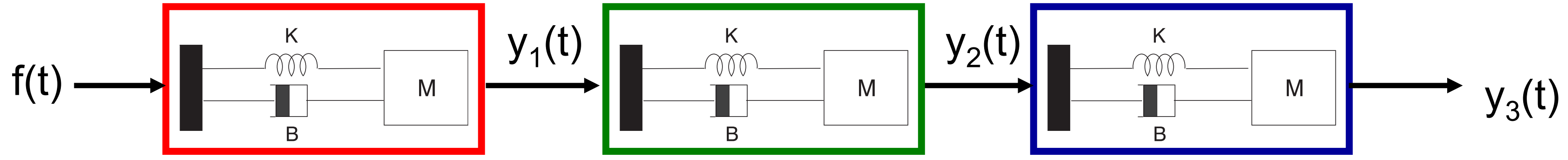
- often computationally intensive to solve in time domain
- in the case of a linear system can simplify using Laplace transforms

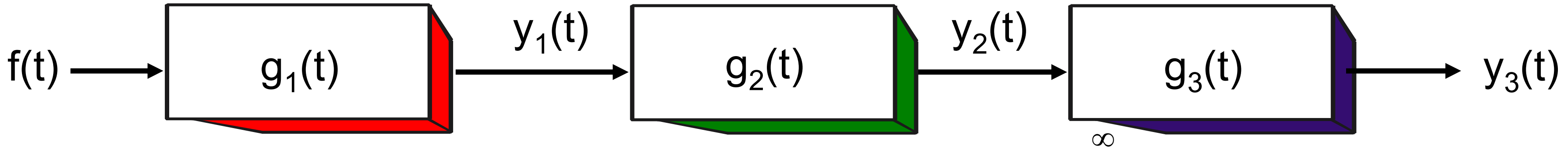
Advantages of Laplace transform descriptions of linear systems

- Advantageous for solving differential equations because the Laplace transform converts a differential equation into an algebraic equation that can be solved using simple algebraic manipulations
- The time domain solution can be obtained simply by taking the inverse Laplace transform
- Convolution in the time domain is a multiplication in the Laplace domain → a simple multiplication of Laplace transform descriptions of inputs and system dynamics gives the output

Cascade of several dynamic systems

In time domain:

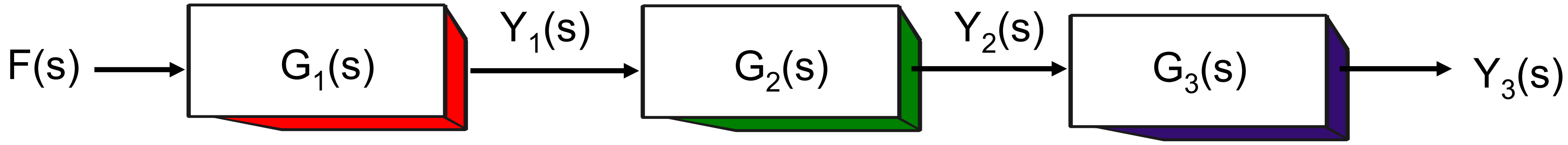




$y_3(t)=[(f(t)*g_1(t))*g_2(t)]*g_3(t)$

$$f(t)*g_1(t)=\int_{-\infty}^{\infty} f(\tau)g_1(t-\tau)d\tau$$

In Laplace (frequency) domain:



$G(s)$: Laplace transform of g(t)

$Y_3(s)=F(s)G_1(s)G_2(s)G_3(s)$

- solution obtained by simple multiplication

The Laplace transform

Definition:

$$\mathcal{L}[x(t)] = \int_{-\infty}^{\infty} x(t)e^{-st}dt \qquad \text{where } s = \sigma + j\omega \qquad j = \sqrt{-1}$$

- similar to Fourier transform but s is has both real and imaginary components

$$\mathcal{F}[x(t)] = \int_{-\infty}^{\infty} x(t)e^{-j\omega t}dt$$

Laplace Transform ⟶ Fourier Transform

$$\mathcal{L}[x(t)] = X(s)|_{s=j\omega} = \mathcal{F}[x(t)]$$

Inverse Laplace Transform

$$\mathcal{L}^{-1}[X(s)] = \frac{1}{2\pi j}\int_{\sigma-j\omega}^{\sigma+j\omega} X(s)e^{st}ds$$

Common Laplace transforms

Impulse: $x(t)=\delta(t) \longleftrightarrow X(s) = 1$

Unit Step: $x(t)=u_s(t) \longleftrightarrow X(s) = \frac{1}{s}$

Exponential Function:

$$x(t)=e^{-at} \longleftrightarrow X(s) = \frac{1}{s+a}$$

Sinusoidal Function:

$$x(t)=\sin(\omega_n t) \longleftrightarrow X(s) = \frac{\omega_n}{s^2+\omega_n^2}$$

Laplace transform properties

1. Multiplication by a constant: $\mathcal{L}[kx(t)]=kX(s)$

2. Sum and Difference: $\mathcal{L}[x_1(t)+x_2(t)]=X_1(s)+X_2(s)$

3. Differentiation: $\mathcal{L}[dx(t)/dt]=sX(s)-x(0)$

   In general for higher order derivatives:

   $\mathcal{L}[d^nx(t)/dt]=s^nX(s)-s^{n-1}x(0)-s^{n-2(}dx/dt)|_{t=0}\ldots-(d^{(n-1)}x/dt)|_{t=0}$

4. Integration: $\mathcal{L}[\int_0^t x(\tau)d\tau]=X(s)/s$

5. Time Shift: $\mathcal{L}[x(t-T)]=e^{-Ts}X(s)$

6. Initial-Value Theorem: $\lim_{t\to 0} x(t) = \lim_{s\to\infty} sX(s)$

7. Final Value Theorem: $\lim_{t\to\infty} x(t) = \lim_{s\to 0} sX(s)$

8. Convolution property: $x_1(t)*x_2(t) \longleftrightarrow X_1(s)X_2(s)$

Properties most important for today

1. Differentiation: $\mathcal{L}\,[dx(t)/dt]=sX(s)-x(0)$

e.g. 1st order system

$$\frac{dx(t)}{dt}+ax(t)=f(t) \longrightarrow sX(s)-x(0)+aX(s)=F(s)$$

- multiplication by s to differentiate for zero initial conditions ($x(0)=0$)

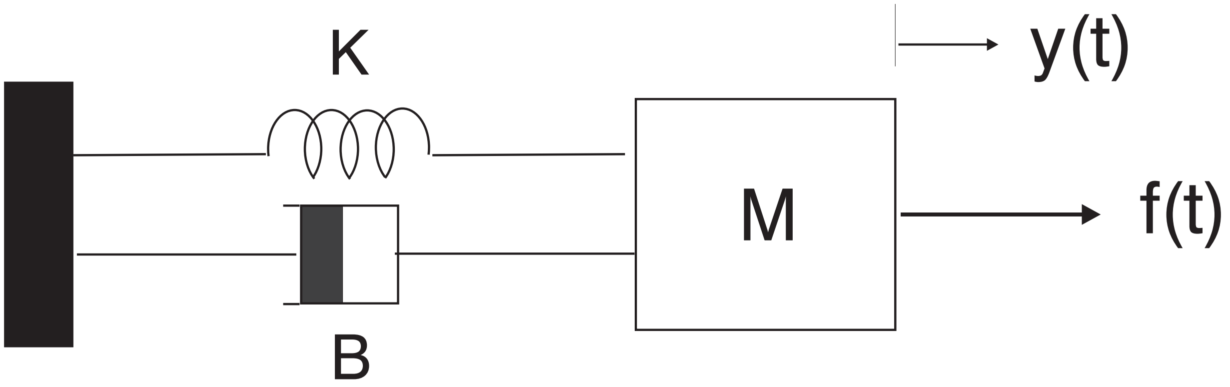
$$sX(s)+aX(s)=F(s)$$

2. Integration: $\mathcal{L}\left[\int_0^t x(\tau)d\tau\right]=\frac{X(s)}{s}$

- division by s to integrate in the Laplace domain

3. Convolution property: $x_1(t)*x_2(t) \longrightarrow X_1(s)X_2(s)$

A simple physical model



$$\Sigma F = Ma$$

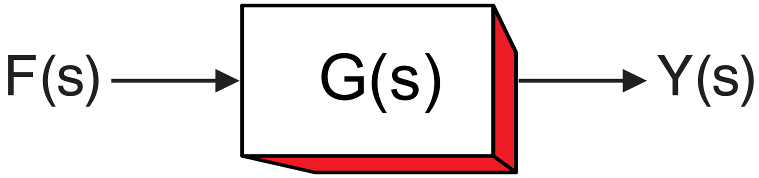
$$M\frac{d^2y(t)}{dt^2} + B\frac{dy}{dt} + Ky(t) = f(t)$$

In the Laplace domain (for zero initial conditions):

$$Ms^2Y(s) + BsY(s) + KY(s) = F(s)$$

$$\frac{Y(s)}{F(s)} = \frac{1}{Ms^2 + Bs + K}$$

Transfer function definition

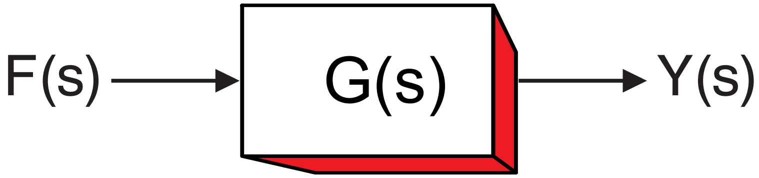


Transfer function: Laplace domain description of the relationship between the input and output of a *linear time-invariant* dynamic system.

$$G(s) = \frac{Y(s)}{F(s)} = \frac{1}{Ms^2 + Bs + K}$$

- The transfer function is the Laplace transform of the unit impulse response (i.e. response to δ(t))

Solution for a particular input



- Suppose we want to know the response of this system to a step input

$$f(t) = u_s(t) \qquad \mathcal{L}\left[u_s(t)\right] = \frac{1}{s} \qquad F(s) = \frac{1}{s}$$

$$Y(s) = F(s)G(s) = \frac{1}{s(Ms^2 + Bs + K)}$$

If M=1, B=5, K=6:

$$Y(s) = F(s)G(s) = \frac{1}{s(s^2 + 5s + 6)} = \frac{1}{s(s+2)(s+3)}$$

Time domain solution

$$Y(s) = F(s)G(s) = \frac{1}{s(s^2+5s+6)} = \frac{1}{s(s+2)(s+3)}$$

- To find y(t) can use partial fraction expansion and then inverse Laplace transformation

$$Y(s) = \frac{1}{s(s+2)(s+3)} = \frac{A}{s} + \frac{B}{s+2} + \frac{C}{s+3}$$

$$\mathrm{A} = \frac{1}{6},\ B = -\frac{1}{2},\ C = \frac{1}{3}$$

$$\mathcal{L}^{-1}\left[\frac{1}{s}\right] = u_s(t) \qquad \mathcal{L}^{-1}\left[\frac{1}{s+a}\right] = e^{-at}u_s(t)$$

$$y(t) = \left(\frac{1}{6} - \frac{1}{2}e^{-2t} + \frac{1}{3}e^{-3t}\right)u_s(t) = \frac{1}{6} - \frac{1}{2}e^{-2t} + \frac{1}{3}e^{-3t} \quad \text{for t} \geq 0$$

Example transfer functions

- Integrator: $G(s) = \dfrac{1}{s}$
- Differentiator: $G(s) = s$
- Low-pass filter: $G(s) = \dfrac{K}{s+a}$ $\qquad G(s) = \dfrac{K'}{Ts+1}$
- High-pass filter: $G(s) = \dfrac{Ks}{s+a}$
- Band-pass filter: $G(s) = \dfrac{K(s+b)}{(s+a_1)(s+a_2)}$ for $b<a_{1,}a_2$

Bandwidth
in rad/s

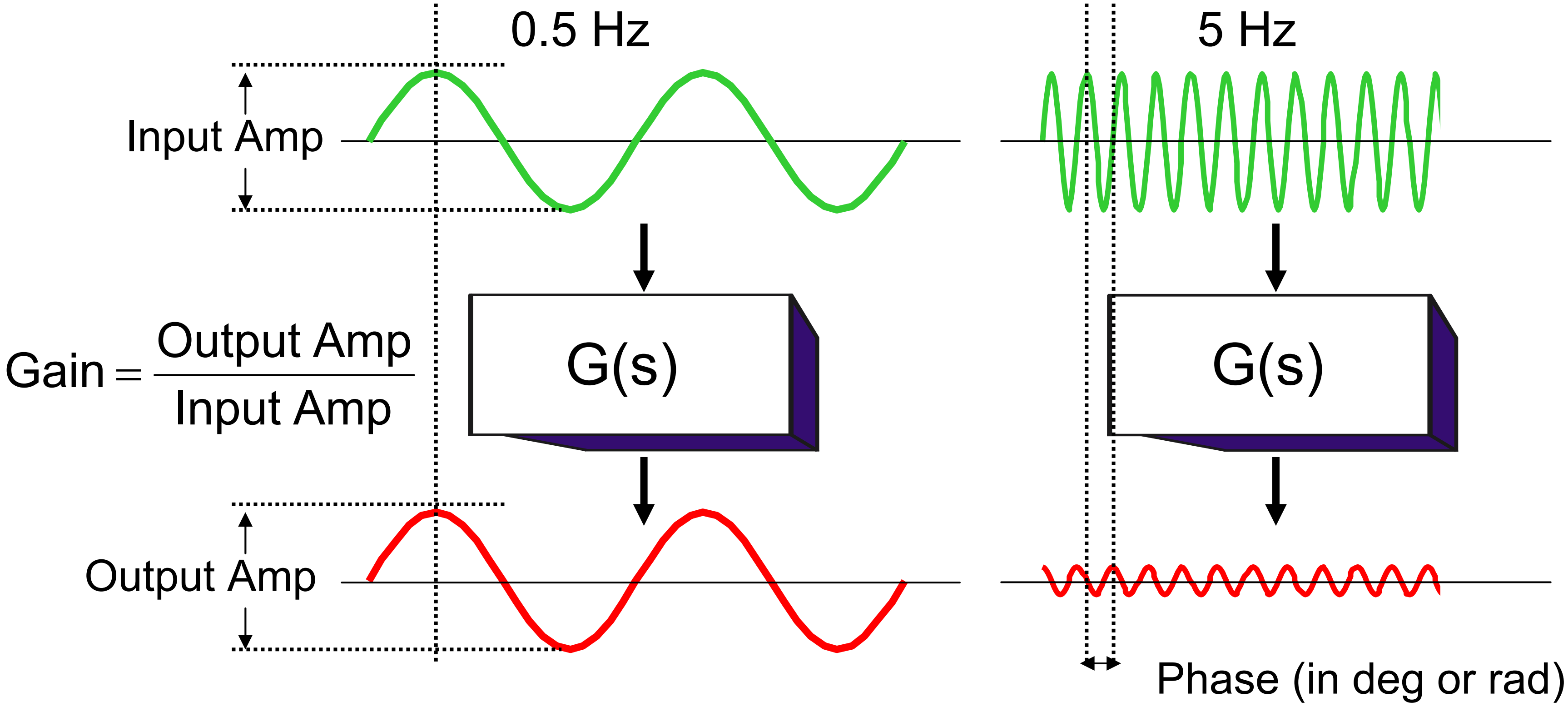
Time
constant

where K' =K/a
and T=1/a

Frequency response evaluation of a transfer function

What is the response of the system for stimuli of different frequencies?

- Quantified in terms of response *Gain* and *Phase*



$$\text{Gain} = \frac{\text{Output Amp}}{\text{Input Amp}}$$

Frequency response evaluation of a transfer function

- Evaluate transfer function for *s*=jω (similar to evaluating the Fourier transform)

$$G(s) = \left.\frac{K(s+z_1)(s+z_2)\ldots(s+z_m)}{(s+p_1)(s+p_2)\ldots(s+p_n)}\right|_{\mathrm{s=j\omega}} = \frac{K(j\omega+z_1)(j\omega+z_2)\ldots(j\omega+z_m)}{(j\omega+p_1)(j\omega+p_2)\ldots(j\omega+p_n)}$$

Gain:

$$|G(j\omega)| = \frac{K\prod_{i=1}^{m}|j\omega+z_i|}{\prod_{i=1}^{n}|j\omega+p_i|} = \frac{K\sqrt{(\omega)^2+z_1^{\,2}}\sqrt{(\omega)^2+z_2^{\,2}}\ldots\sqrt{(\omega)^2+z_m^{\,2}}}{\sqrt{(\omega)^2+p_1^{\,2}}\sqrt{(\omega)^2+p_2^{\,2}}\ldots\sqrt{(\omega)^2+p_n^{\,2}}}$$

Simplify evaluation of the contribution of each term by taking logarithm:

$$\log_{10}|G(j\omega)| = \log_{10}K + \sum_{i=1}^{m}\log_{10}|j\omega+z_i| - \sum_{i=1}^{n}\log_{10}|j\omega+p_i|$$

In decibels (dB):

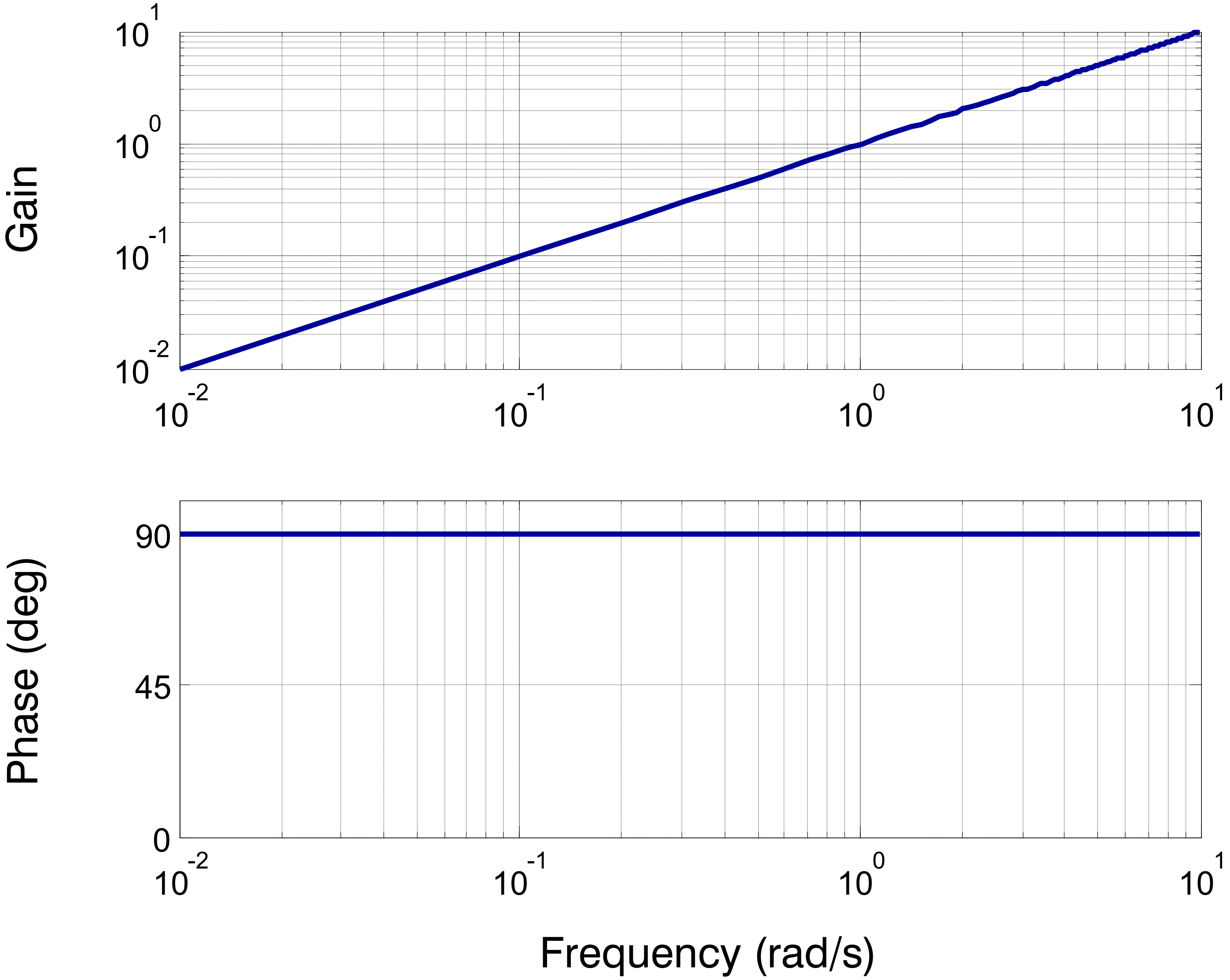
$$|G(j\omega)|_{\mathrm{dB}} = 20\log_{10}K + 20\sum_{i=1}^{m}\log_{10}|j\omega+z_i| - 20\sum_{i=1}^{n}\log_{10}|j\omega+p_i|$$

Phase:

$$\angle G(j\omega) = \sum_{i=1}^{m}\tan^{-1}\left(\frac{\omega}{z_i}\right) - \sum_{i=1}^{n}\tan^{-1}\left(\frac{\omega}{p_i}\right)$$

Differentiator

$$G(s) = s\Big|_{s=j\omega} = j\omega$$



$$|j\omega| = \sqrt{\omega^2}$$

$$= \omega$$

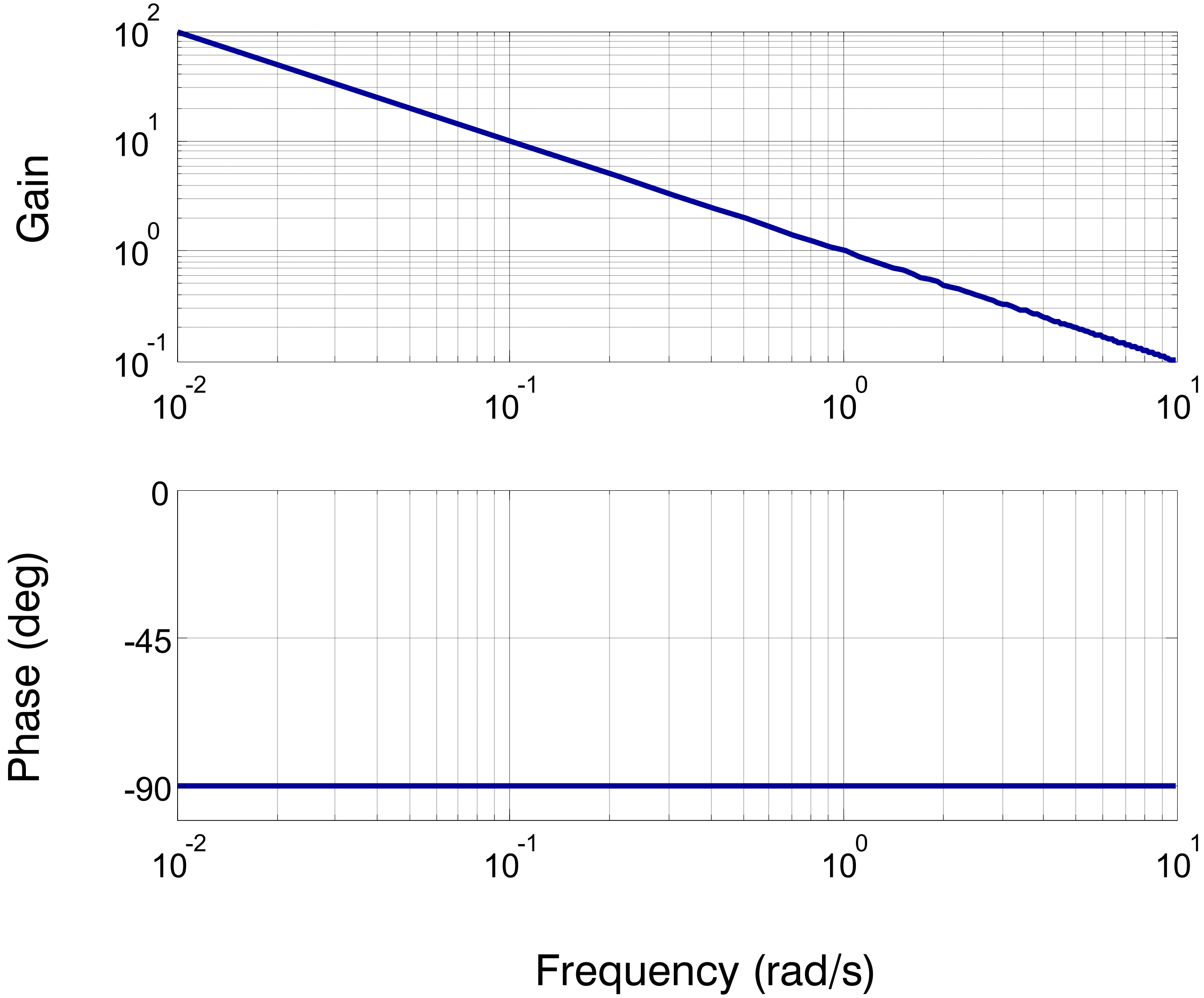
$$\tan^{-1}\left(\frac{\omega}{0}\right)$$

$$= \tan^{-1}(\infty)$$

$$= 90^{\circ}$$

Integrator

$$G(s) = \frac{1}{s}\bigg|_{s = j\omega} = \frac{1}{j\omega}$$



$$\left|\frac{1}{j\omega}\right| = \frac{1}{\sqrt{\omega^2}}$$

$$= \frac{1}{\omega}$$

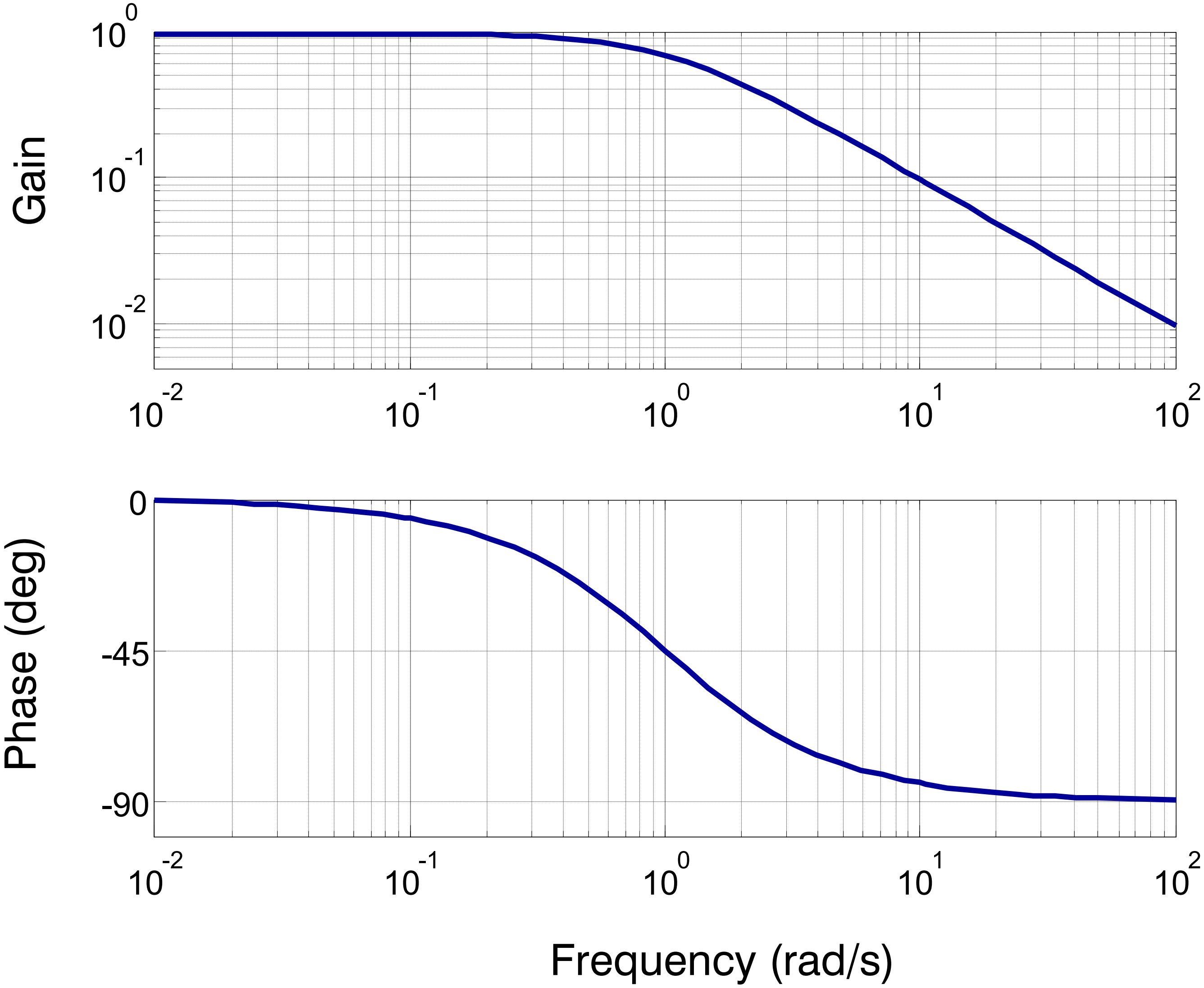
$$\tan^{-1}(0) - \tan^{-1}\left(\frac{\omega}{0}\right)$$

$$= -\tan^{-1}(\infty)$$

$$= -90^{\circ}$$

Low-pass filter

$$G(s) = \frac{1}{(s+1)}\Bigg|_{s=j\omega} = \frac{1}{(j\omega+1)}$$



$$\left|\frac{1}{(j\omega+1)}\right| = \frac{1}{\sqrt{\omega^2+1}}$$

≈ 1 for $\omega << 1$

$\approx 1/\omega$ for $\omega >> 1$

$= 1/\sqrt{2}$ for $\omega = 1$

$$-\tan^{-1}(\omega)$$

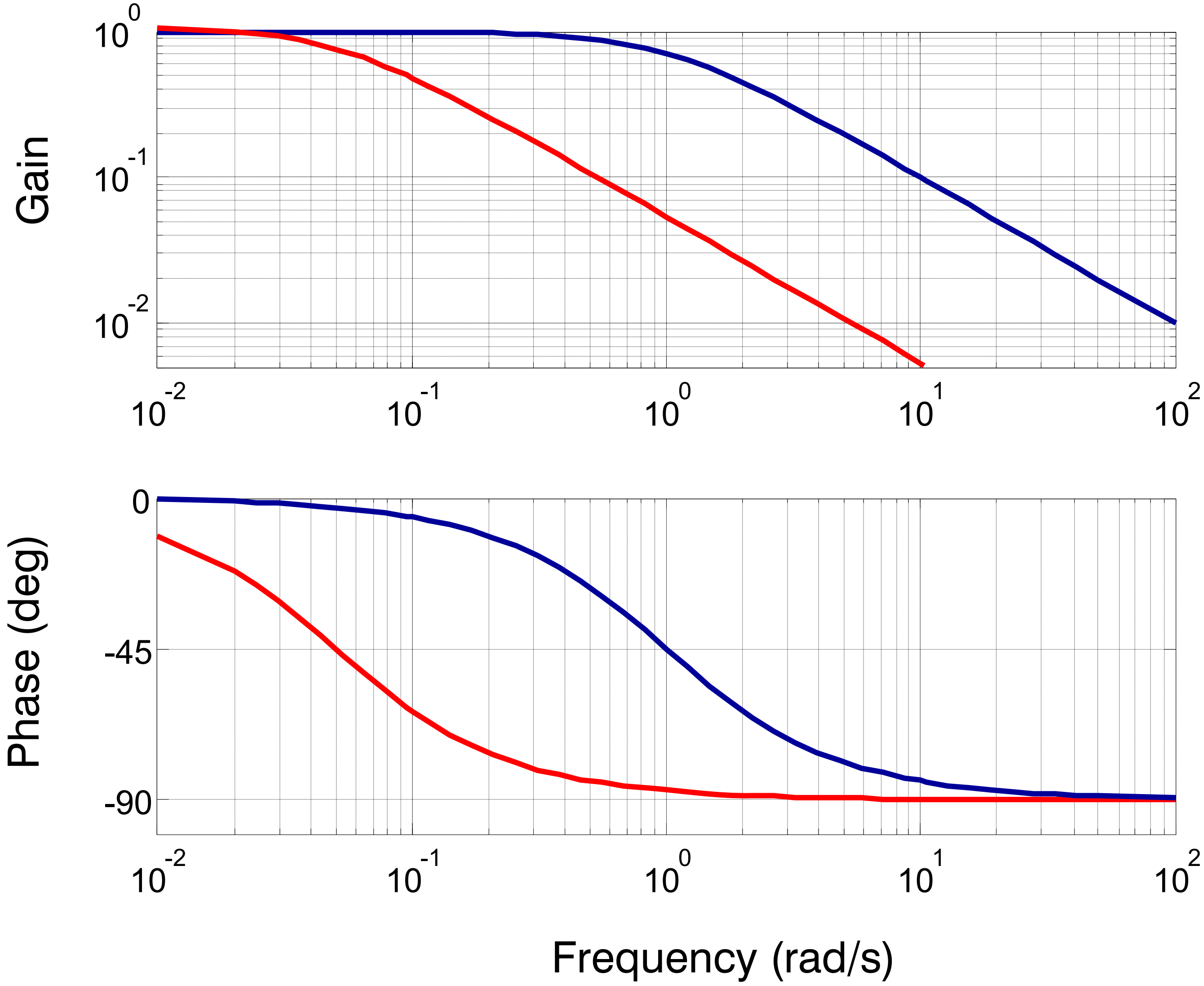
$\approx 0^o$ for $\omega << 1$

$\approx -90^o$ for $\omega >> 1$

$= -45^o$ for $\omega = 1$

Low-pass filter

$$G(s) = \frac{1}{(20s+1)}\bigg|_{s=j\omega} = \frac{1}{(20j\omega+1)}$$



$$\left|\frac{0.05}{(j\omega+0.05)}\right| = \frac{0.05}{\sqrt{(\omega)^2+(0.05)^2}}$$

≈ 1 for $\omega << 0.05$

$\approx 0.05/\omega$ for $\omega >> 0.05$

$= 1/\sqrt{2}$ for $\omega = 0.05$

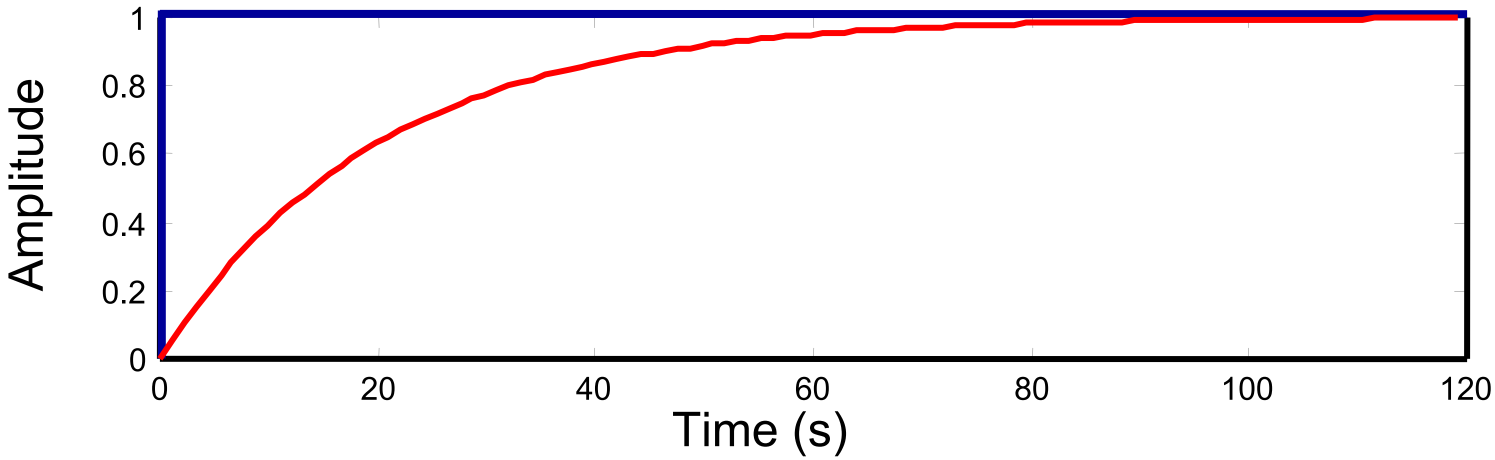
$$-\tan^{-1}\left(\frac{\omega}{0.05}\right)$$

$\approx 0^{o}$ for $\omega << 0.05$

$\approx -90^{o}$ for $\omega >> 0.05$

$= -45^{o}$ for $\omega = 0.05$

Step response: low-pass filter



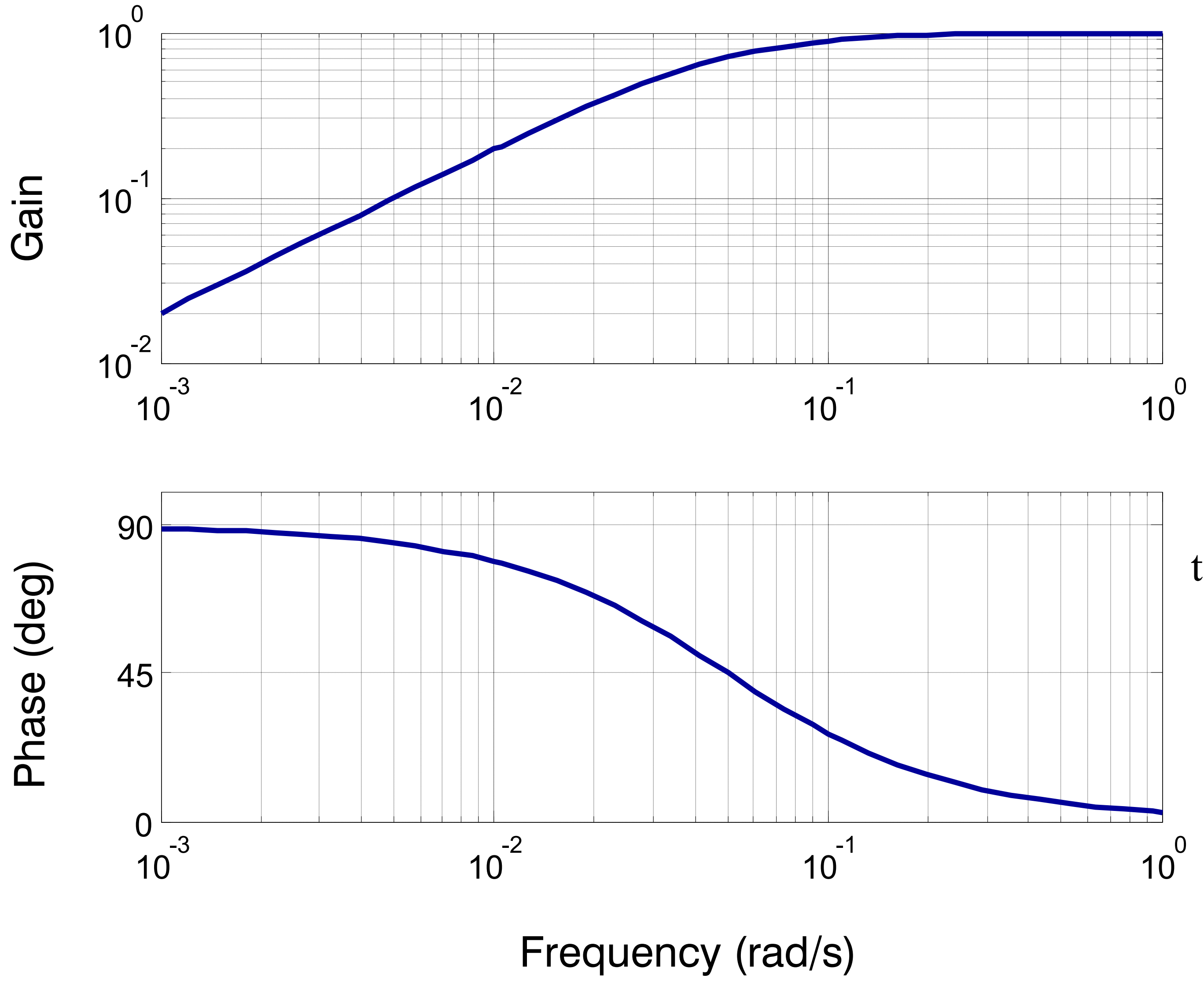
$$G(s) = \frac{1}{(20s+1)}$$

Step Response: $Y(s) = G(s)\frac{1}{s} = \frac{1}{s(20s+1)} = \frac{1}{s} + \frac{-20}{(20s+1)}$

Time Domain: $y(t) = (1 - e^{-t/20})u_s(t)$

High-pass filter

$$G(s) = \frac{20s}{(20s+1)}\bigg|_{s=j\omega} = \frac{20j\omega}{(20j\omega+1)}$$



$$\left|\frac{j\omega}{(j\omega+0.05)}\right| = \frac{\omega}{\sqrt{(\omega)^2+(0.05)^2}}$$

$\approx \omega/0.05$ for $\omega \ll 0.05$

≈ 1 for $\omega \gg 0.05$

$= 1/\sqrt{2}$ for $\omega = 0.05$

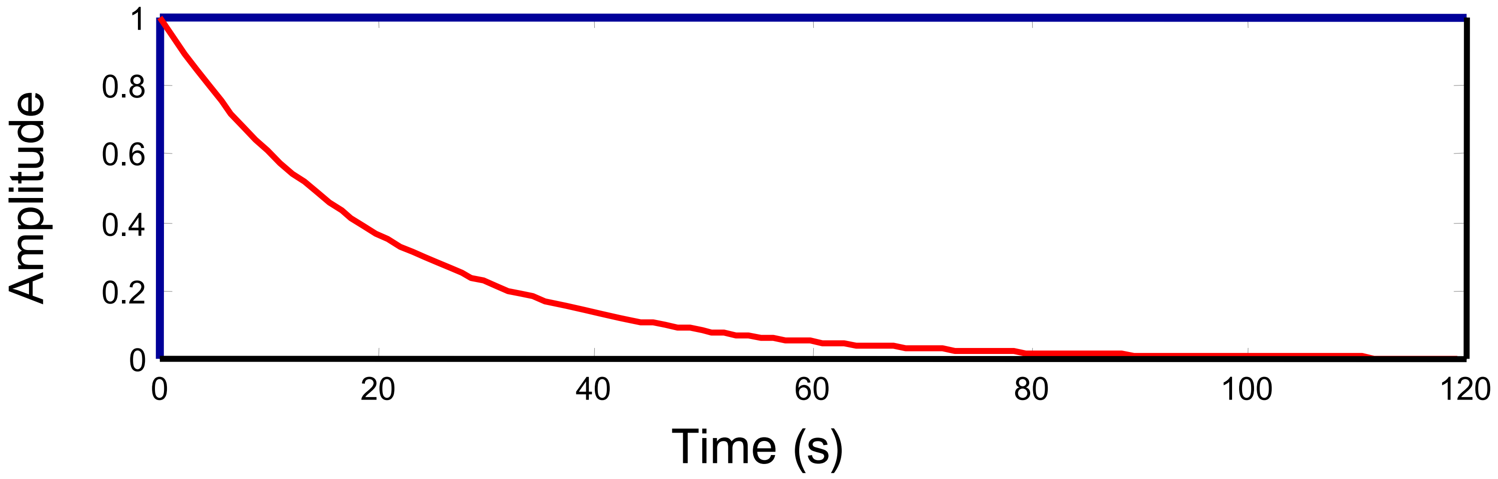
$$\tan^{-1}(\infty) - \tan^{-1}\left(\frac{\omega}{0.05}\right)$$

$\approx 90^{o}$ for $\omega \ll 0.05$

$\approx 0^{o}$ for $\omega \gg 0.05$

$= 45^{o}$ for $\omega = 0.05$

Step response: high-pass filter

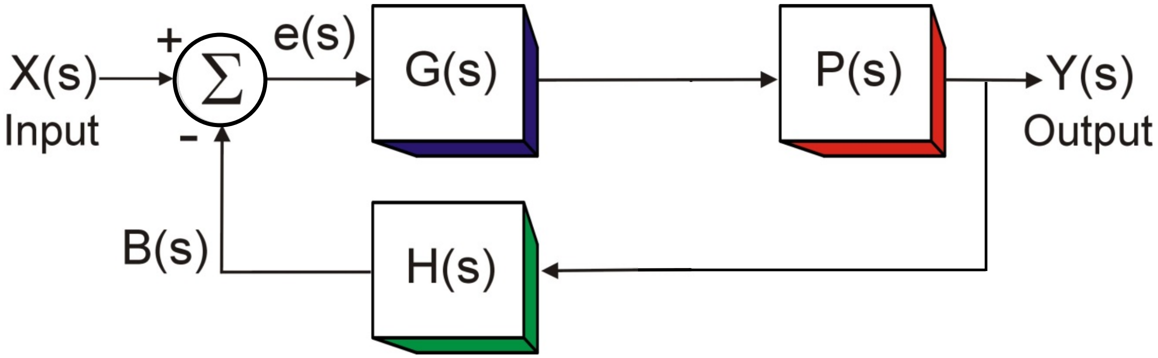


System transfer function: $G(s) = \dfrac{20s}{(20s+1)}$

Step Response: $Y(s) = G(s)\dfrac{1}{s} = \dfrac{20}{(20s+1)}$

Time Domain: $y(t) = e^{-t/20}u_s(t)$

Example feedback system



$$e(s)=X(s)-B(s)$$

$$B(s)=G(s)P(s)H(s)e(s)$$

$$Y(s)=e(s)G(s)P(s)$$

$$e(s)=X(s)-G(s)P(s)H(s)e(s)$$

$$e(s)=\frac{X(s)}{1+G(s)P(s)H(s)}$$

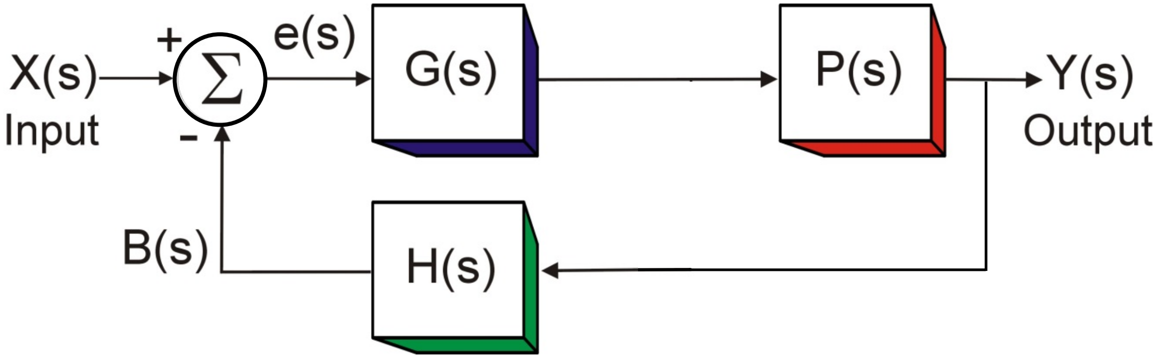
$$Y(s)=\frac{X(s)G(s)P(s)}{1+G(s)P(s)H(s)}$$

$$\frac{Y(s)}{X(s)}=\frac{G(s)P(s)}{1+G(s)P(s)H(s)} \longleftarrow \text{Transfer function}$$

Advantages of Feedback

- Improve response characteristics
- Reduce sensitivity of a system to parameter variations
- Reduce sensitivity to external disturbances
- Stabilize an unstable system

Example feedback system



Change characteristics of response to input:

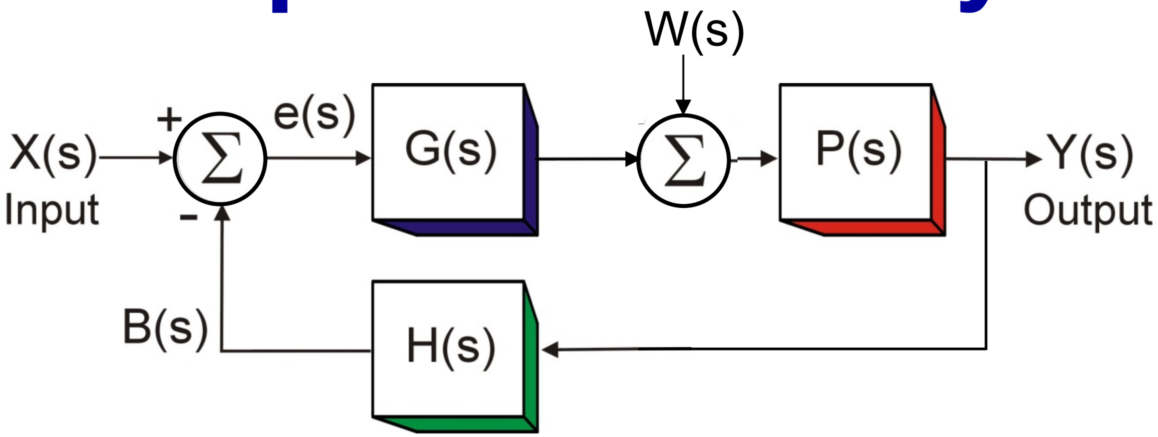
Suppose $G(s)$=K, $H(s)$=1, $P(s) = \dfrac{1}{Ts+1}$

Without feedback: $\dfrac{Y(s)}{X(s)} = KP(s) = \dfrac{K}{Ts+1}$

With feedback: $\dfrac{Y(s)}{X(s)} = \dfrac{KP(s)}{1+KP(s)} = \dfrac{G_{FB}}{T_{FB}s+1}$ where $G_{FB}=K/(1+K)$,
$T_{FB}=T/(1+K)$

- Response now reflects new steady-state gain G_{FB} and smaller time constant T_{FB} (i.e., faster response)

Example feedback system



Reduced sensitivity to external disturbances:

Suppose $G(s)$=K, $H(s)$=1, $P(s) = \dfrac{1}{Ts+1}$

Without feedback: $\dfrac{Y(s)}{W(s)} = P(s) = \dfrac{1}{Ts+1}$

With feedback: $\dfrac{Y(s)}{W(s)} = \dfrac{P(s)}{1+KP(s)} = \dfrac{G_{Dist}}{T_{FB}s+1}$ where $G_{Dist}=1/(1+K)$,
$T_{FB}=T/(1+K)$

- Gain of response to an external disturbance is reduced by ≈1/K for K>>1

Poles and Zeros and Stability

Poles: Values of complex variable *s* for which the transfer function becomes infinite

Zeros: Values of complex variable *s* for which the transfer function becomes zero

e.g.

$$G(s) = \frac{10(s+2)}{s(s+1)(s+3)}$$

- $G(s)$ has one zero at $s = -2$ and three poles at $s = 0$, $s = -1$ and $s = -3$

System Stability

Definition of Stability:

A system is stable if the output is bounded for any bounded input.

Criterion for Stability:

The real portion of all poles must be negative.

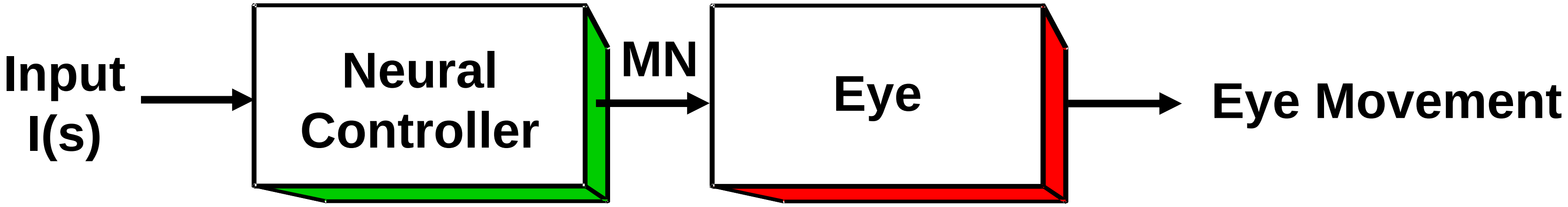
Why?

$$G(s) = \frac{P(s)}{(s+a_1)(s+a_2)....(s+a_n)} = \frac{K_1}{(s+a_1)} + \frac{K_2}{(s+a_2)} + \ldots \frac{K_n}{(s+a_n)}$$

$$\mathcal{L}^{-1}\left[G(s)\right] = K_1 e^{-a_1 t} + K_2 e^{-a_2 t} + \ldots K_n e^{-a_n t}$$

- For $a_1 \ldots a_n > 0$ poles are negative (i.e., poles at $-a_1 \ldots -a_n$)
- System response reflects decaying exponentials → STABLE
- For $a_1 \ldots a_n < 0$ poles are positive (i.e., poles at $a_1 \ldots a_n$)
- System response reflects rising exponentials → UNSTABLE

What neural control mechanisms are required for different eye movements?



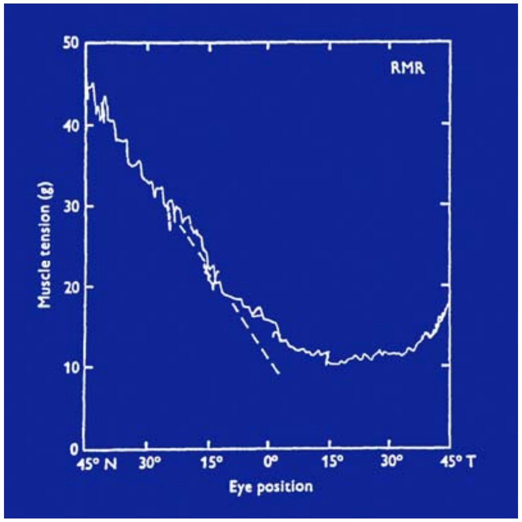
- What are the dynamic properties of the eye?
- What forces do eye muscles need to generate?
- What should motor neurons do to generate this muscle force?

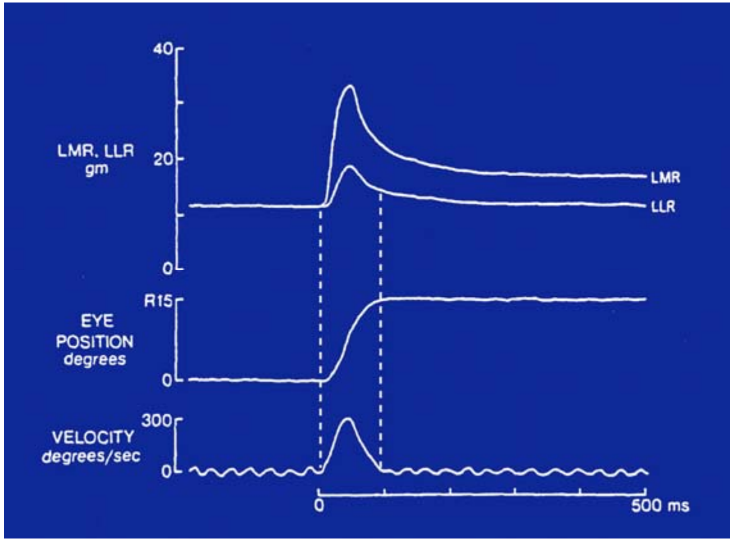
Physical characteristics of the eye

- **What are the dynamic characteristics of the eye?**
  - The eye globe has viscosity and elasticity but negligible inertia

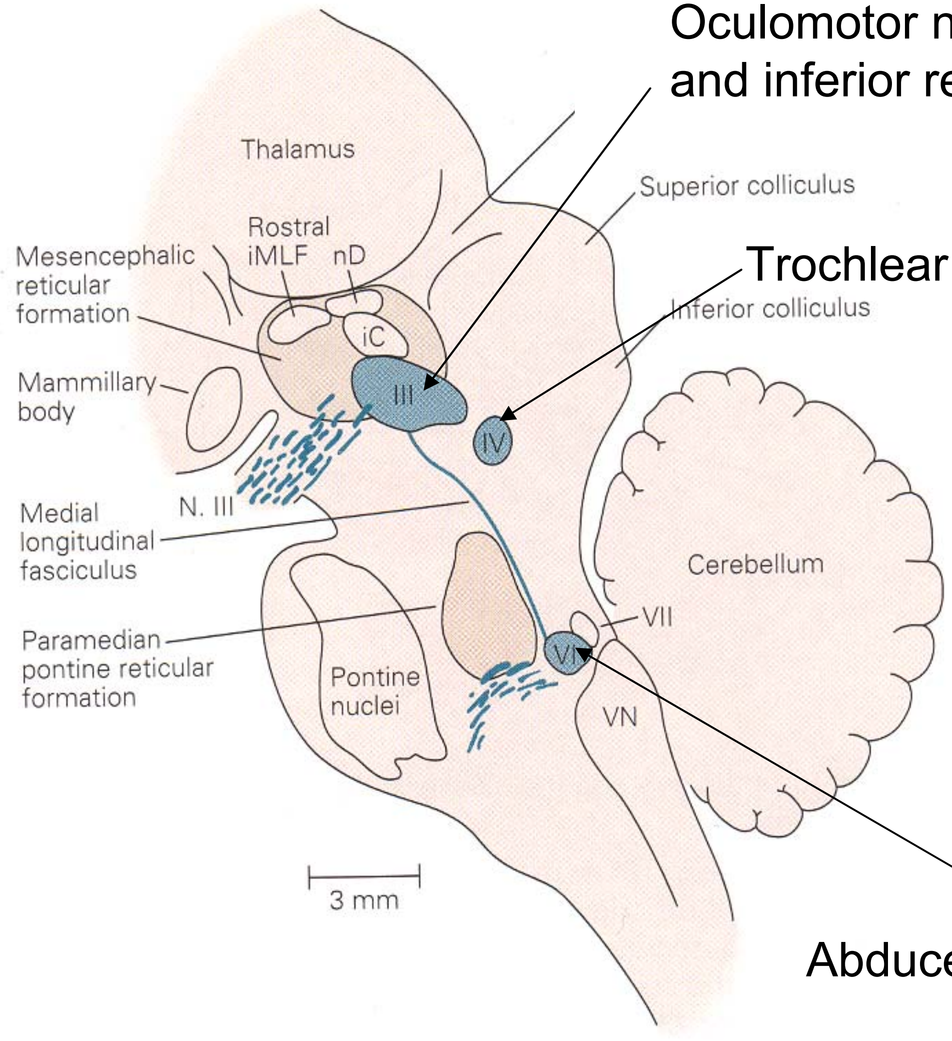
$$\text{Force} = k \times (\text{position}) + b \times (\text{velocity}) + \xcancel{I \times (\text{acceleration})}$$

- **Physical eye properties are reflected in the muscle force required to fixate and move the eye**





Motoneuron response properties

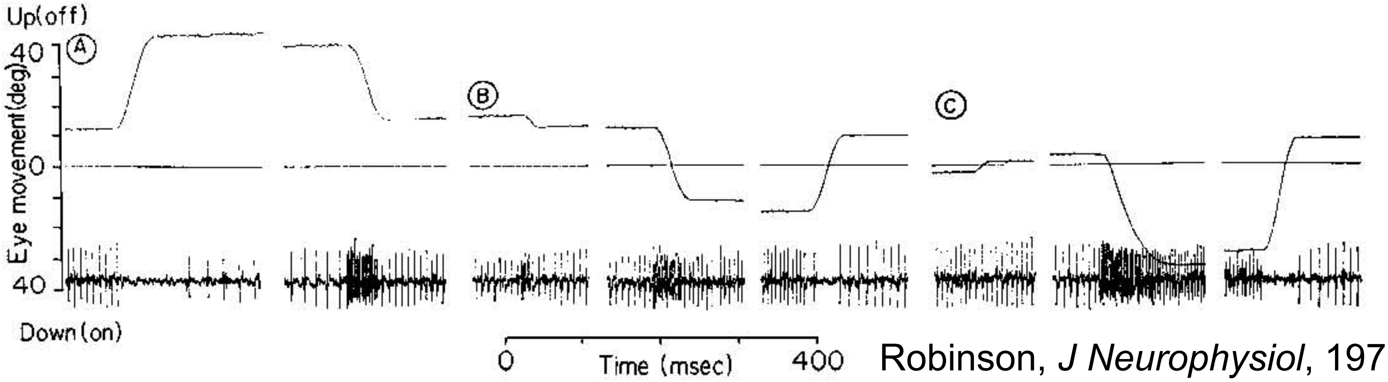


Oculomotor nucleus (III): medial, superior and inferior rectii and inferior oblique

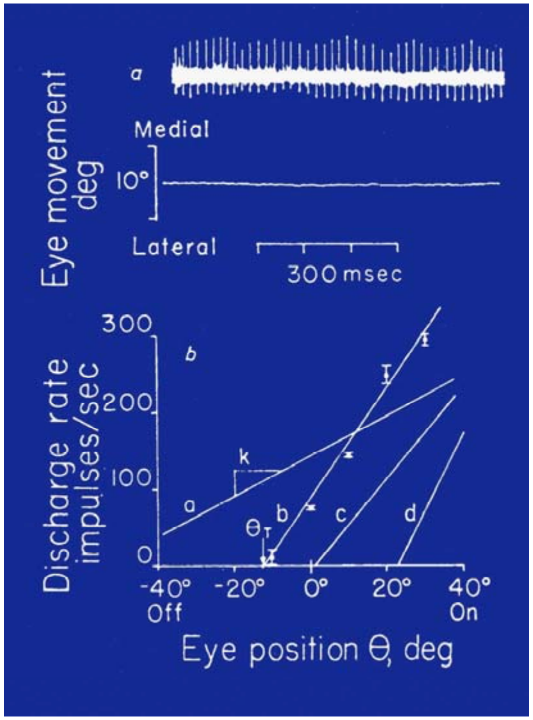
Trochlear nucleus (IV): superior oblique

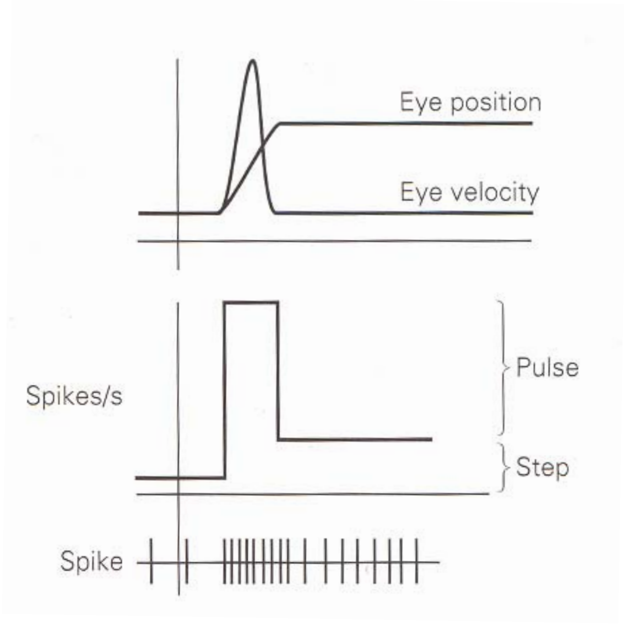
Abducens nucleus (VI): lateral rectus

Motoneuron activity during saccades



Robinson, *J Neurophysiol*, 1970

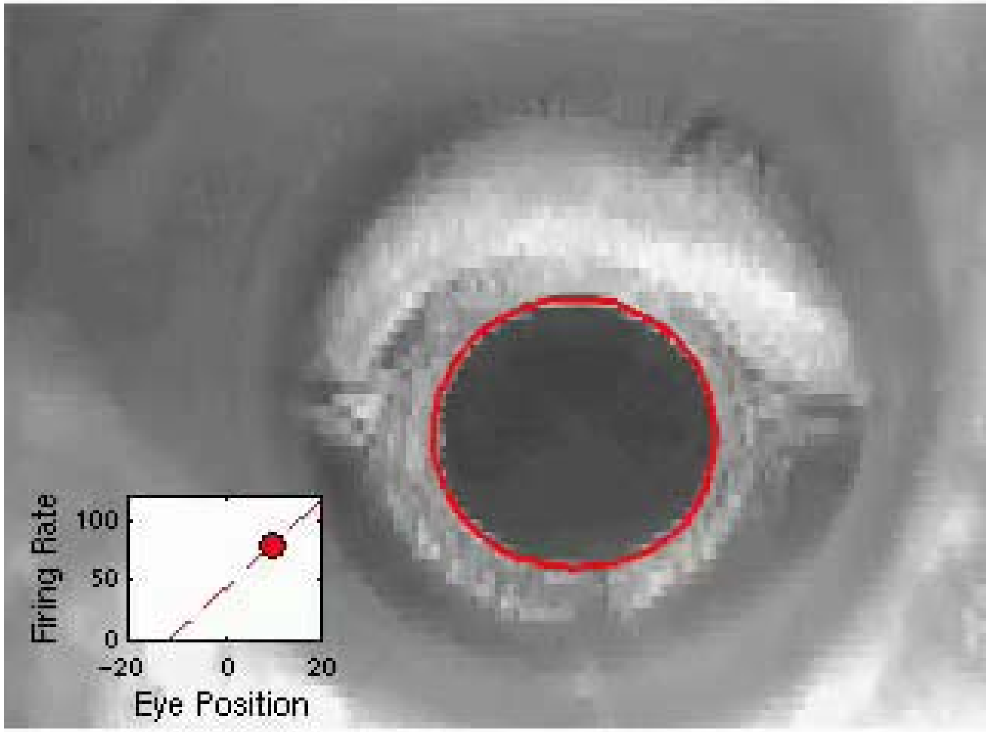




Firing rate = K × (eye position) + B × (eye velocity)

Motor neuron firing rate ≈ proportional to muscle force

Example motor neuron in goldfish



Dynamic characteristics of the "eye plant"

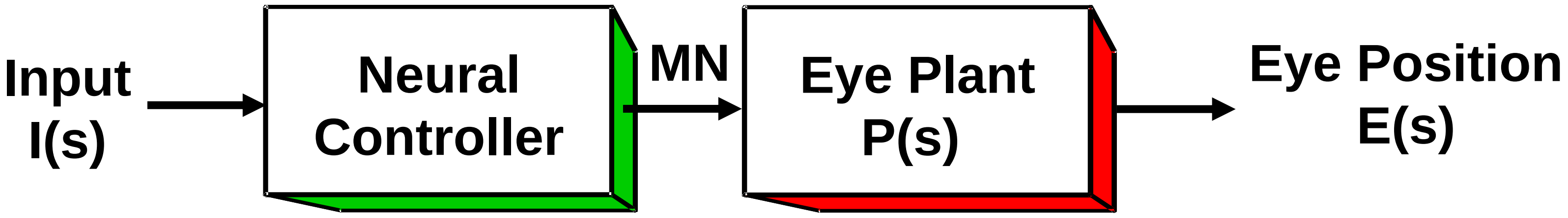
How can we model the dynamic properties of the eye plant?

Time domain description: $MN(t) = kE(t) + B\dfrac{dE(t)}{dt}$

Laplace domain description: $MN(s) = kE(s) + BsE(s)$

Transfer function: $\dfrac{E(s)}{MN(s)} = \dfrac{1}{Bs+k} = \dfrac{1/k}{T_p s+1}$ for $T_p = B/k$

$T_p \approx 250\text{ms}$



Input I(s)

Neural Controller

MN

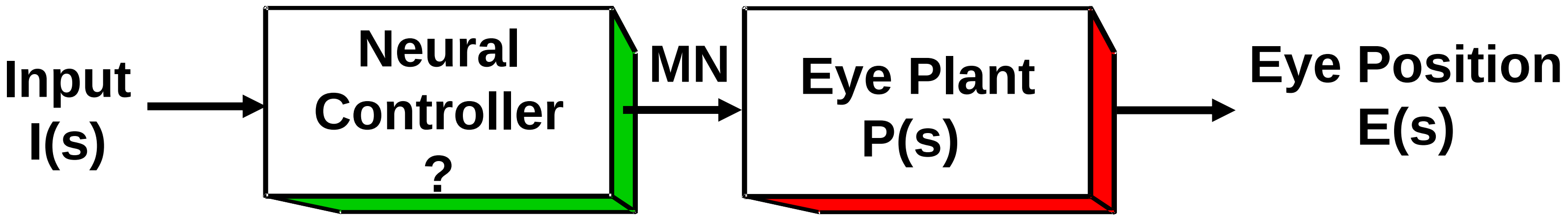
Eye Plant P(s)

Eye Position E(s)

$$\frac{1}{T_p s+1} \longleftarrow$$

Low-pass filter
$T_p \approx 250\text{ms}$
$(1/(2\pi T_p) \approx 0.6\text{ Hz})$

What are the characteristics of the neural controller?


Input I(s)

Neural Controller ?

MN

Eye Plant P(s)

Eye Position E(s)

$$\frac{1}{T_p s + 1}$$

←

low-pass filter

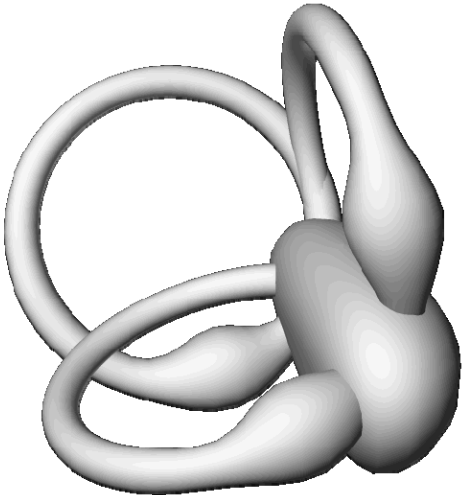
$T_p \approx 250\text{ms}$

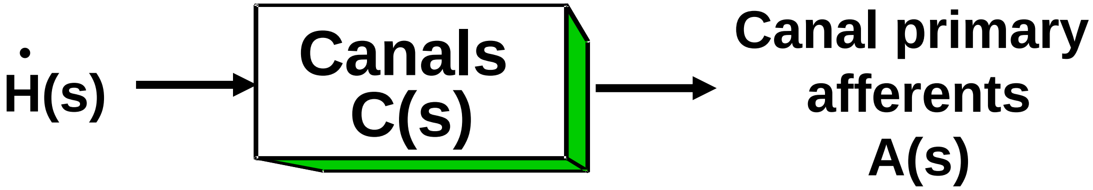
$(1/(2\pi T_p) \approx 0.6\text{ Hz})$

- Depends on input I(s)……

Semicircular canal dynamics

- Head rotation sensors that consist of three fluid-filled semicircular ducts that are approximately perpendicular to one other
- When there is a change in head rotation speed (i.e., angular acceleration) the endolymph fluid lags behind because of inertia, pushing on a membrane that causes the bending of hair cells





$\dot{H}(s)$ → **Canals C(s)** → **Canal primary afferents A(s)**

Low-pass filter of angular acceleration → $\frac{A(s)}{\ddot{H}(s)} = \frac{1}{T_c s + 1}$

High-pass filter of angular velocity → $\frac{A(s)}{\dot{H}(s)} = \frac{T_c s}{T_c s + 1}$

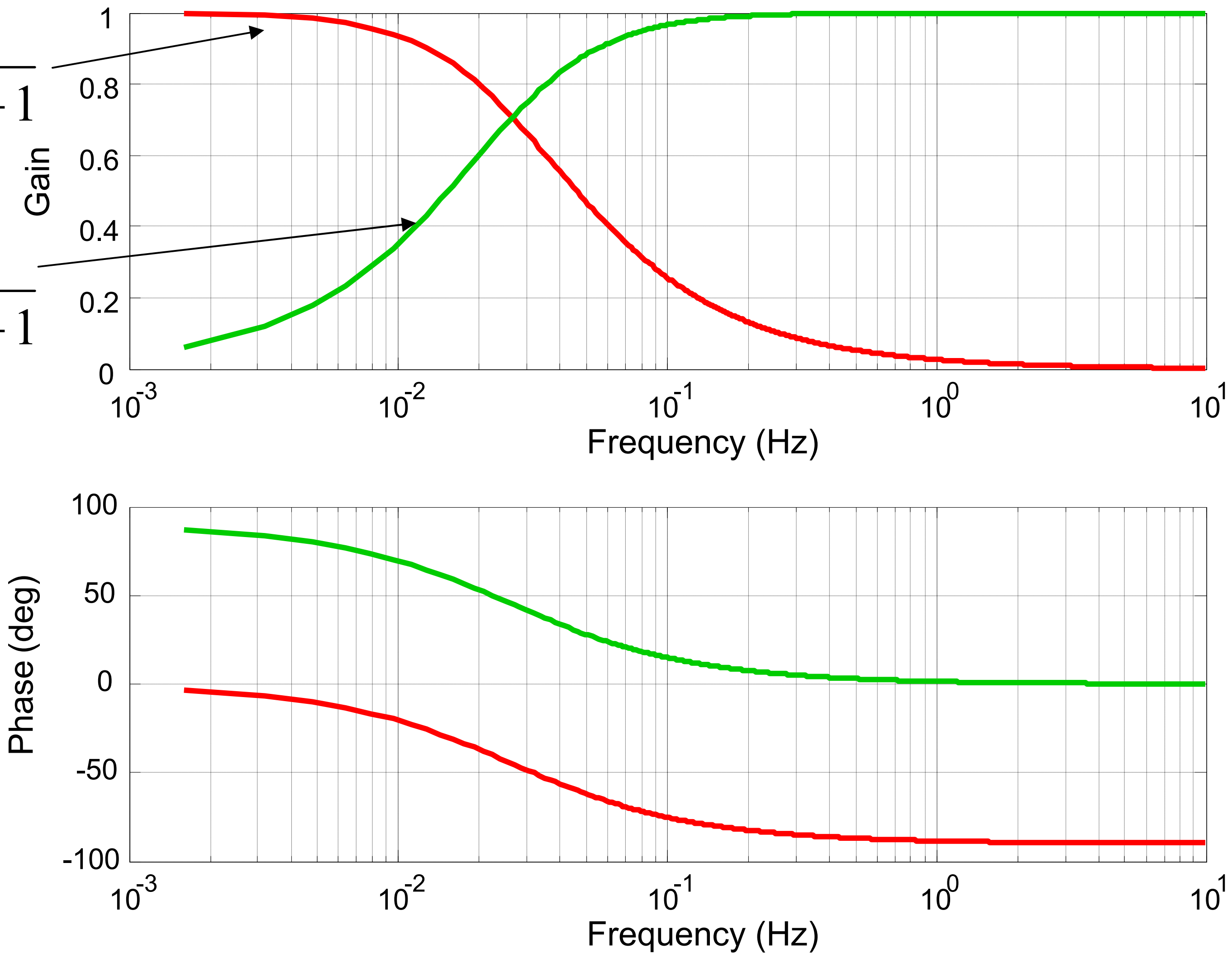
$T_c \approx$ 4-6s

The canals provide an accurate estimate of angular head velocity at frequencies f>$(1/(2\pi T_c) \approx 0.03$ Hz

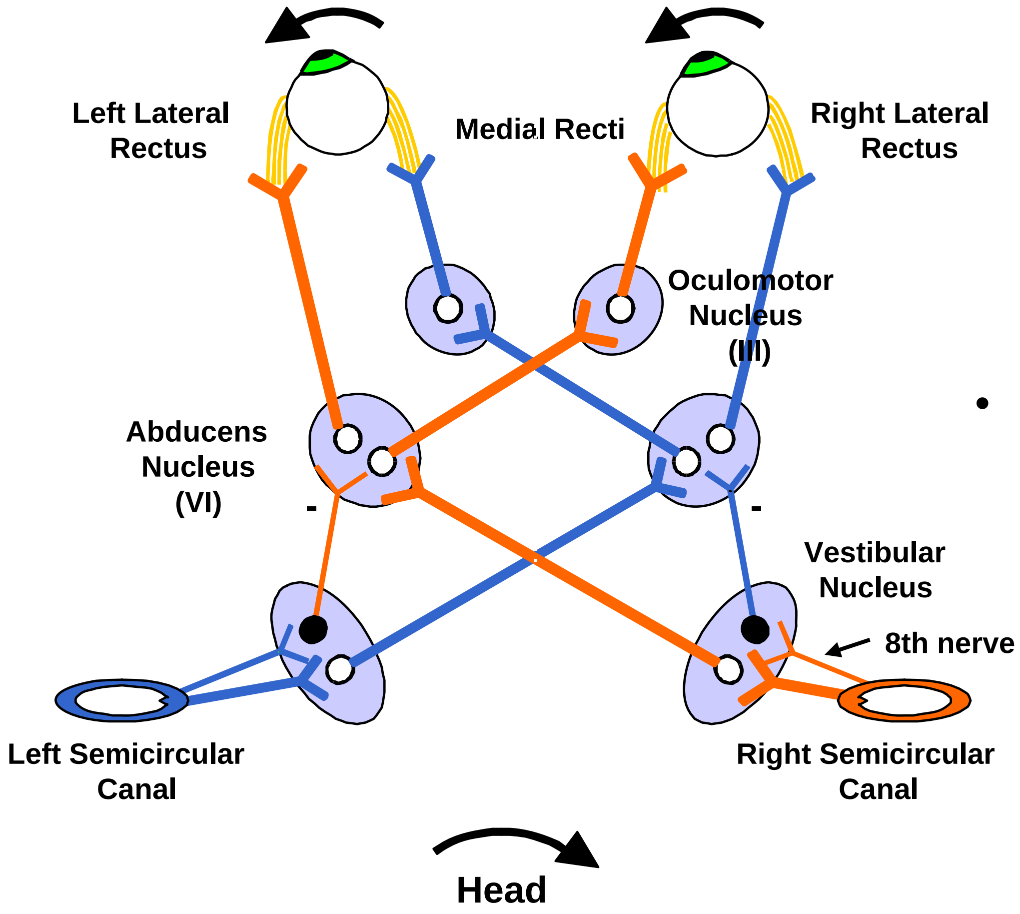
Semicircular canal dynamics

$$\frac{A(s)}{\ddot{H}(s)} = \frac{1}{T_c s + 1}$$

$$\frac{A(s)}{\dot{H}(s)} = \frac{T_c s}{T_c s + 1}$$

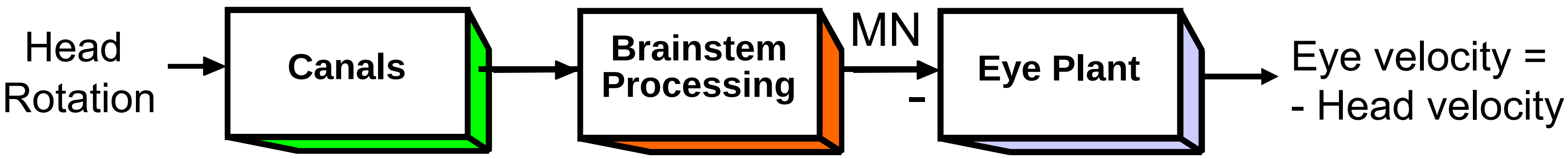


Neural substrate of the VOR: “three-neuron-arc” pathways



- Direct path of the VOR is a short tri-synaptic reflex pathway consisting of:
  - 1) primary afferents innervating the semicircular canals
  - 2) secondary neurons in the vestibular nuclei (VN)
  - 3) extraocular motor neurons
- When the head rotates rightward:
  - Right semicircular canal activity increases; left decreases
  - The right VN activity increases; left decreases
  - Motoneurons in the left abducens and (VI) right oculomotor (III) nuclei fire at a higher frequency; those in the right VI and left III fire at a lower frequency
  - Both eyes rotate leftward

Sensorimotor transformations in the VOR pathways

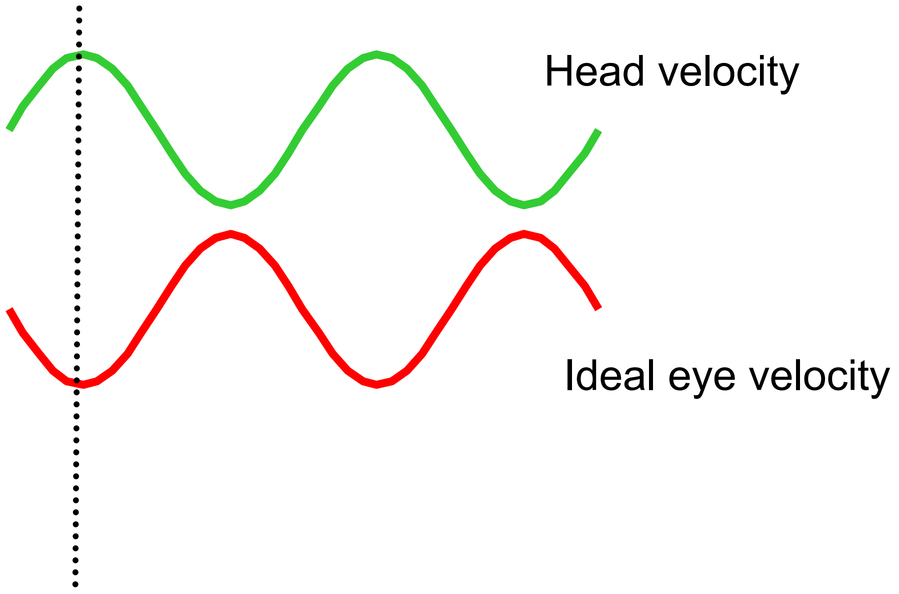


Head Rotation → **Canals** → **Brainstem Processing** → MN - → **Eye Plant** → Eye velocity = - Head velocity

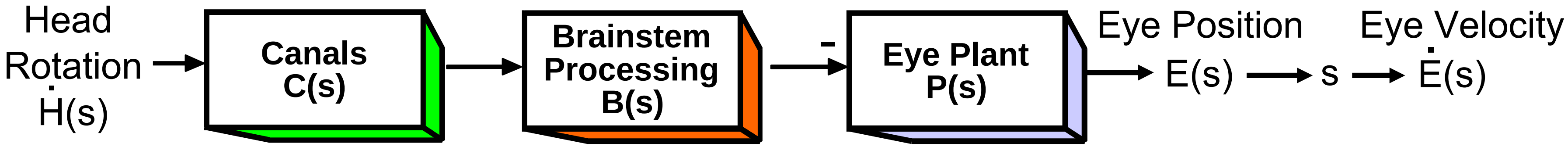
- Canal afferents provide an accurate estimate of angular head velocity at frequencies >~0.03 Hz

?

- The motoneural command requires signal components related to both eye position and eye velocity



Sensorimotor transformations in the VOR pathways



Head Rotation $\dot{H}(s)$

Canals C(s)

Brainstem Processing B(s)

-

Eye Plant P(s)

Eye Position E(s) → s → Eye Velocity $\dot{E}(s)$

Semicircular Canals
High Pass Sensors of $\dot{H}$
(encode $\dot{H}$ > 0.03 Hz)

Low Pass Filter
Time constant ≈ 0.25 s
Bandwidth ≈ 0.6 Hz

$$\dot{H}(s) \longrightarrow \frac{T_c s}{T_c s+1} \longrightarrow B(s) \longrightarrow \frac{1}{T_p s+1} \longrightarrow E(s) \rightarrow s \rightarrow \dot{E}(s)$$

$T_c \approx 6\text{ s} \quad (1/(2\pi T_c)) \approx 0.03\text{Hz}$

$T_p \approx 0.25\text{ s} \quad (1/(2\pi T_p)) \approx 0.6\text{Hz}$

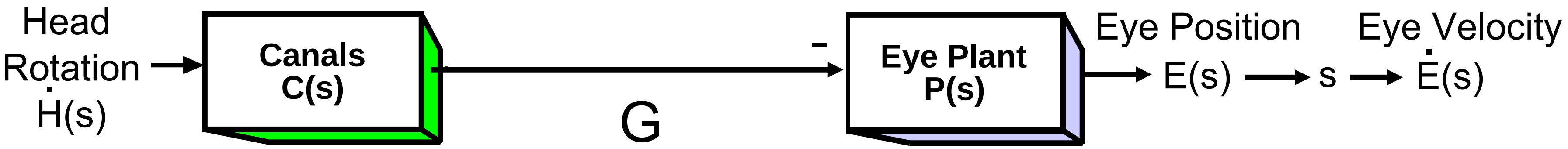
$$\dot{E}(s) = -C(s)B(s)P(s)s\dot{H}(s)$$

$$\frac{\dot{E}(s)}{\dot{H}(s)} = -C(s)B(s)P(s)s$$

For ideal reflex behavior: $\dfrac{\dot{E}(s)}{\dot{H}(s)} = -1$

- The VOR behaves close to ideally over a frequency range of ≈0.03-30Hz

Sensorimotor transformations in the VOR pathways



Head Rotation $\dot{H}(s)$

Canals C(s)

G

-

Eye Plant P(s)

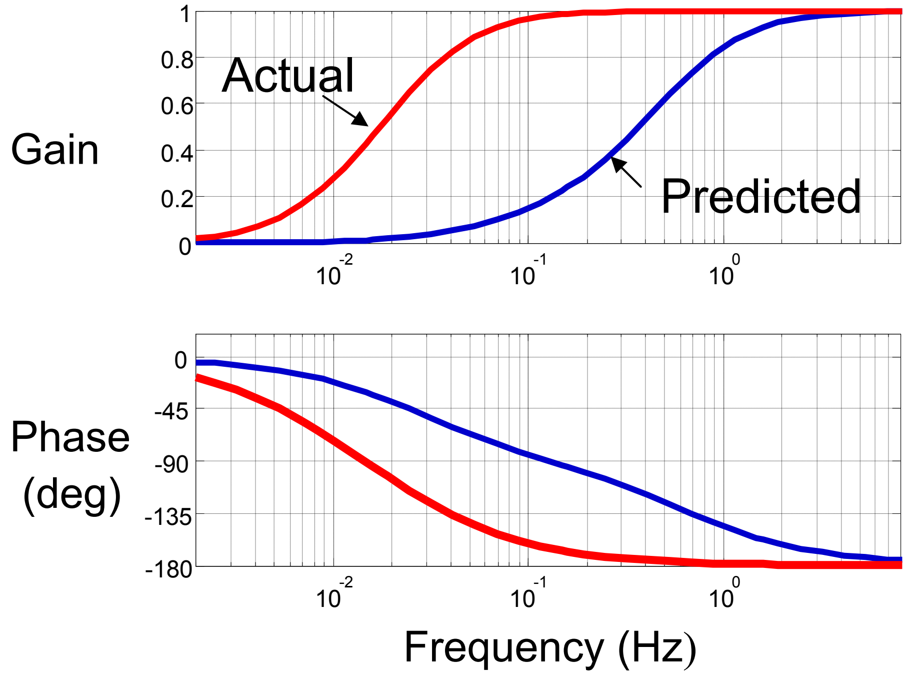
Eye Position E(s) → s → Eye Velocity $\dot{E}(s)$

Suppose *B(s)* = *G* (a gain term – no dynamic properties)

$$\frac{\dot{E}(s)}{\dot{H}(s)} = -C(s)B(s)P(s)s = -\frac{T_c s}{T_c s + 1}\frac{Gs}{T_p s + 1} \approx -\frac{Gs}{T_p s + 1}$$

for $s = j\omega >> 1/T_c$,
$f = \omega/(2\pi) >> 0.03\text{Hz}$

High-pass filter with cutoff frequency ≈ 0.6 Hz



Sensorimotor transformations in the VOR pathways


Head Rotation

Canals

G

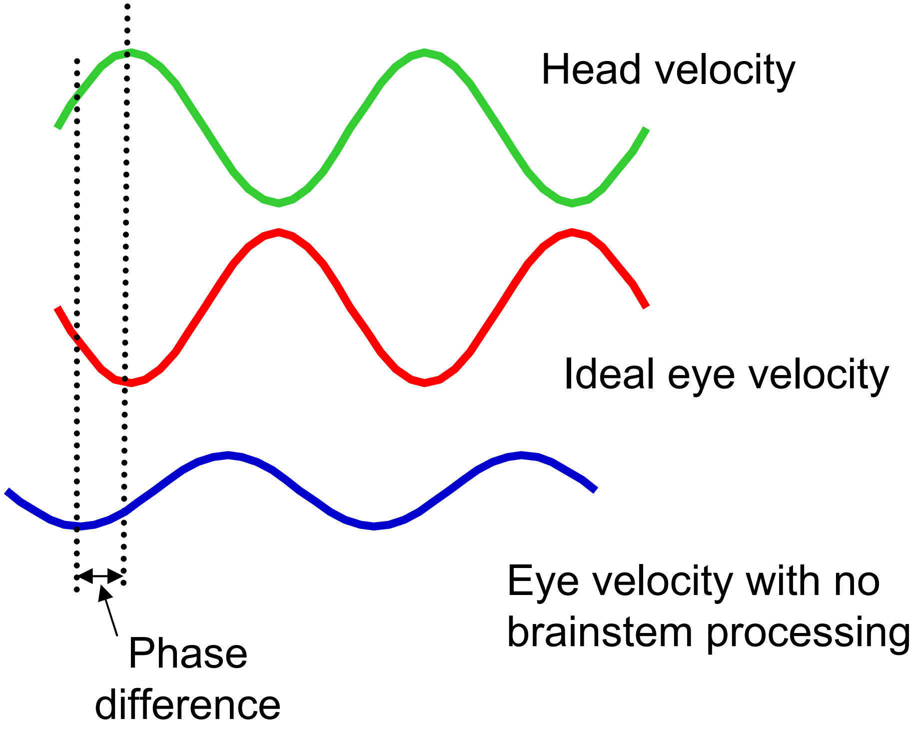
MN

-

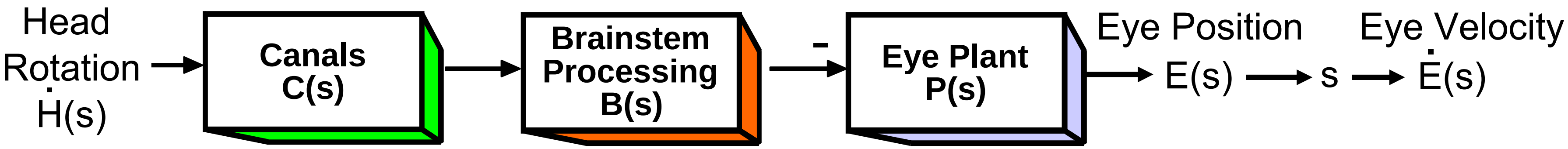
Eye Plant

Eye velocity = - Head velocity

- Canal afferents provide an estimate of head velocity at frequencies >~0.03 Hz
- motoneuron signal needs to have a combination of components related to eye velocity and eye position



Sensorimotor transformations in the VOR pathways

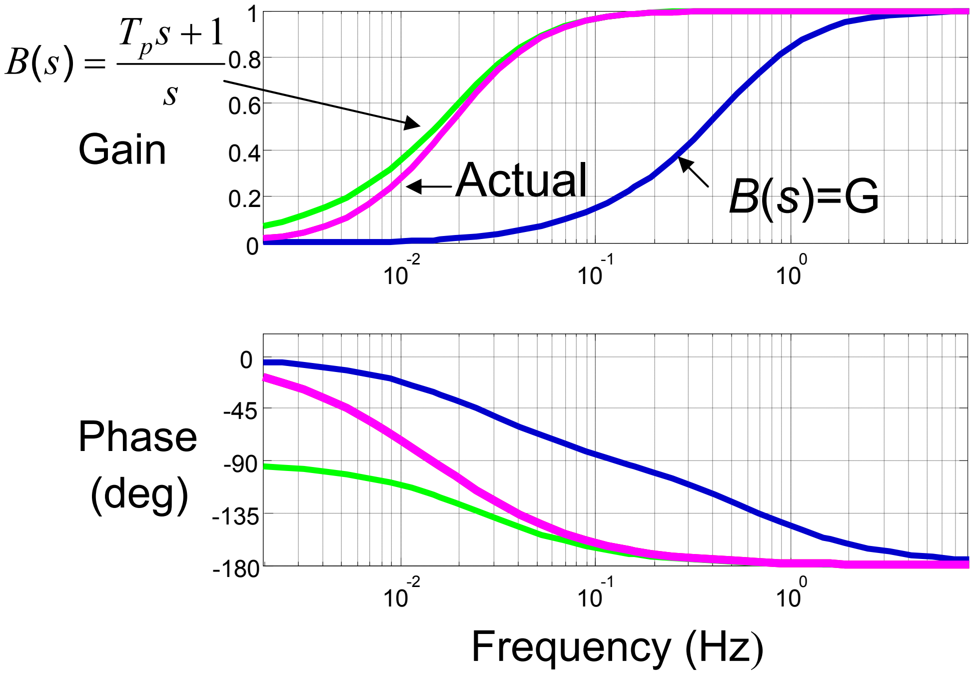


Head Rotation $\dot H(s)$ → **Canals C(s)** → **Brainstem Processing B(s)** → - **Eye Plant P(s)** → Eye Position E(s) → s → Eye Velocity $\dot E(s)$

Suppose $B(s) = \frac{T_p s + 1}{s}$ *B(s)* includes the inverse dynamics of *P(s)*

$$\frac{\dot E(s)}{\dot H(s)} = -C(s)B(s)P(s)s = -\frac{T_c s}{(T_c s + 1)} \frac{\cancel{(T_p s + 1)}}{\cancel{s}} \frac{\cancel{s}}{\cancel{(T_p s + 1)}} \approx -1$$

for $s = j\omega >> 1/T_c$,
$f = \omega/(2\pi) >> 0.03\text{Hz}$

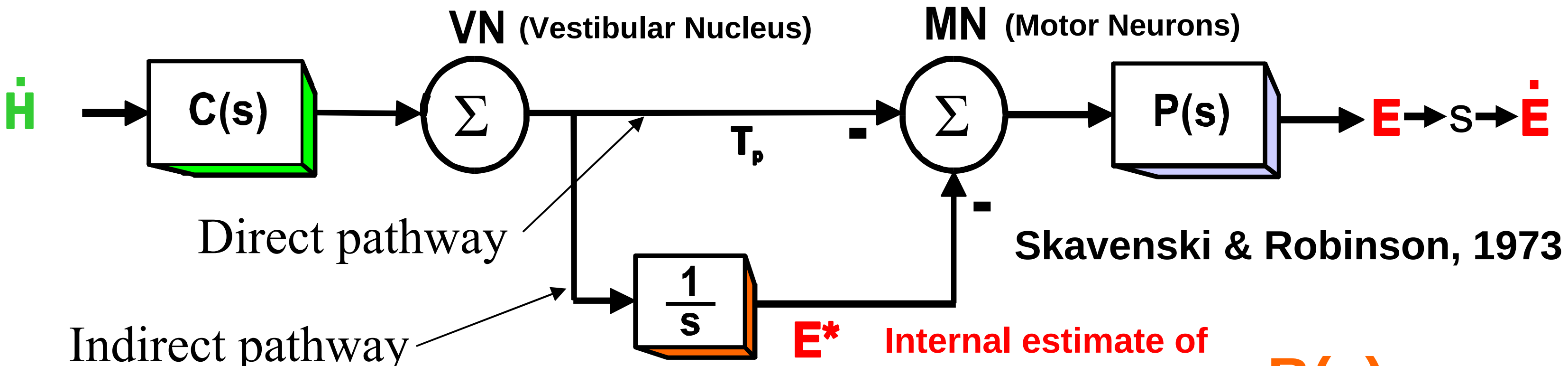


Conclusion:

- *B*(*s*) includes an inverse model of the eye plant dynamics
- *B*(*s*) includes an integrator (1/s)
- It is not a perfect neural integrator

$$B(s) = \frac{T_p s + 1}{T_I s + 1} \qquad T_I \text{ is large} \approx 20\text{s}$$

A simple feedforward model of the VOR system



Skavenski & Robinson, 1973

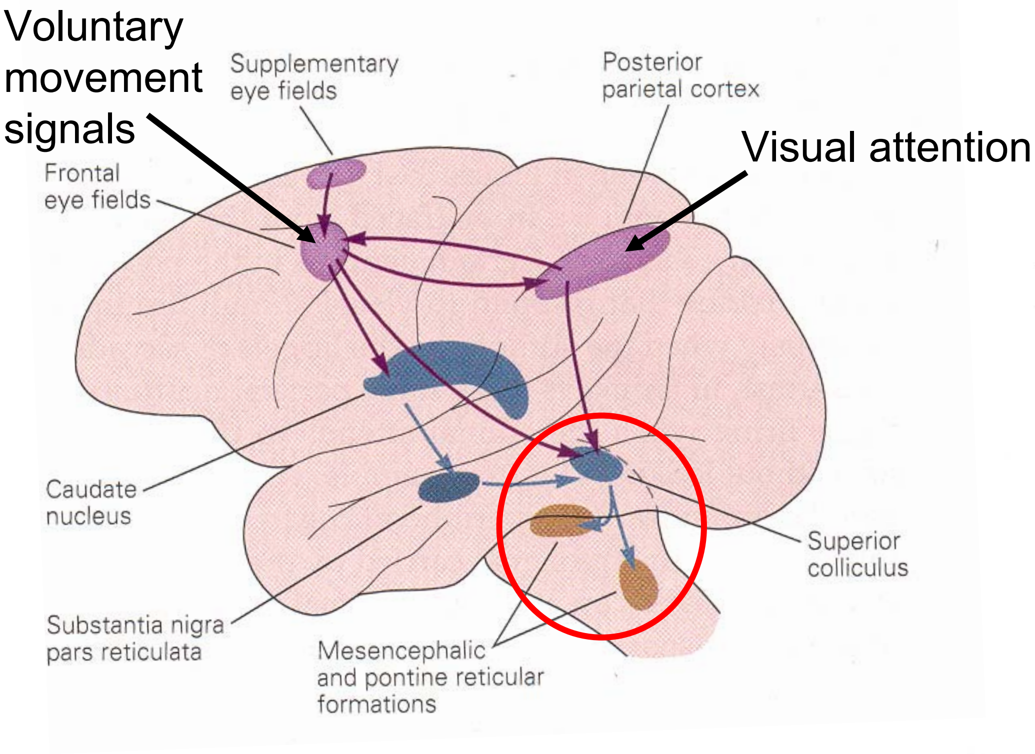
$$\frac{\dot{E}(s)}{\dot{H}(s)} = -C(s)\left[T_p + \frac{1}{s}\right]P(s)s = -\frac{T_c s}{(T_c s+1)}\overset{B(s)}{\left[\frac{\cancel{(T_p s+1)}}{\cancel{s}}\right]}\frac{\cancel{s}}{\cancel{(T_p s+1)}}$$

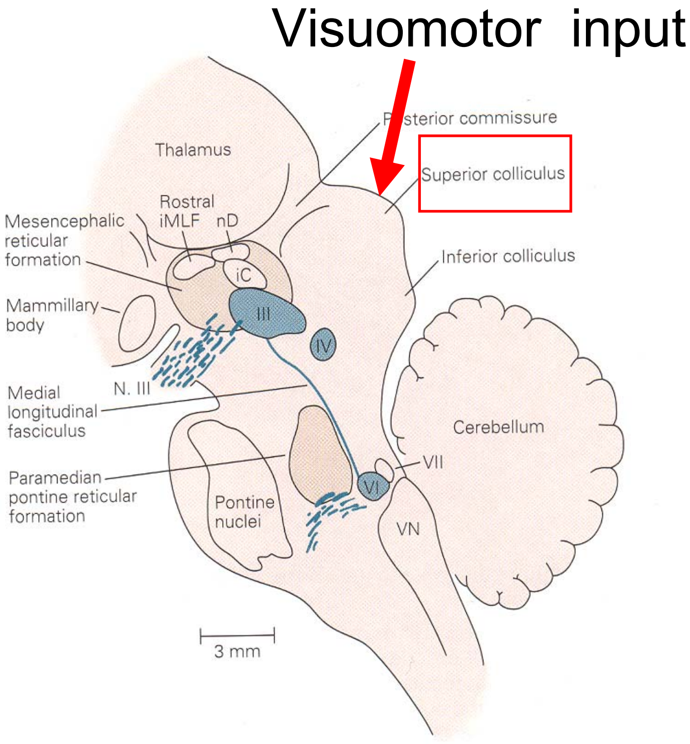
$$= -\frac{T_c s}{(T_c s+1)} \approx -1 \ \text{ for f} >> 0.03\ \text{Hz}$$

- The brainstem networks compute an inverse model of the plant using parallel pathways: a direct pathway and an indirect pathway through a neural integrator

<u>Prediction</u>: There should exist a neural integrator that can be identified by cells that encode an internal estimate (E*) of actual eye position (E)

Neural control of saccades

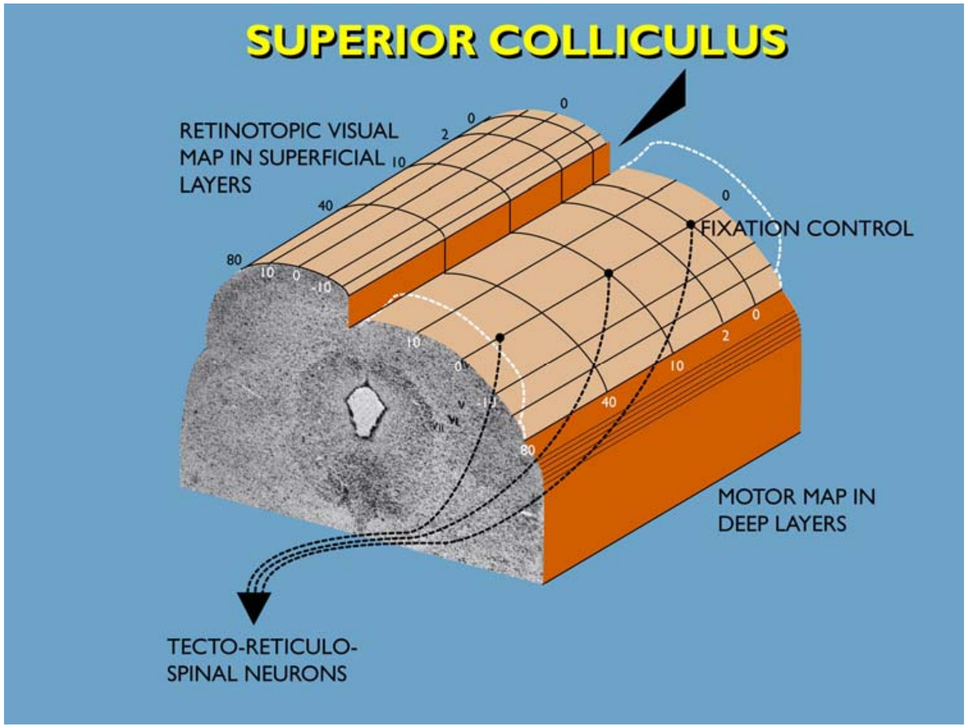


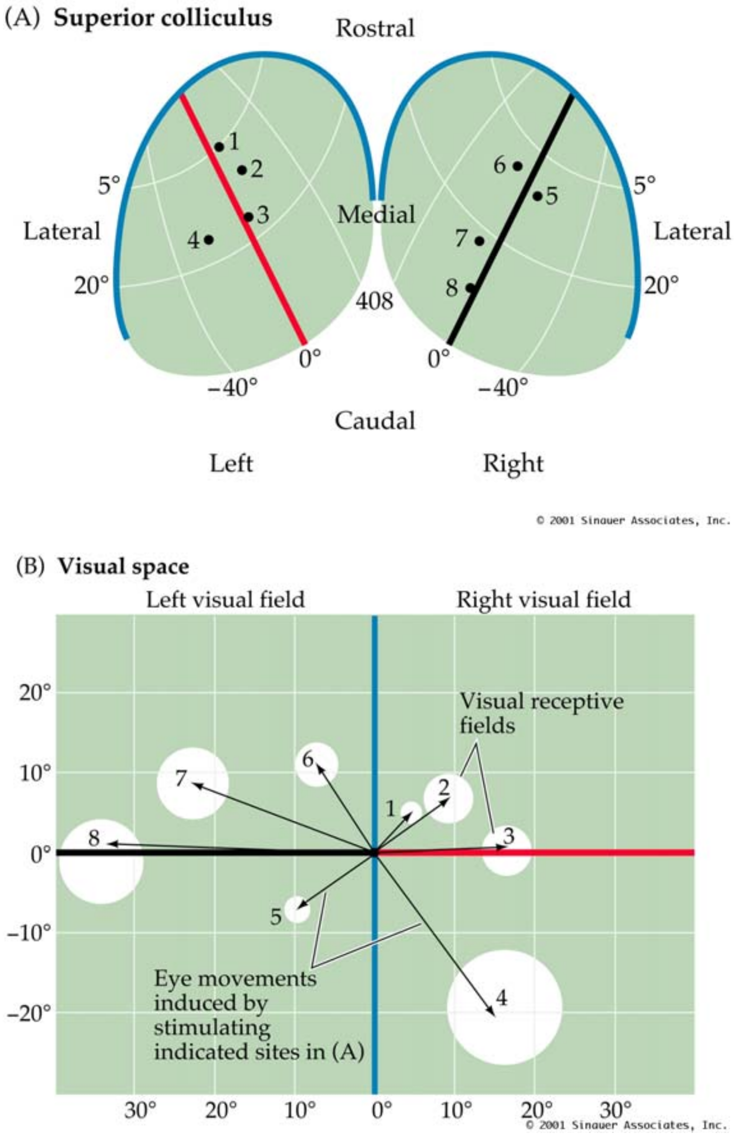


- Visual fixation and saccade initiation are controlled by a network of brain areas

- The command to move the eyes to a new position normally arises from visuomotor signals in the superior colliculus

The superior colliculus





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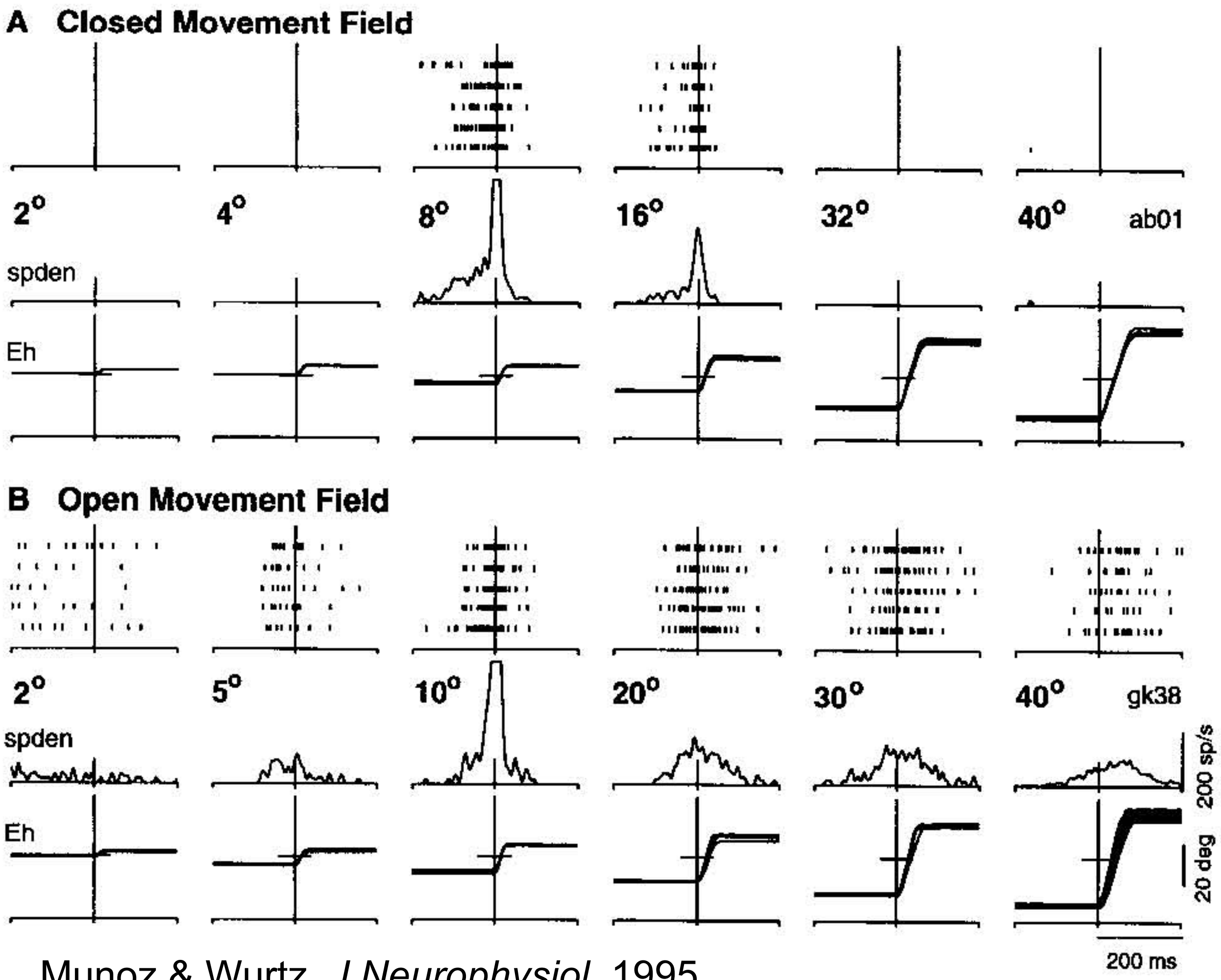
- The superior colliculus contains a topographic motor map composed of neurons that discharge a high frequency burst of activity before saccades
- The location of the burst on this map defines the vector direction and amplitude of the saccade

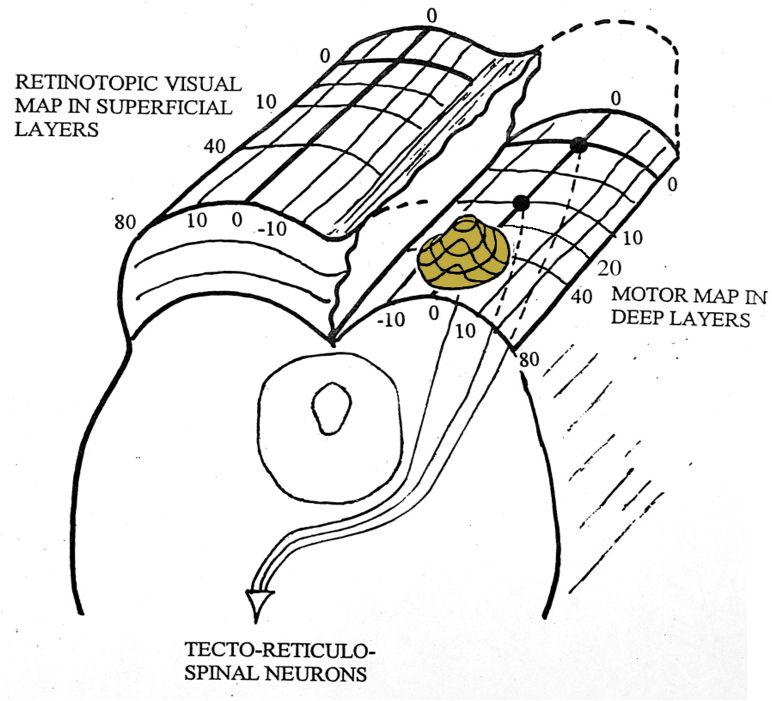
Superior colliculus saccade neurons

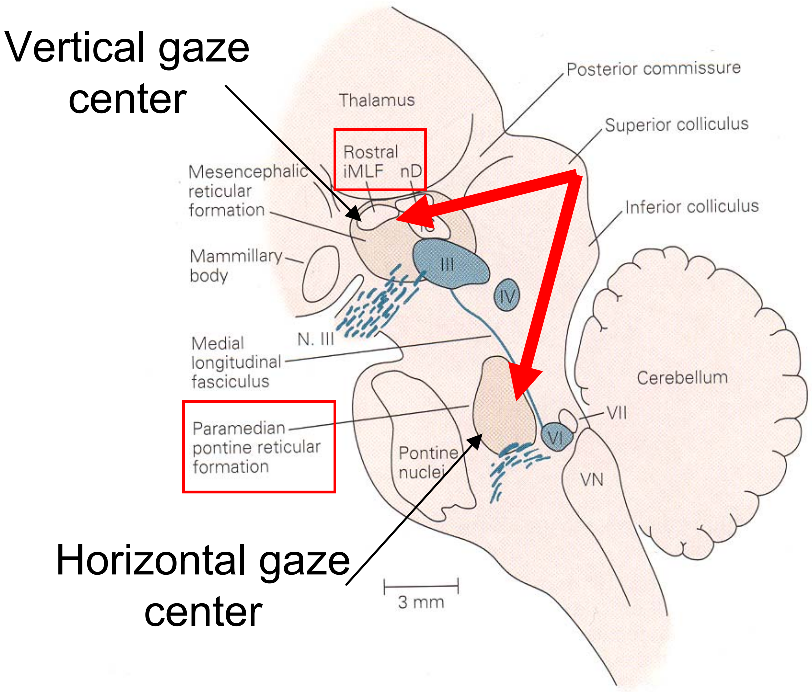


Munoz & Wurtz, *J Neurophysiol*, 1995

- Superior colliculus saccade neurons burst maximally for the amplitude and direction of saccade encoded by the region of the colliculus in which they are located

How is the motor command for saccades generated?

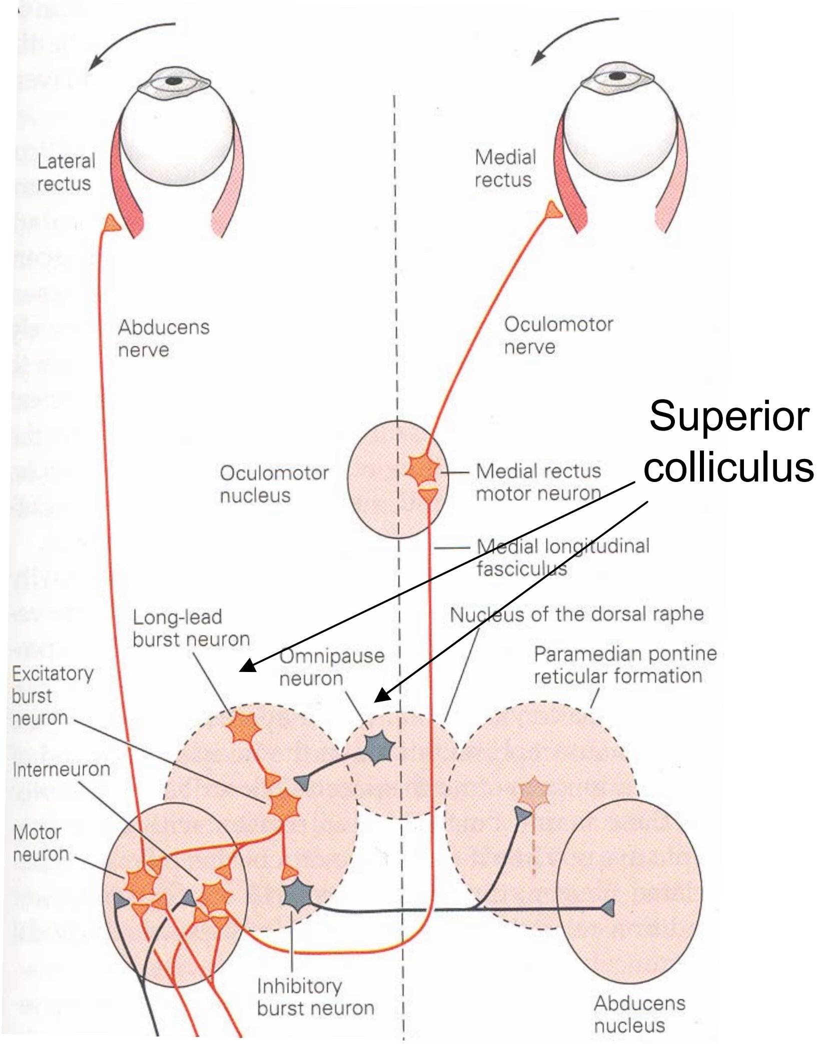



Vertical gaze center

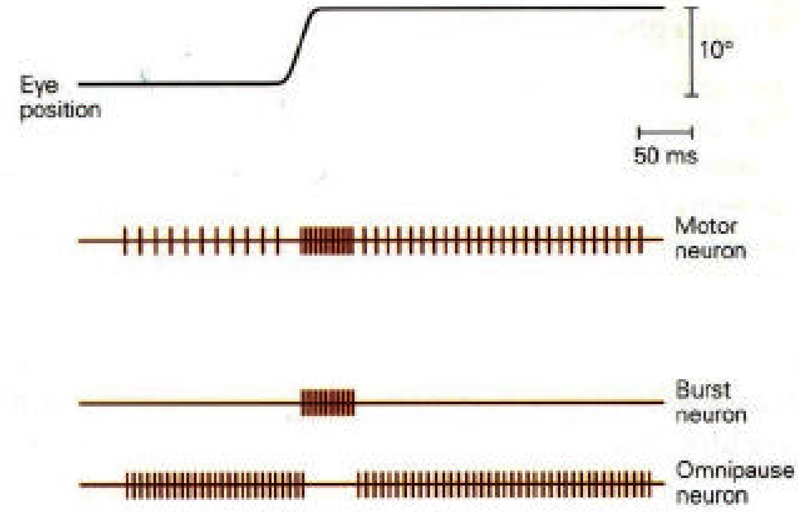
Horizontal gaze center

- The superior colliculus projects to horizontal and vertical gaze centers in the paramedian pontine reticular formation (PPRF) and rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF) that provide the burst (phasic or pulse) of activity that drives saccadic eye movements

How is the motor command for saccades generated?

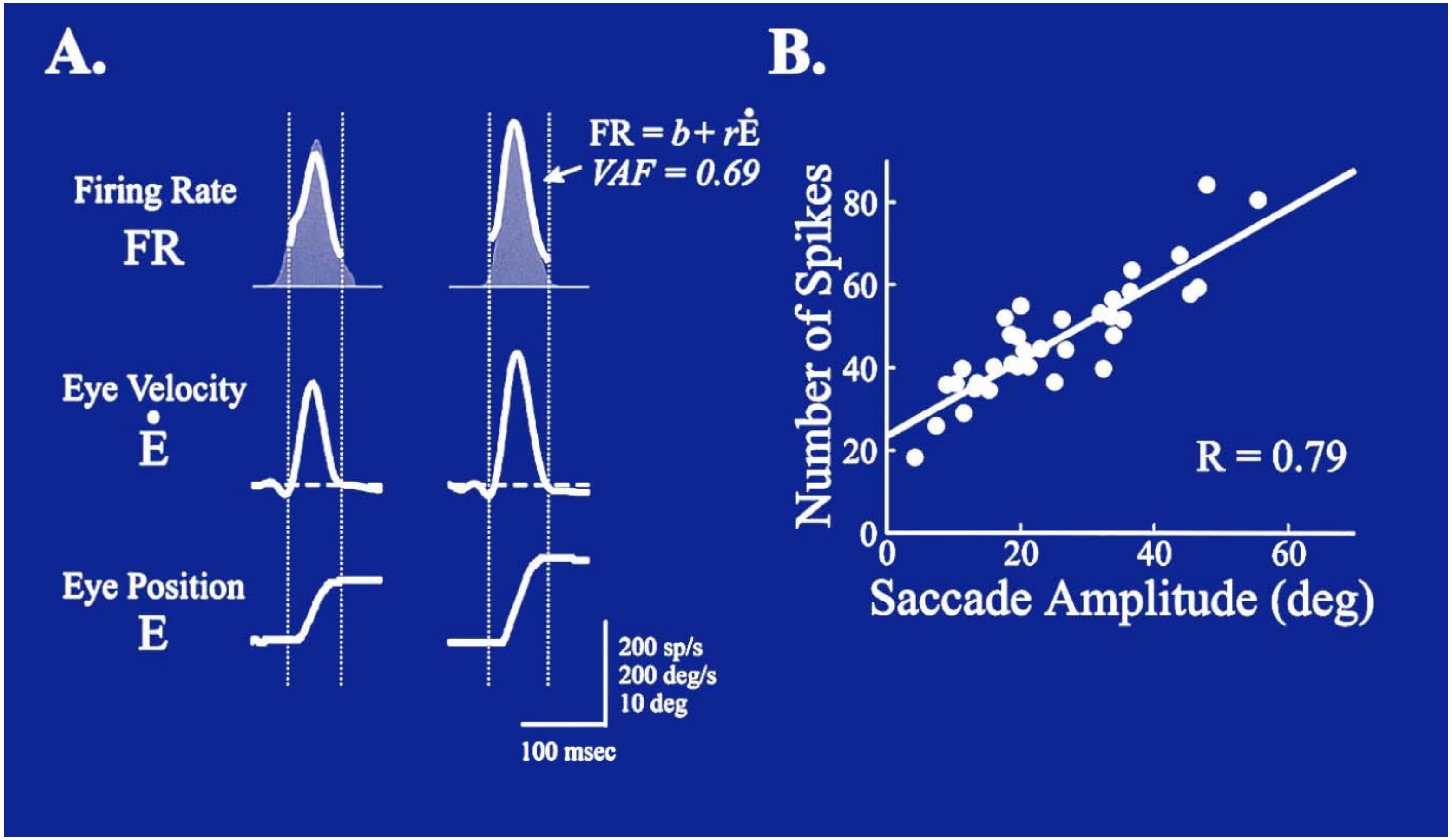


Superior colliculus



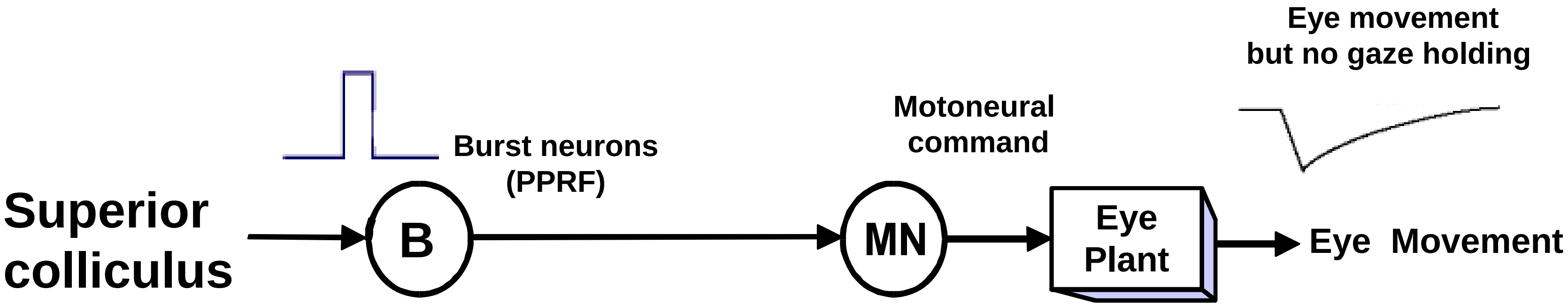
- Excitatory burst neurons in these gaze centers provide the excitatory phasic signal to agonist motor neurons
- Inhibitory burst neurons send signals to silence antagonist muscles
- Omnipause neurons inhibit burst neurons to prevent saccades during fixations and these cells must be silenced to generate a saccade

Burst neuron activity during saccades



- Burst neuron firing rate is directly correlated with saccade velocity
- The number of spikes in the burst is correlated with saccade amplitude

Saccade processing requires the generation of an eye position signal



Eye movement
but no gaze holding

Motoneural
command

Burst neurons
(PPRF)

Superior
colliculus

B

MN

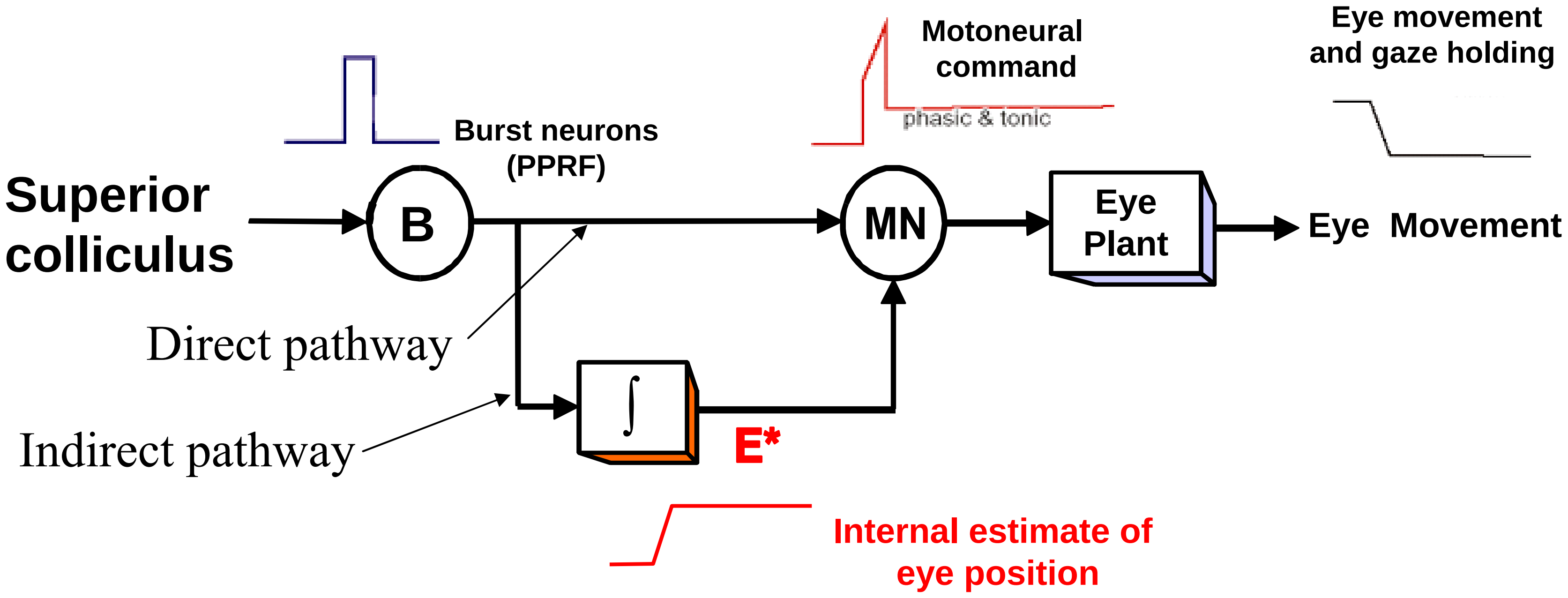
Eye
Plant

Eye Movement

- The pulse compensates for the visco-elastic properties of the eye plant and makes the eyes move to a new location as fast as possible
- However, there is no signal to keep the eyes in the new position so eye position decays back to center

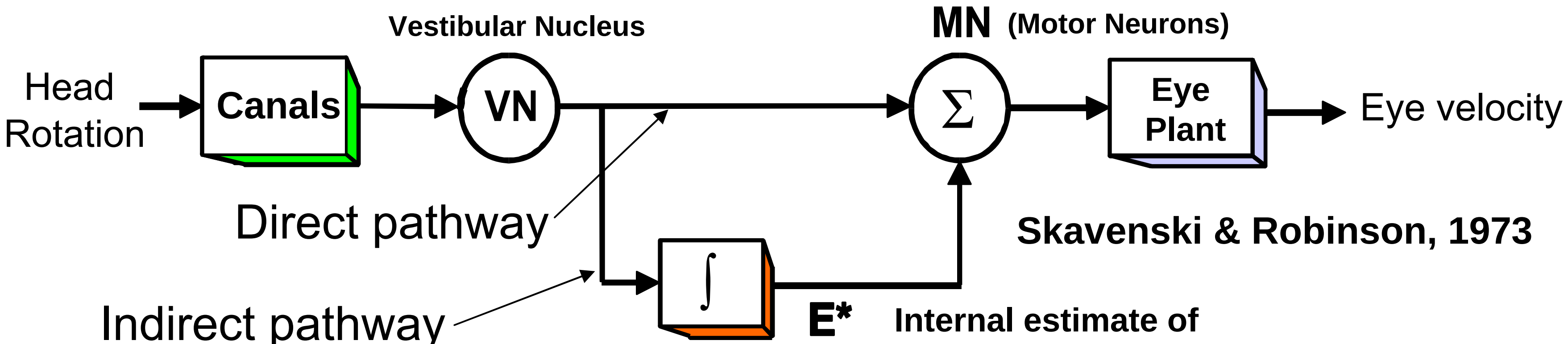
Where does the tonic (step) activity to hold the eye in a new position come from?

Saccade processing also requires a neural integrator



- David A. Robinson proposed that the tonic component of the motoneural command is generated by integrating the burst neuron signal

Comparison of the models proposed for saccades and the VOR



Vestibular Nucleus

MN (Motor Neurons)

Head Rotation

Canals

VN

Σ

Eye Plant

Eye velocity

Direct pathway

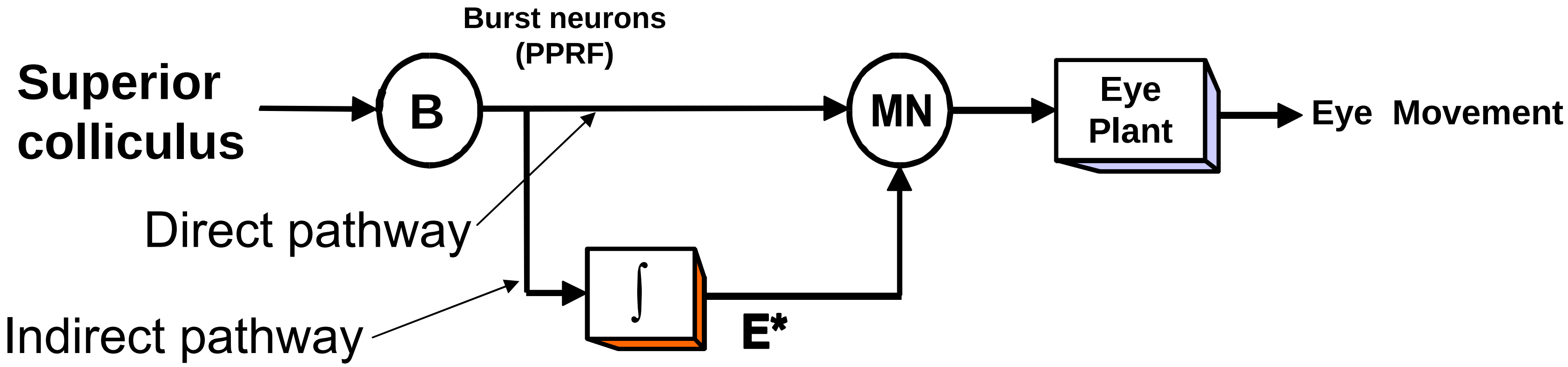
Indirect pathway

∫

E*

Internal estimate of eye position

Skavenski & Robinson, 1973



Burst neurons (PPRF)

Superior colliculus

B

MN

Eye Plant

Eye Movement

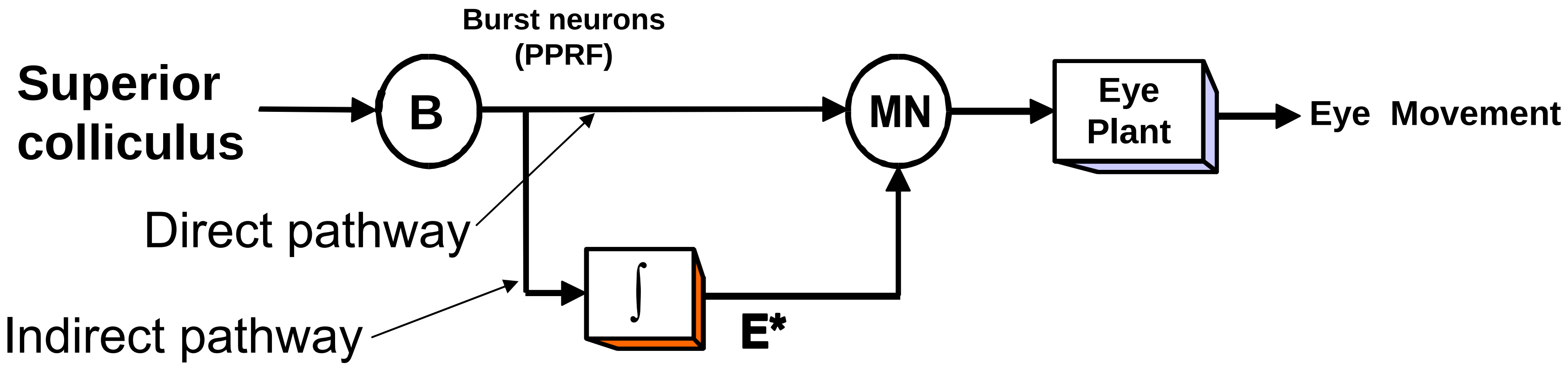
Direct pathway

Indirect pathway

∫

E*

Saccades are controlled by a feedback circuit



Burst neurons
(PPRF)

Superior colliculus

B

MN

Eye Plant

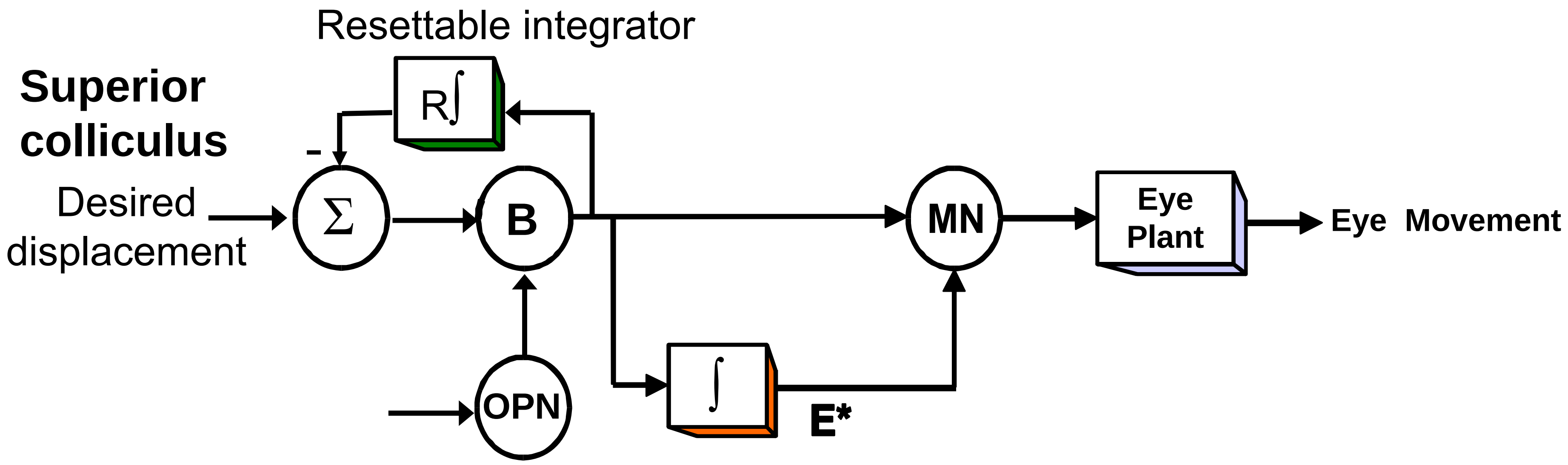
Eye Movement

Direct pathway

Indirect pathway

∫

E*



Resettable integrator

Superior colliculus

Desired displacement

R∫

-

Σ

B

MN

Eye Plant

Eye Movement

OPN

∫

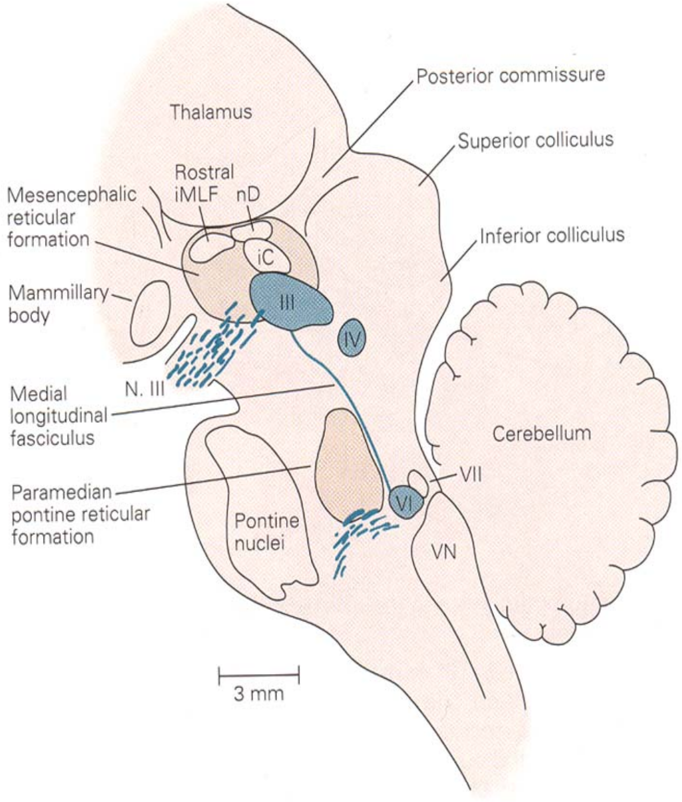
E*

Neurophysiological studies of oculomotor brainstem regions

- Correlation of cell responses with oculomotor behavior for different combinations of sensory stimuli

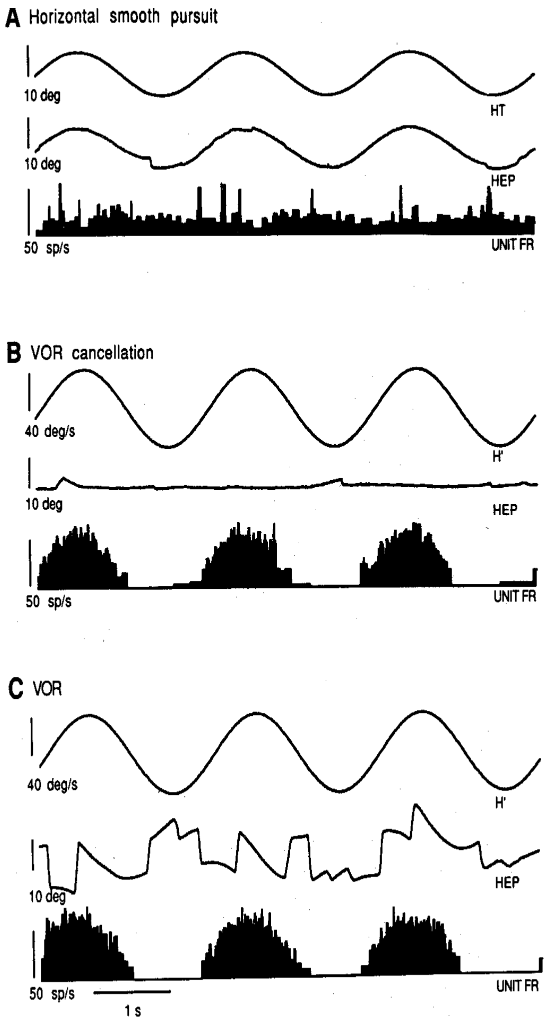
<u>Common Protocols</u>:

- Saccades and fixations
- Head movement in the dark
- Smooth Pursuit
- Visual-vestibular interaction conditions

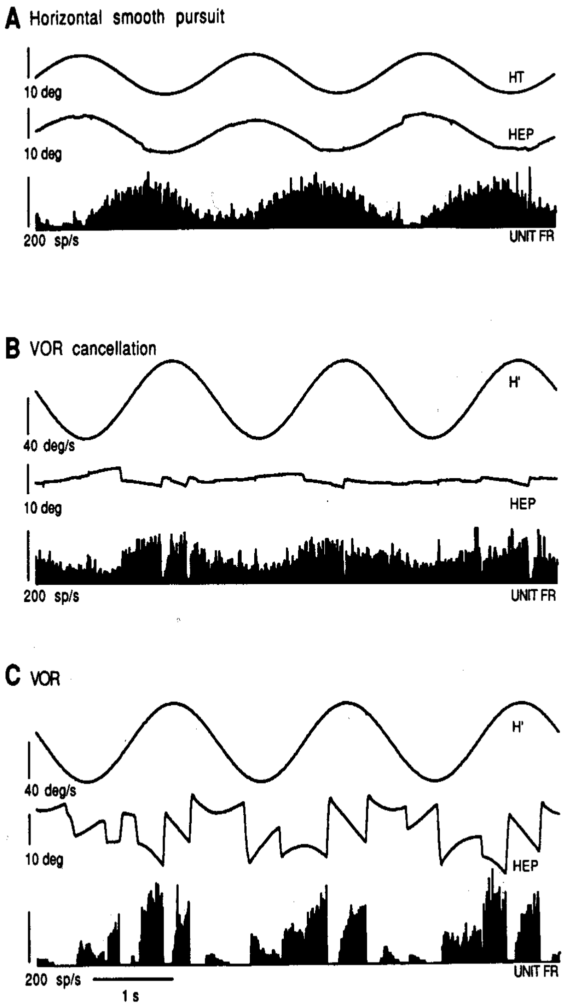


Vestibular nucleus neurons

Vestibular-Only Cell



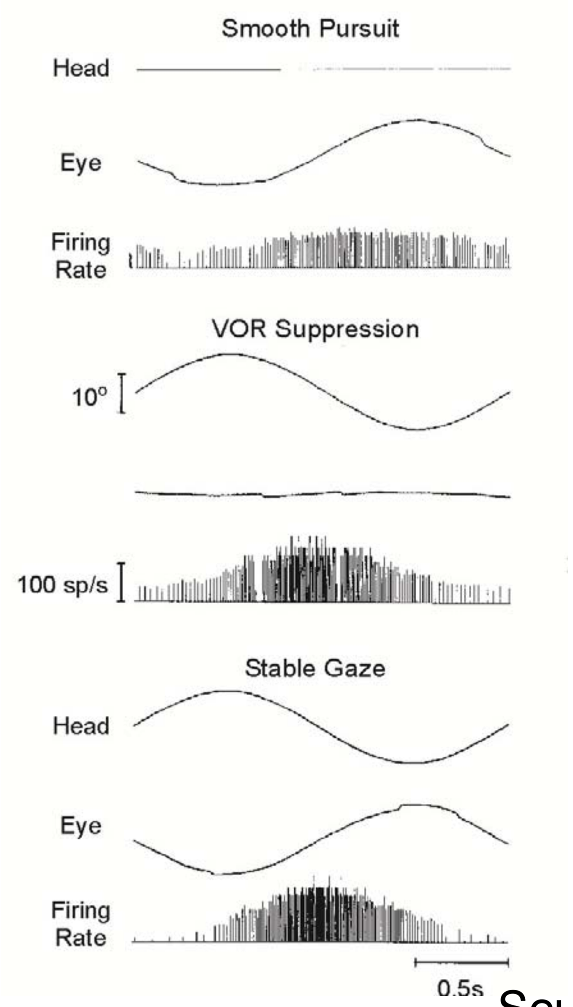
Position-Vestibular Cell



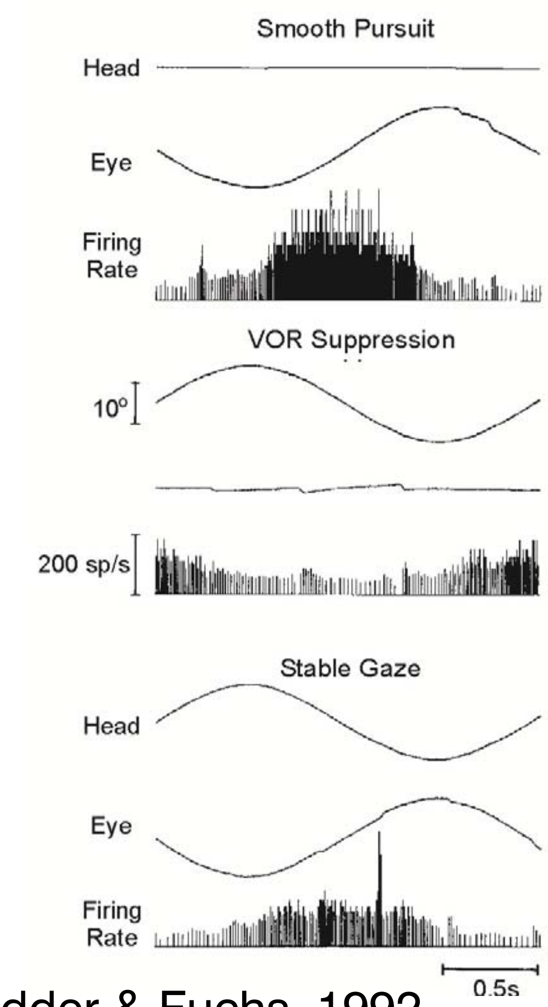
Cullen & McCrea, 1993a,b

Position-vestibular subtypes

Position-Vestibular-Pause (PVP)



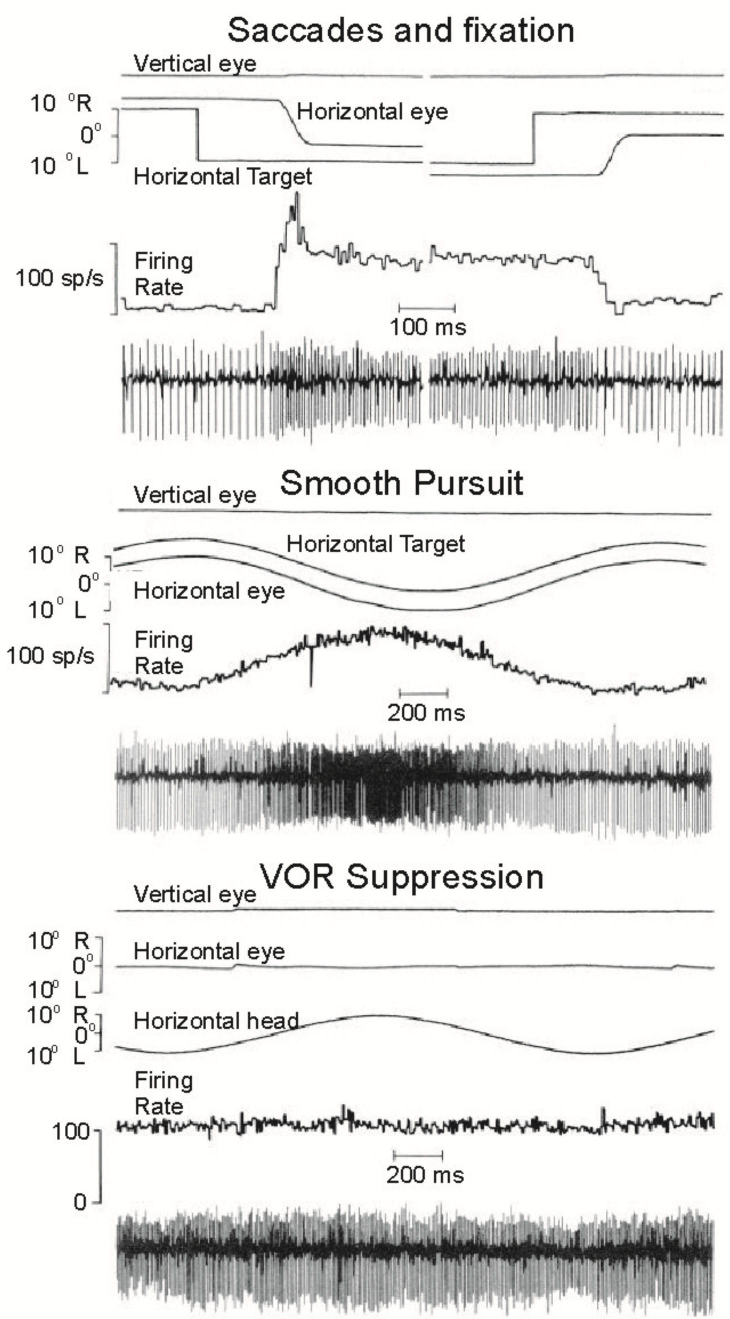
Eye-Head-Velocity (EHV)



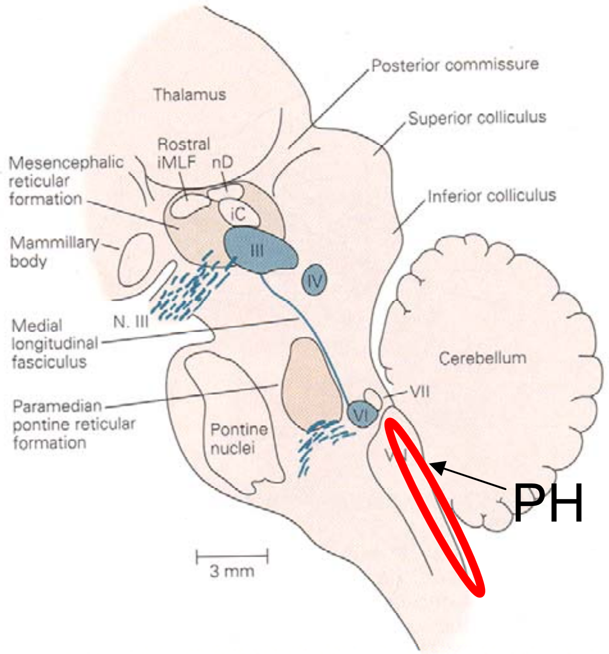
Scudder & Fuchs, 1992

- Both cell types make direct projections to extraocular motor neurons
- The different subtypes can be distinguished functionally by their distinct patterns of responses to combined vestibular and visual stimuli
- Many EHV cells receive direct projections from the cerebellar flocculus

Burst-position cell in the Prepositus Hypoglossi (PH)

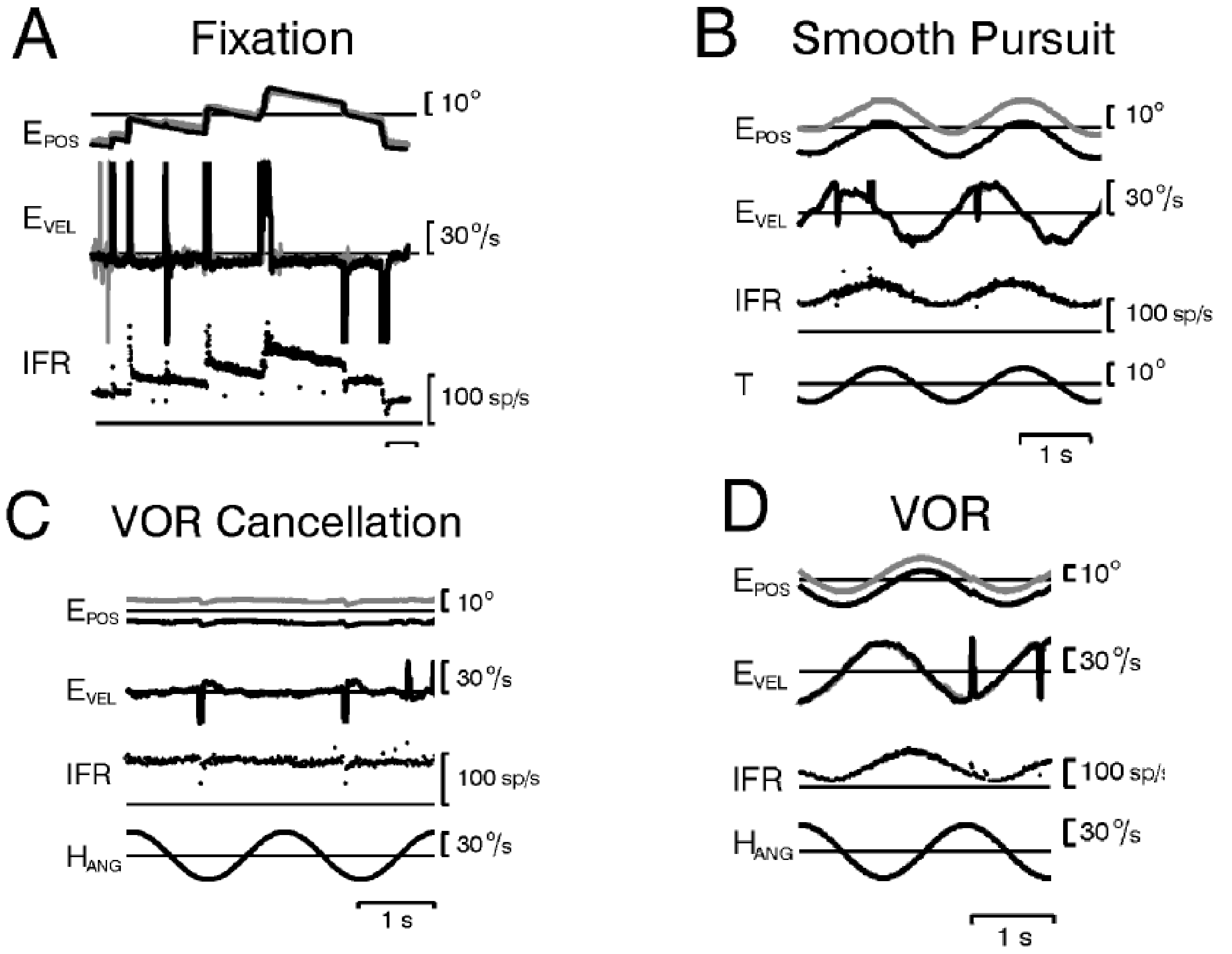


McFarland & Fuchs, 1992



- Neural responses closely correlated with eye position (often burst-position activity)
- No response to head movement in the absence of eye movement

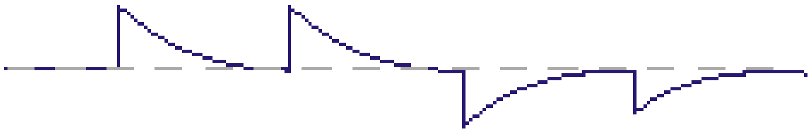
Burst-Position Neuron in the Prepositus Hypoglossi

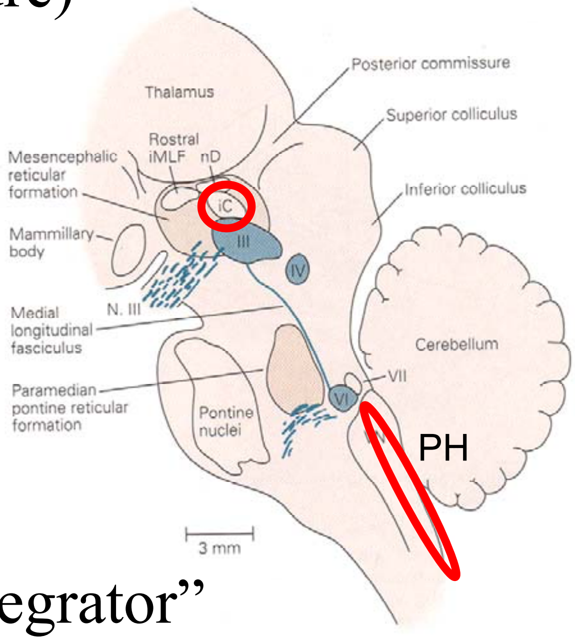


Green et al, 2007

Neurons in the Prepositus Hypoglossi

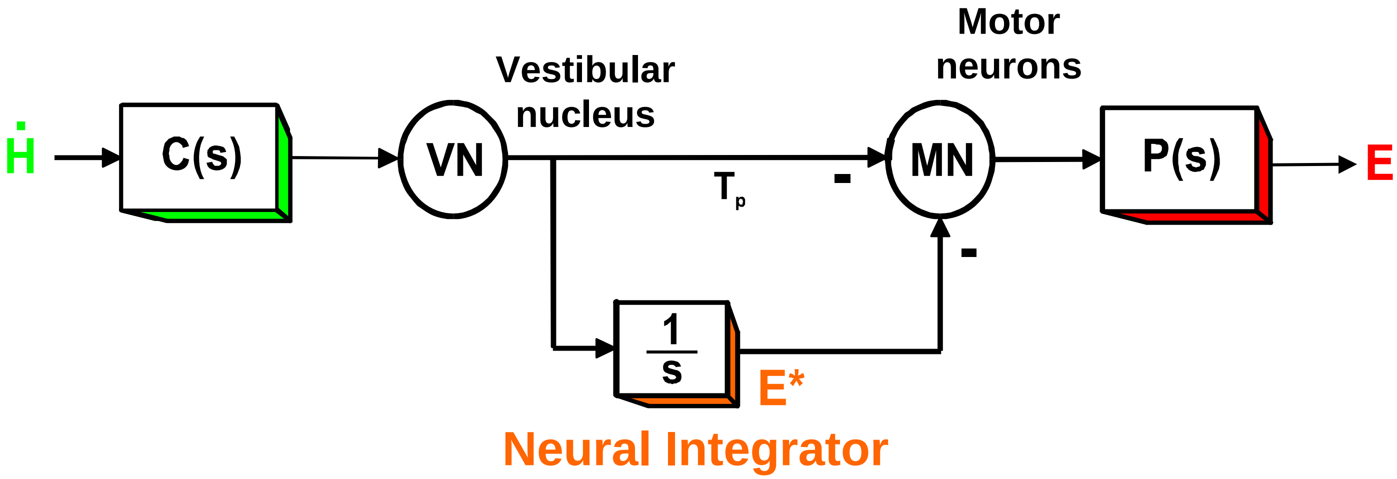
- Many cells exhibit responses closely correlated with eye position (often burst-position activity)
- Lesions to this area result in a severe deterioration in integrator performance (e.g. severe gaze-holding failure)

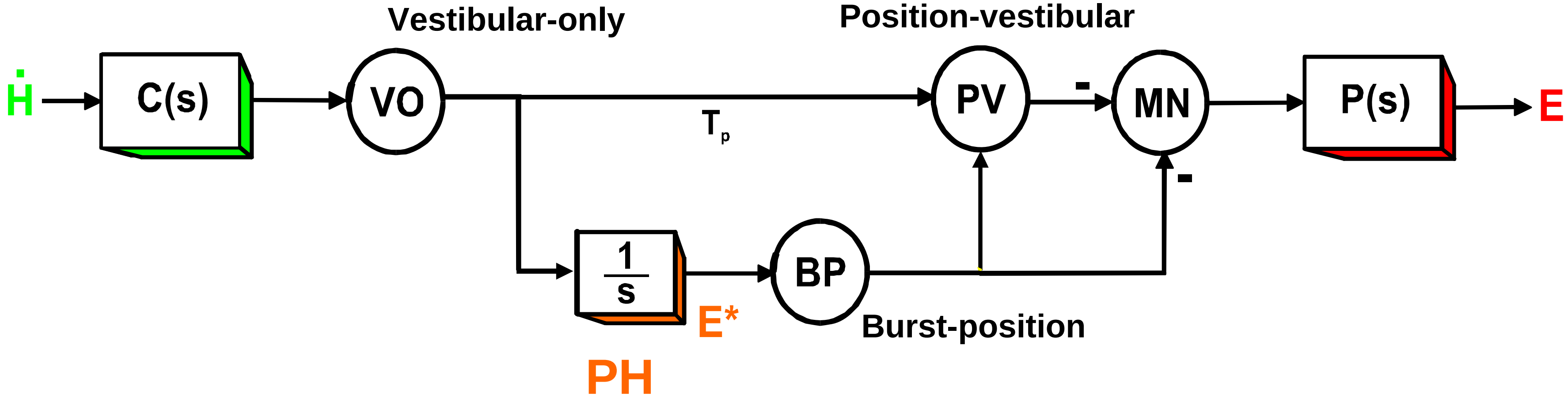




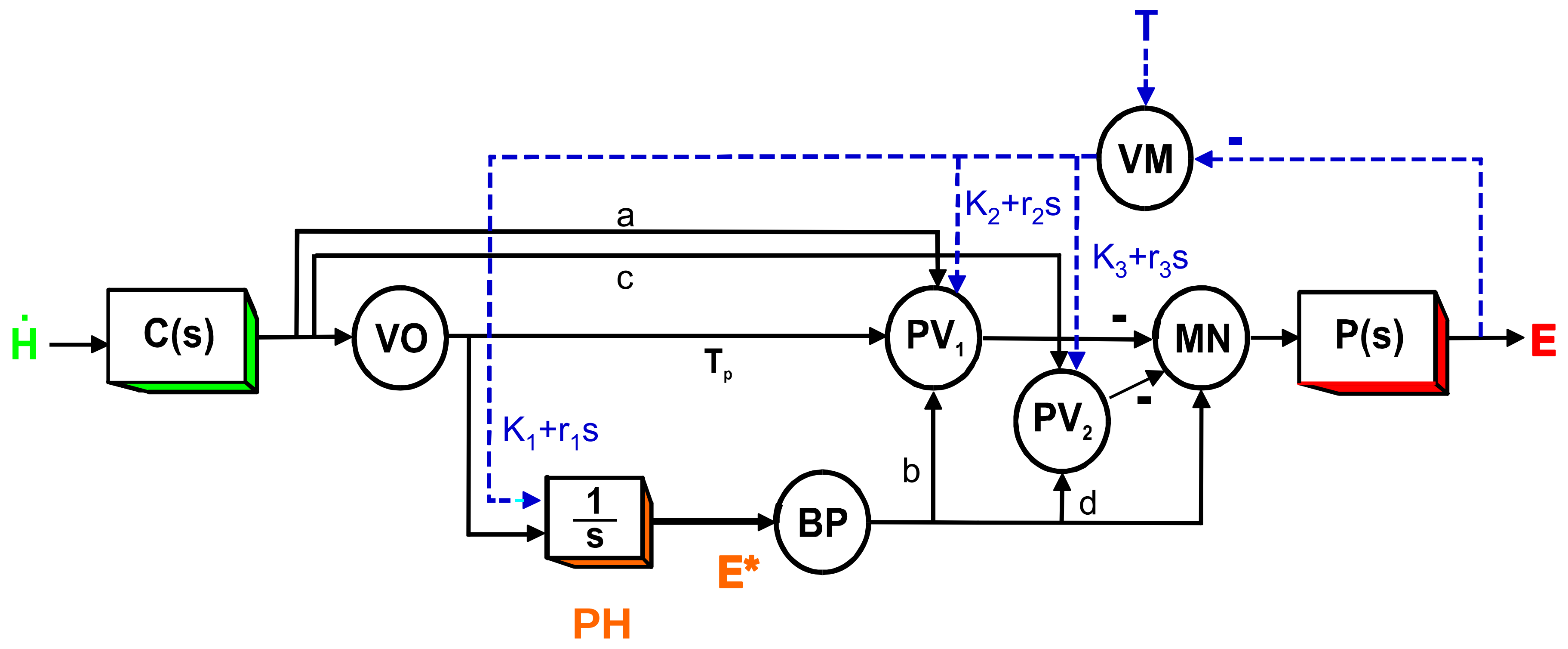
→ Postulated as the site of the “neural integrator”

Incorporating distinct cell types in VOR models



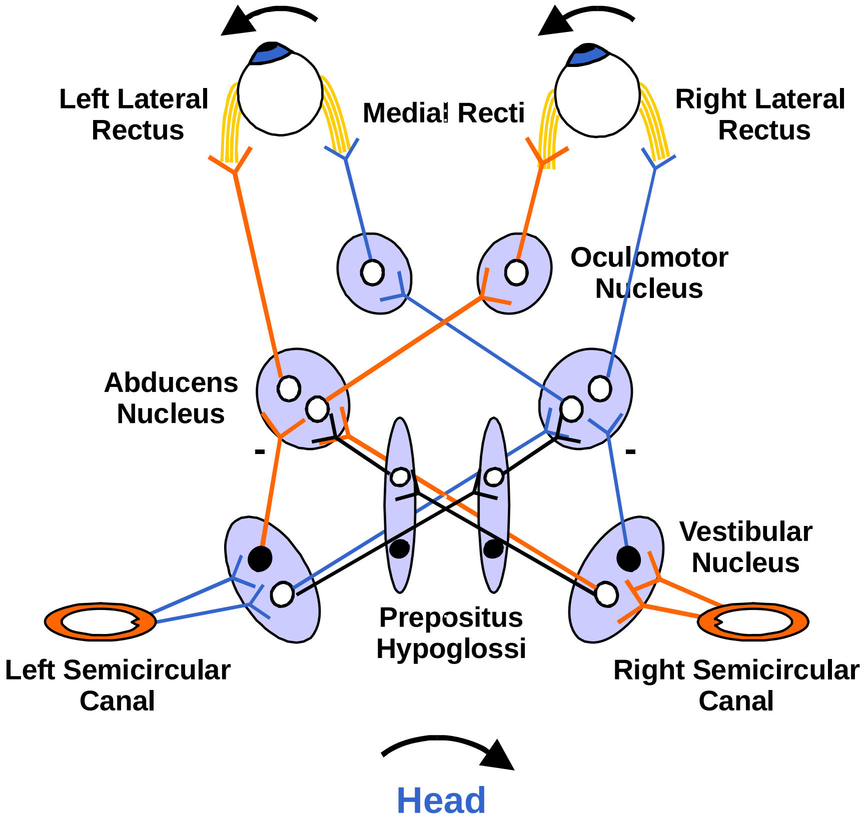


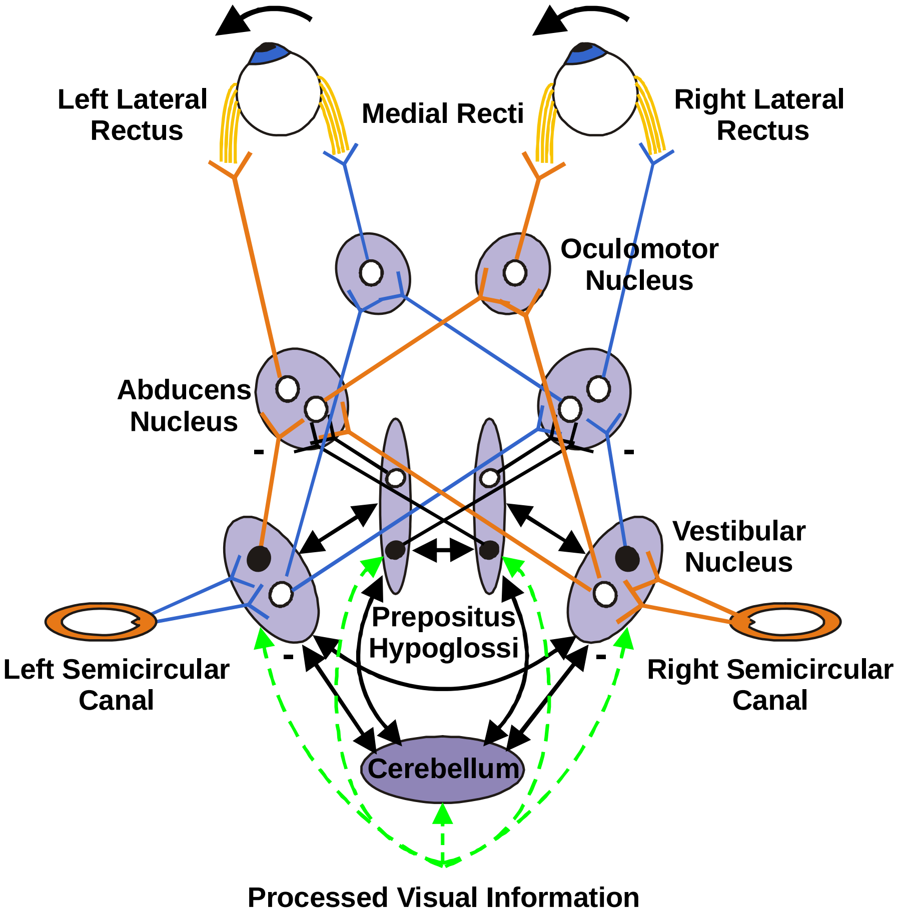
Incorporating different position-vestibular (PV) cell subtypes



- Cell types with unique dynamic characteristics emerge by virtue of different signal projection weights

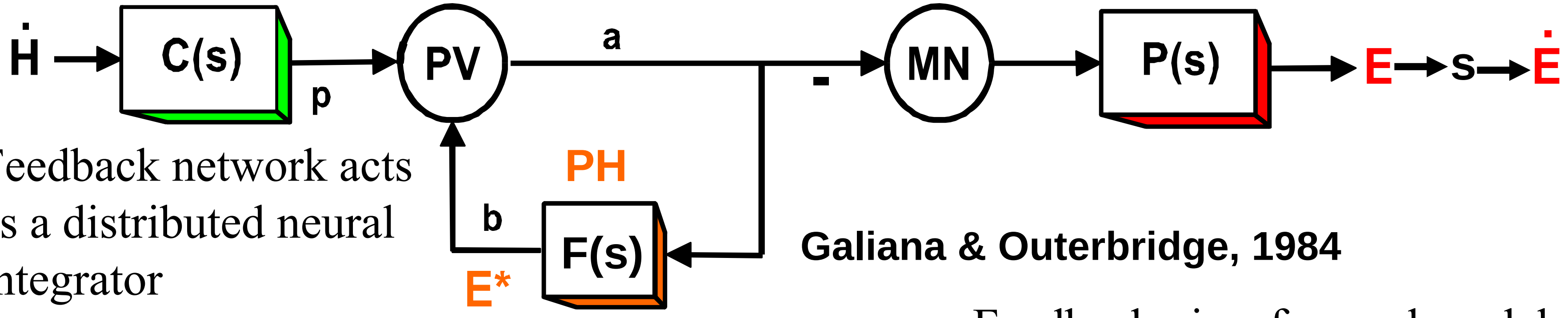
Brainstem premotor network





- The actual premotor network is highly interconnected with reciprocal (feedback) projections between the vestibular nuclei, prepositus hypoglossi and cerebellum
- Lesions anywhere within this circuit give rise to changes in integrator function

Feedback model of the premotor eye movement network



- Feedback network acts as a distributed neural integrator

Galiana & Outerbridge, 1984

Internal Forward Model of Eye Plant

F(s)=P(s)=1/(T_ps+1)

- Feedback via a forward model so that the network implements the inverse dynamics of the eye plant

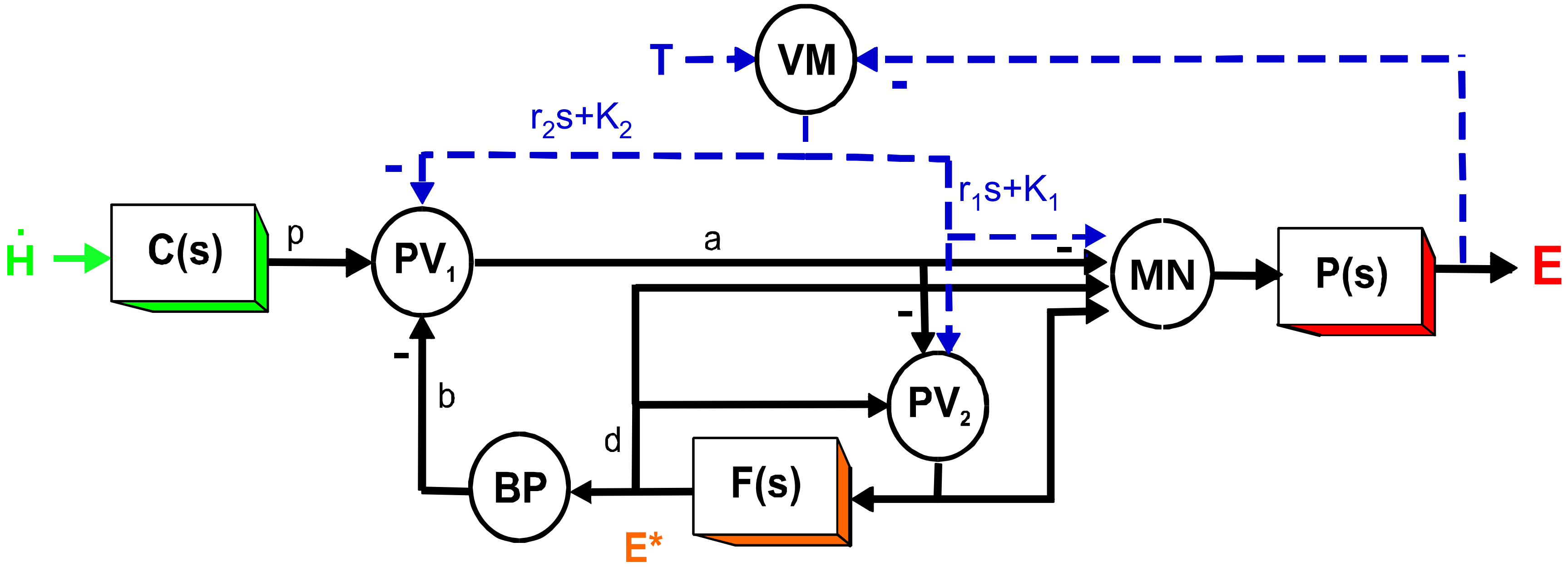
$$\frac{\dot{E}(s)}{\dot{H}(s)} = -s\left[\frac{T_c s}{T_c s+1}\right]\left[\frac{pa}{1-abF(s)}\right]\left[\frac{1}{T_p s+1}\right] = -s\left[\frac{T_c s}{T_c s+1}\right]\left[\frac{G(\cancel{T_p s+1})}{T_I s+1}\right]\left[\frac{1}{\cancel{T_p s+1}}\right]$$

$$T_I = \frac{T_p}{1-ab} \qquad G = \frac{pa}{1-ab} \qquad = -\left[\frac{T_c s}{T_c s+1}\right]\left[\frac{G\cancel{s}}{\cancel{T_I s+1}}\right] \approx -1 \text{ for } G/T_I=1$$

f>>0.03Hz

set parameters so $T_I >> T_p \approx 20$ s → $\frac{1}{T_I s+1}$ approximates an integrator $\frac{1}{s}$

Distinct cell types in a feedback model



$$E(s) = \frac{G_E}{(T_I s + 1)} \frac{T_c s}{(T_c s + 1)} \dot{H}(s)$$

$$BP(s) = \frac{G_{BP}}{(T_I s + 1)} \frac{T_c s}{(T_c s + 1)} \dot{H}(s)$$

$$PV(s) = \frac{G_{PV}(T_{PV} s + 1)}{(T_I s + 1)} \frac{T_c s}{(T_c s + 1)} \dot{H}(s)$$

$$T_I = \frac{T_p}{1 - ab - d}$$

- Each cell type has different dynamic properties

$$T_{PV1} = \frac{T_p}{1 - d} \qquad T_{PV2} = T_P$$

Distinctions between feedforward and feedback implementations

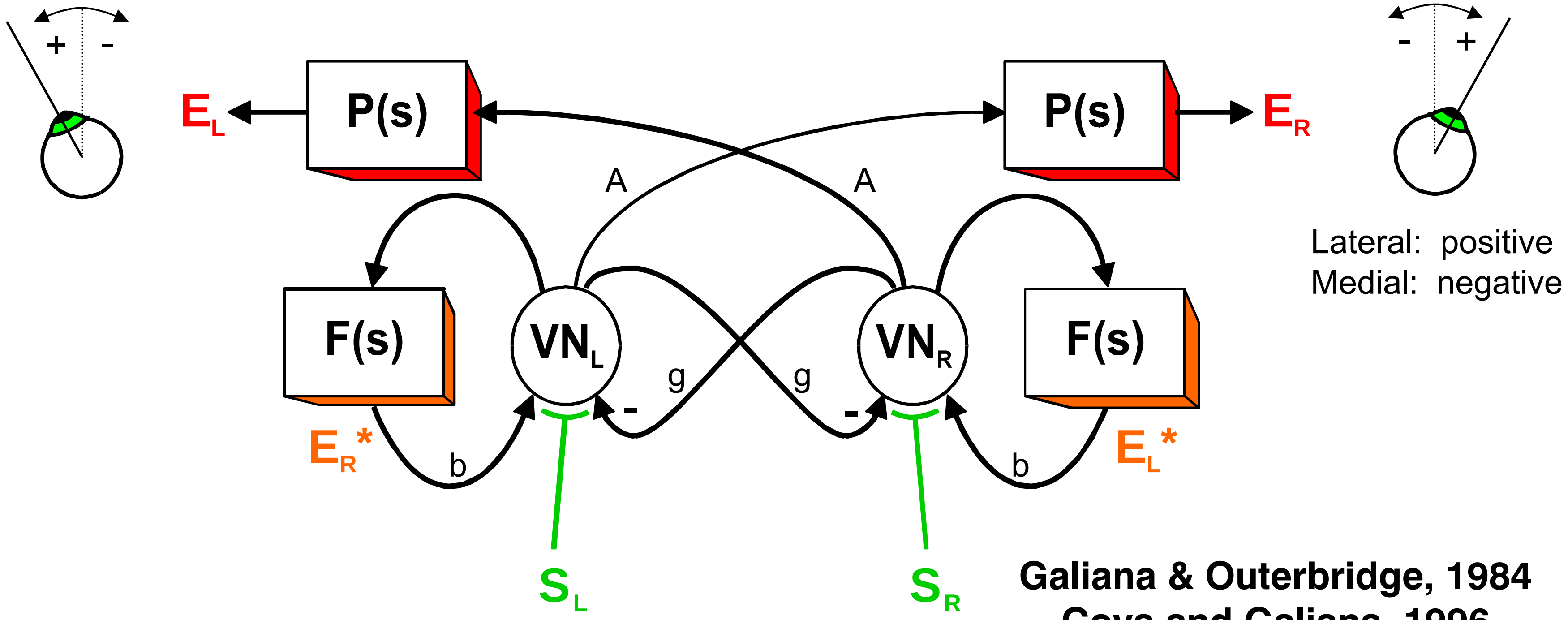
Feedforward:

- a localized neural integrator is assumed
- the integrator generates an internal eye position signal
- the emergence of distinct cell types depends on the weights of signal projections

Feedback:

- network performs a distributed integration
- internal forward model of the plant generates an internal estimate of eye position
- network topology plays a significant role in the emergence of distinct cell types
- More physiologically

Bilateral premotor structure



Galiana & Outerbridge, 1984
Cova and Galiana, 1996

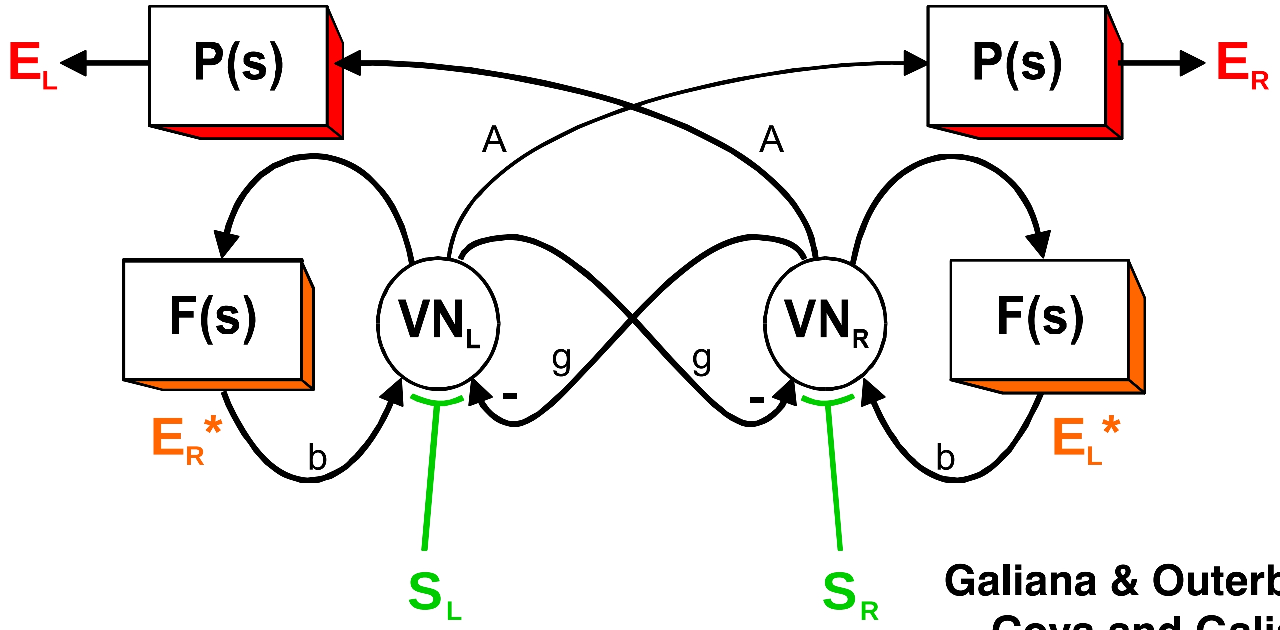
$E_{conj}(s) = (E_R(s) - E_L(s))/2 \longrightarrow$ Conjugate eye movement

$E_{verg}(s) = -(E_R(s) + E_L(s)) \longrightarrow$ Vergence eye movement

$S_R(s) - S_L(s) \longrightarrow$ Differential sensory input

$S_R(s) + S_L(s) \longrightarrow$ Common sensory input

Bilateral premotor structure



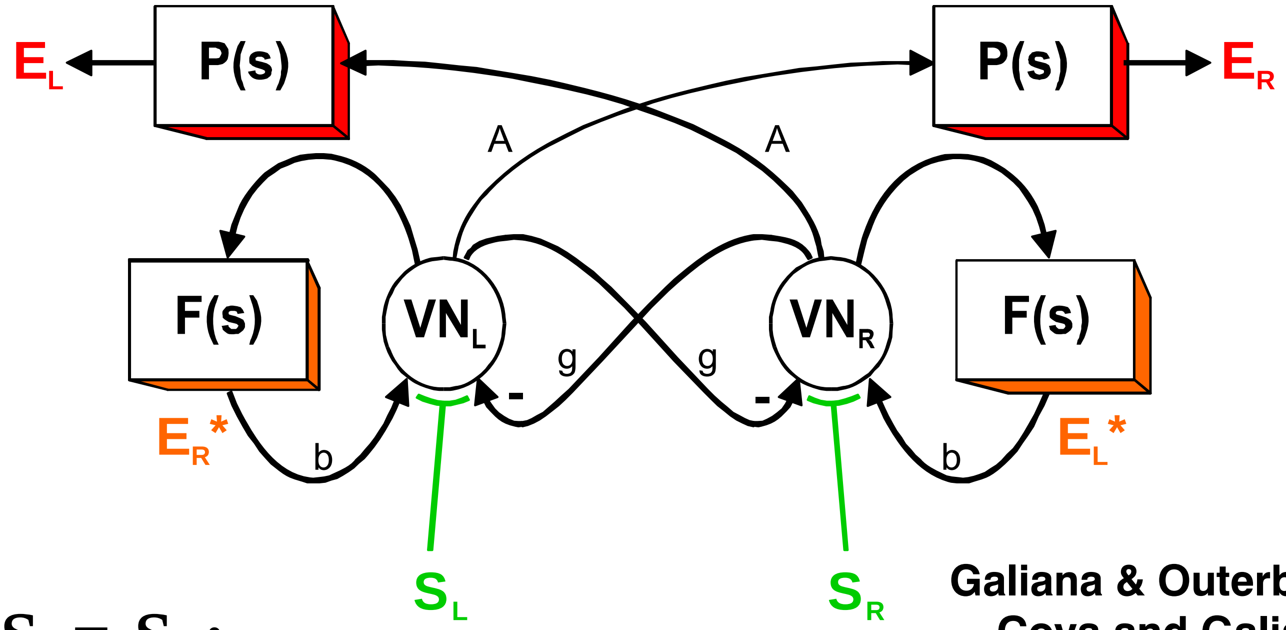
Galiana & Outerbridge, 1984
Cova and Galiana, 1996

$$E_R(s) = -G_d(s)\left[S_R(s) - S_L(s)\right] + G_c(s)\left[S_R(s) + S_L(s)\right]$$

$$E_L(s) = G_d(s)\left[S_R(s) - S_L(s)\right] + G_c(s)\left[S_R(s) + S_L(s)\right]$$

$$E_{conj}(s) = -G_d(s)\left[S_R(s) - S_L(s)\right] \qquad E_{verg}(s) = -2G_c(s)\left[S_R(s) + S_L(s)\right]$$

Bilateral premotor structure



Galiana & Outerbridge, 1984
Cova and Galiana, 1996

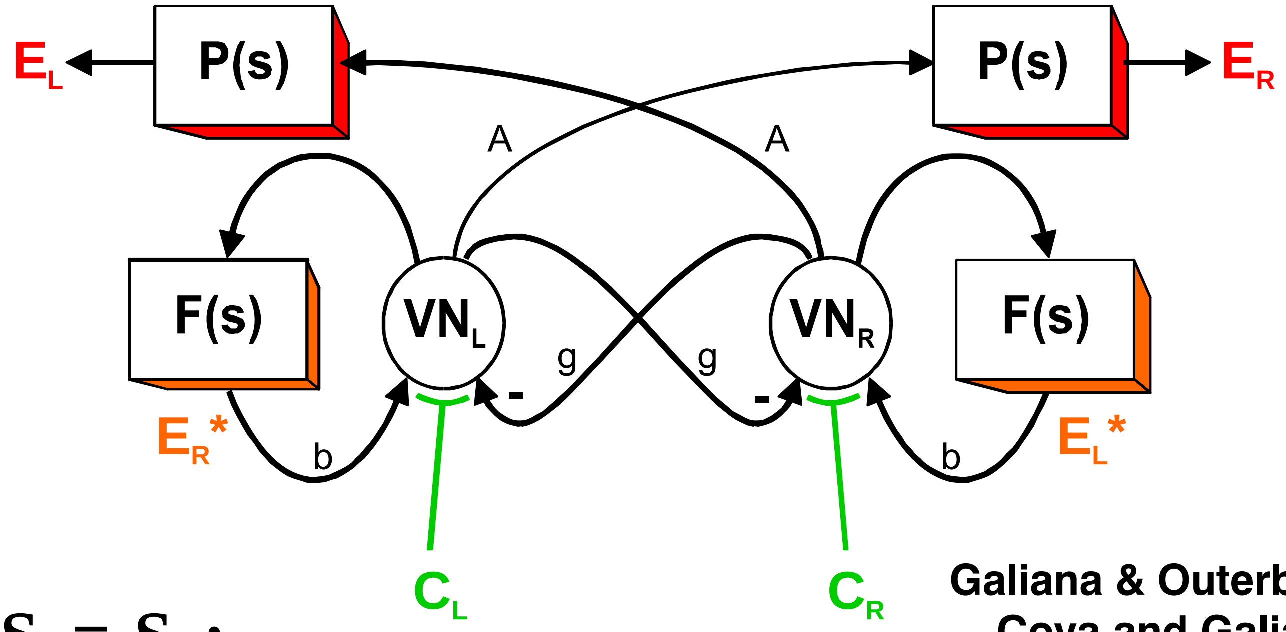
When S_R=-S_L:

$$E_R(s) = -G_d(s)\left[S_R(s) - S_L(s)\right] + G_c(s)\xcancel{\left[S_R(s) + S_L(s)\right]}$$

$$E_L(s) = G_d(s)\left[S_R(s) - S_L(s)\right] + G_c(s)\xcancel{\left[S_R(s) + S_L(s)\right]}$$

$$E_{conj}(s) = -G_d(s)\left[S_R(s) - S_L(s)\right] \qquad \xcancel{E_{verg}(s) = -2G_c(s)\left[S_R(s) + S_L(s)\right]}$$

Bilateral premotor structure



Galiana & Outerbridge, 1984
Cova and Galiana, 1996

When S_R=-S_L:

$$E_R(s) = -G_d(s)\left[S_R(s) - S_L(s)\right] + \xcancel{G_c(s)\left[S_R(s) + S_L(s)\right]}$$

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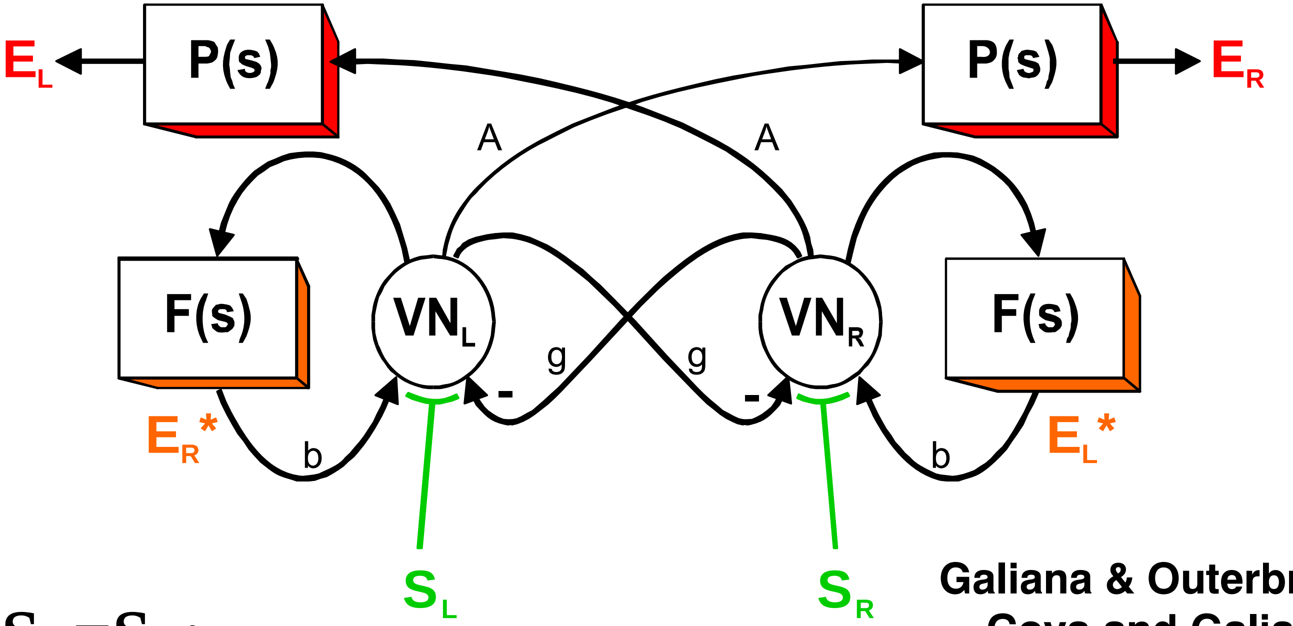
Bilateral premotor structure



Galiana & Outerbridge, 1984
Cova and Galiana, 1996

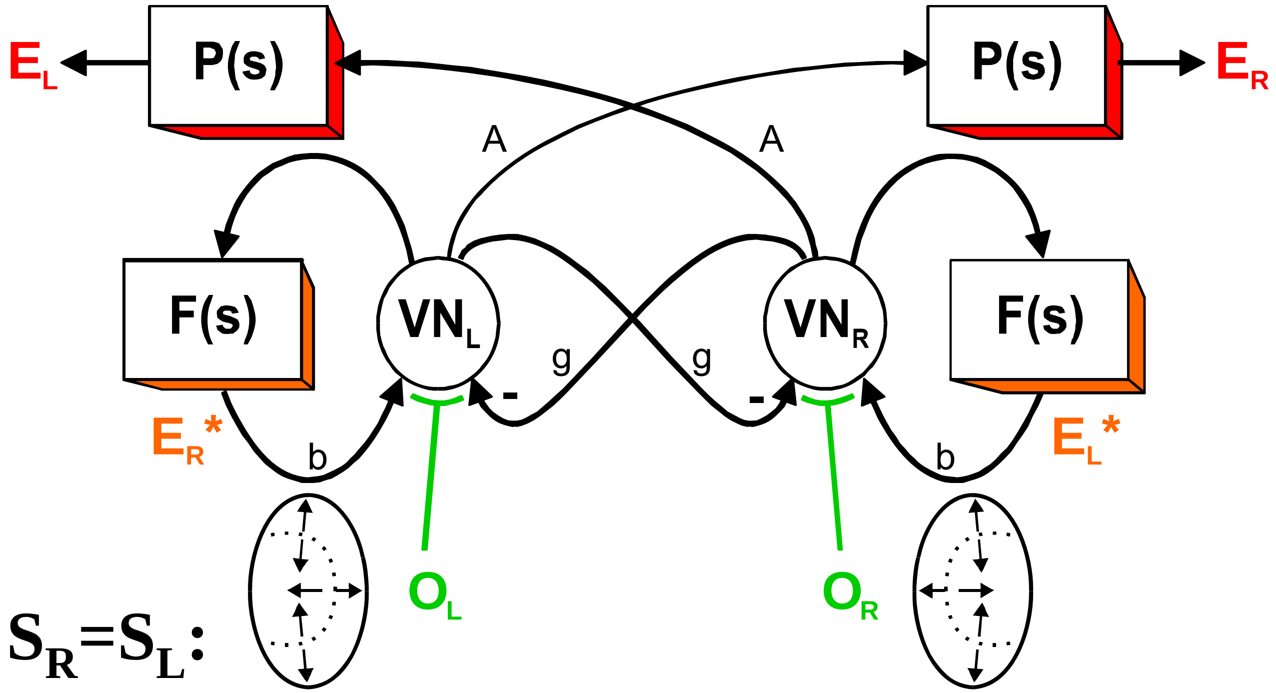
When $S_R=S_L$:

$$E_R(s) = \cancel{-G_d(s)\left[S_R(s)-S_L(s)\right]} + G_c(s)\left[S_R(s)+S_L(s)\right]$$

$$E_L(s) = \cancel{G_d(s)\left[S_R(s)-S_L(s)\right]} + G_c(s)\left[S_R(s)+S_L(s)\right]$$

$$\cancel{E_{conj}(s) = -G_d(s)\left[S_R(s)-S_L(s)\right]} \qquad E_{verg}(s) = -2G_c(s)\left[S_R(s)+S_L(s)\right]$$

Bilateral premotor structure



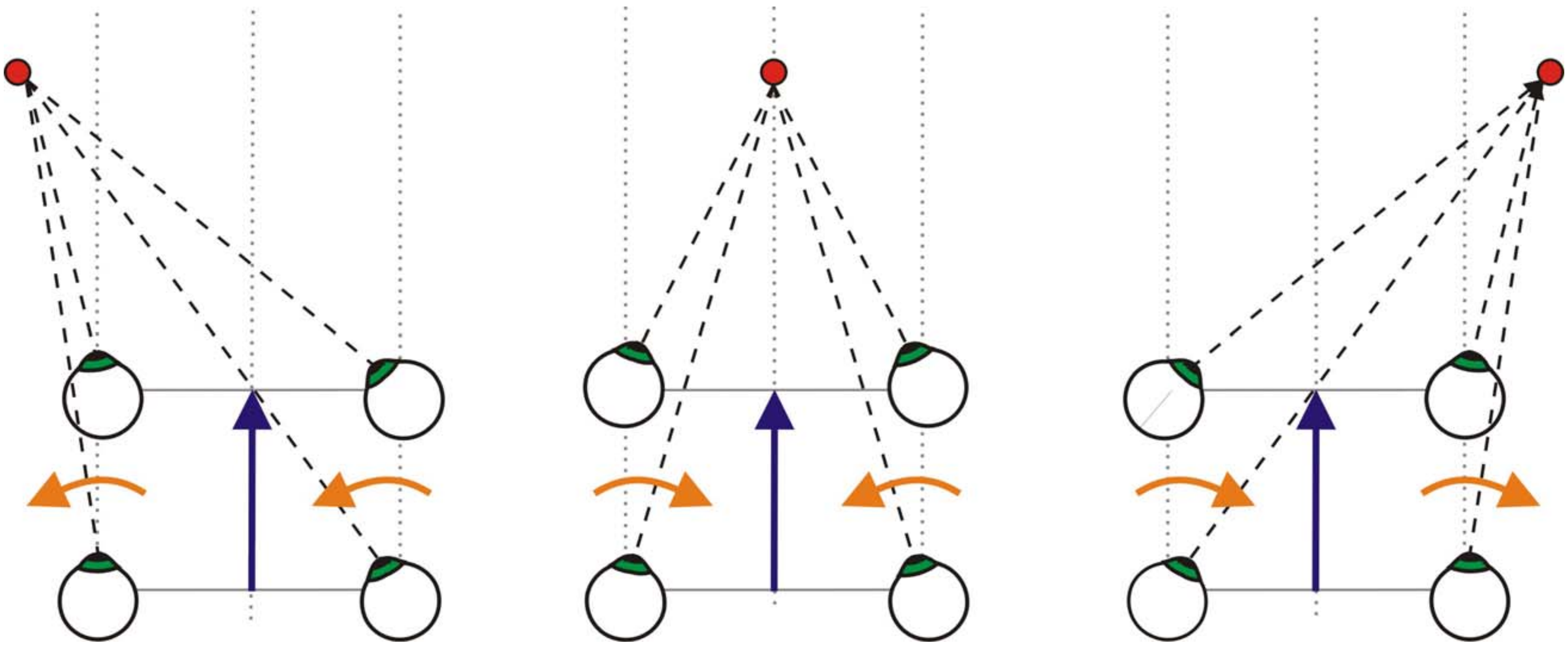
When $S_R=S_L$:

$$E_R(s) = \xcancel{-G_d(s)\left[S_R(s) - S_L(s)\right]} + G_c(s)\left[S_R(s) + S_L(s)\right]$$

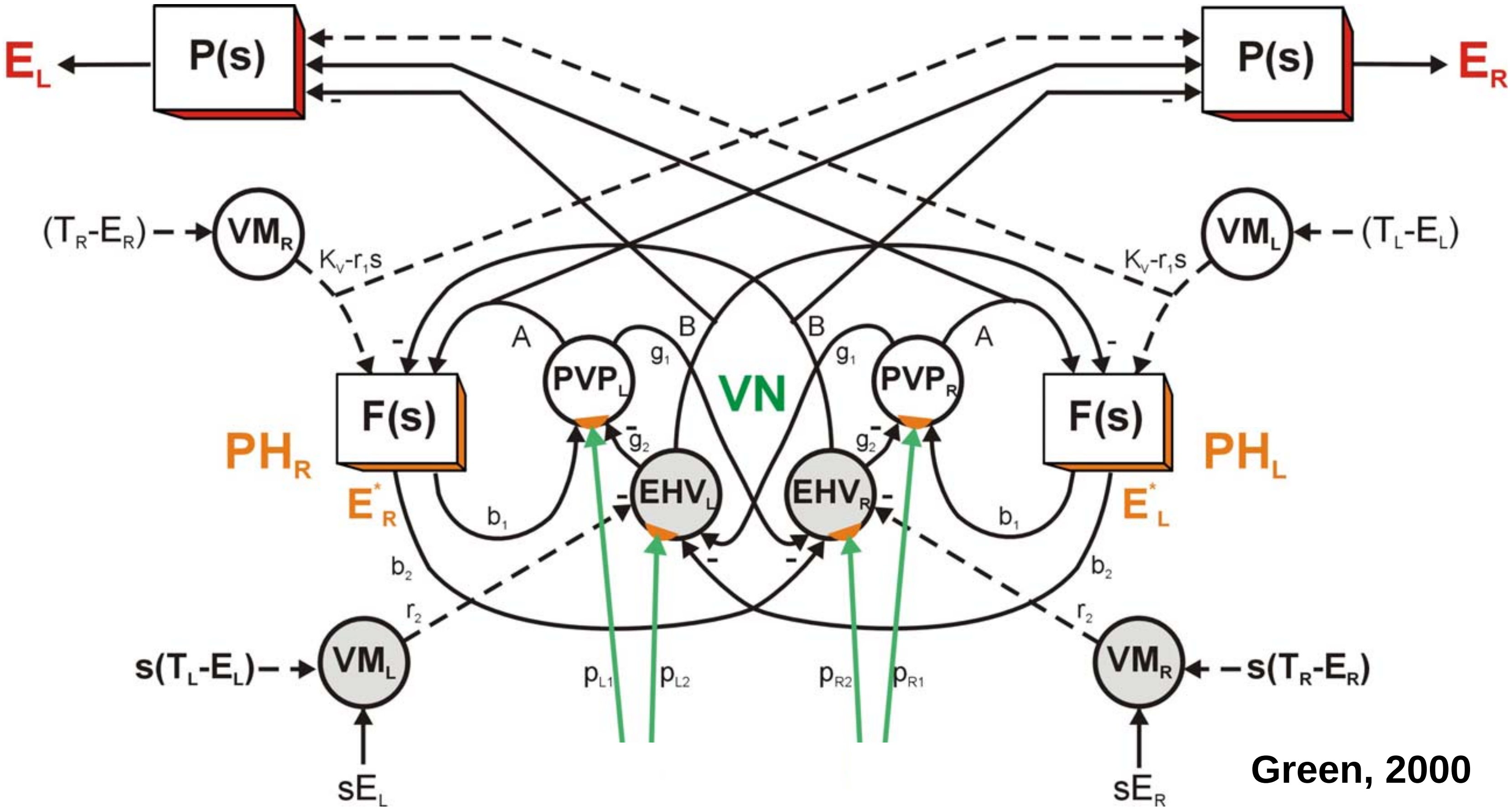
$$E_L(s) = \xcancel{G_d(s)\left[S_R(s) - S_L(s)\right]} + G_c(s)\left[S_R(s) + S_L(s)\right]$$

$$\xcancel{E_{conj}(s) = -G_d(s)\left[S_R(s) - S_L(s)\right]} \qquad E_{verg}(s) = -2G_c(s)\left[S_R(s) + S_L(s)\right]$$

Viewing-location-dependent compensation for translation



Model for binocular control with multiple cell types and sensory inputs



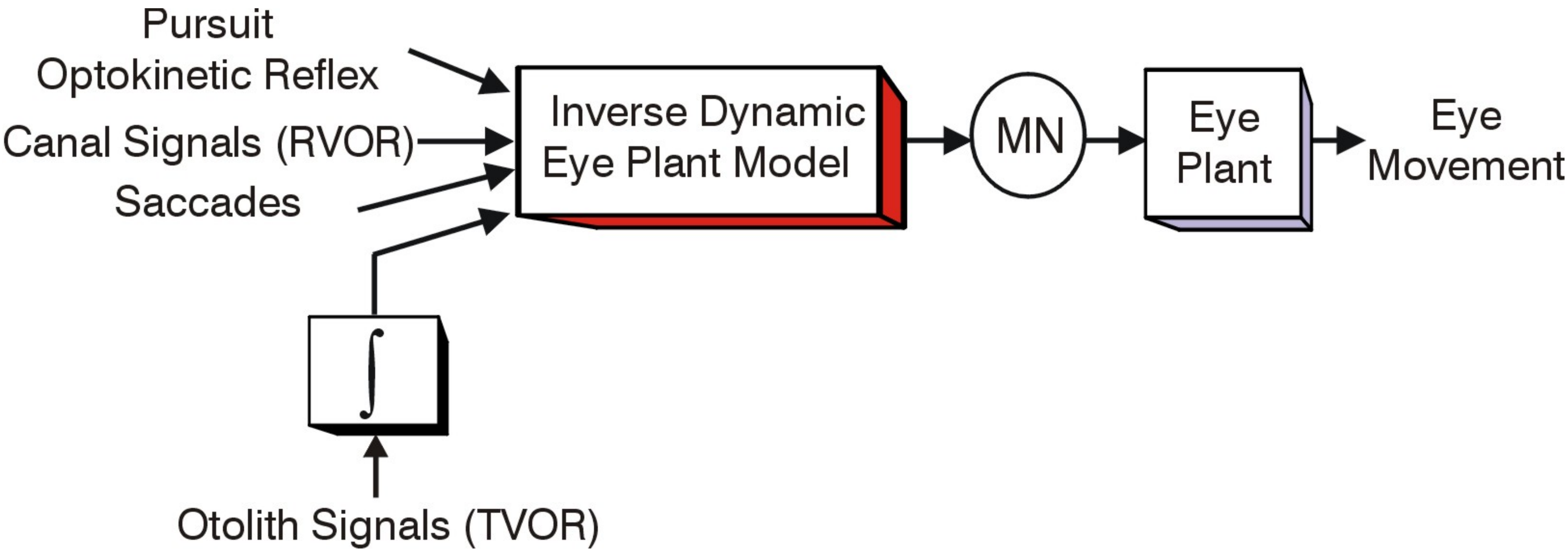
Green, 2000

How are otolith signals processed in the translational VOR (TVOR)?

Otolith and canal signals have distinct dynamic properties:

Semicircular canals → angular head velocity

Otolith organs → linear head acceleration



Pursuit

Optokinetic Reflex

Canal Signals (RVOR)

Saccades

Inverse Dynamic Eye Plant Model

MN

Eye Plant

Eye Movement

$\int$

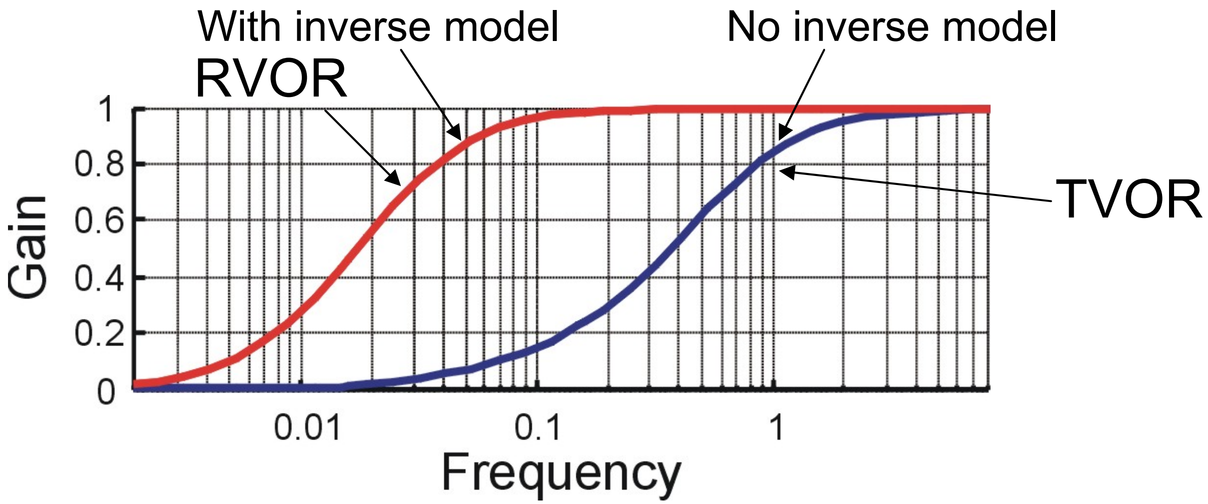
Otolith Signals (TVOR)

How are otolith signals processed in the translational VOR (TVOR)?

Otolith and canal signals have distinct dynamic properties:

Semicircular canals → angular head velocity
Otolith organs → linear head acceleration

The RVOR and TVOR have distinct dynamic characteristics:



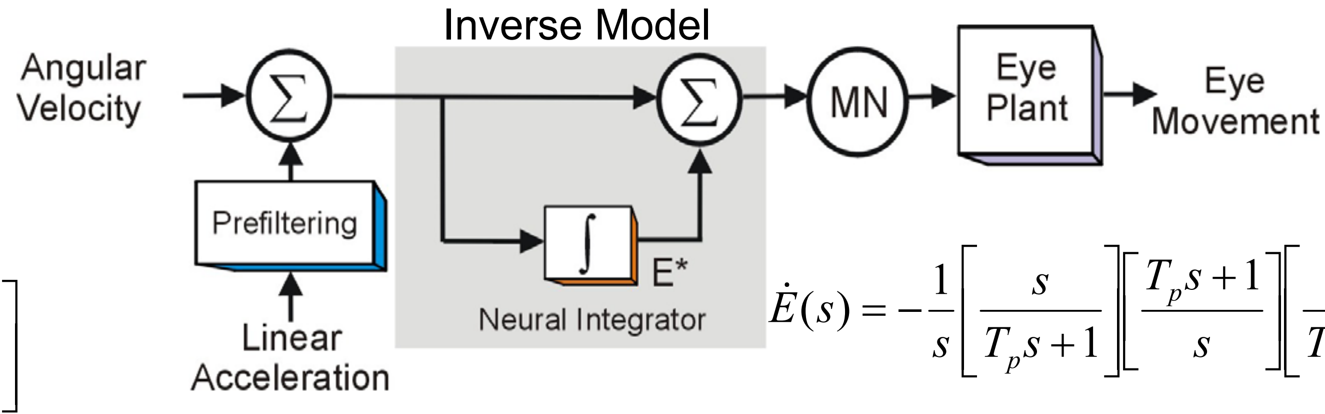
- The TVOR does not appear to reflect processing by an internal model

Two potential hypotheses

Common internal model

Integrator

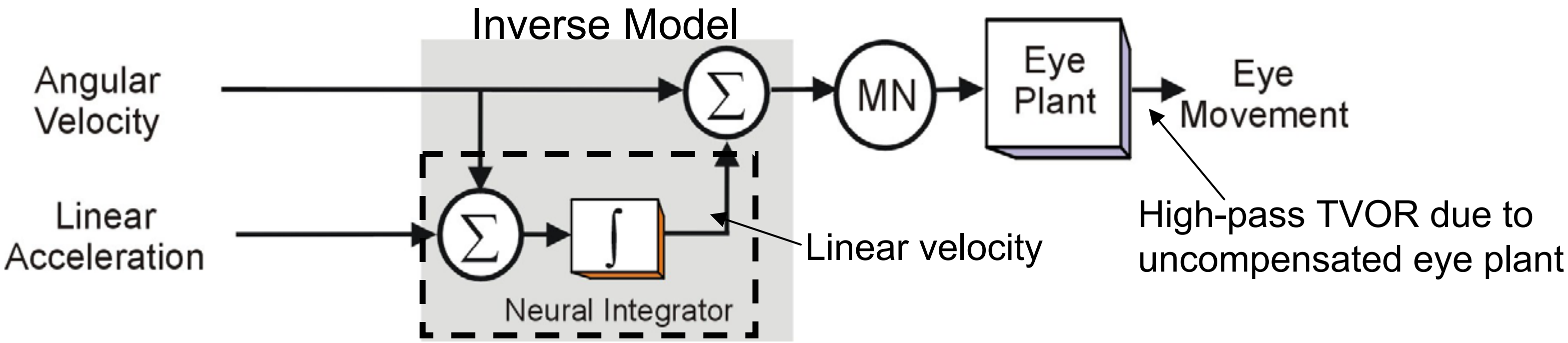
$$\frac{1}{s}\left[\frac{s}{T_p s+1}\right]$$



$$\dot{E}(s) = -\frac{1}{s}\left[\frac{s}{T_p s+1}\right]\left[\frac{T_p s+1}{s}\right]\left[\frac{s}{T_p s+1}\right]s\dot{H}_{lin}(s)$$

$$= -\frac{s}{T_p s+1}\dot{H}_{lin}(s)$$

Distributed dynamic processing



Linear velocity

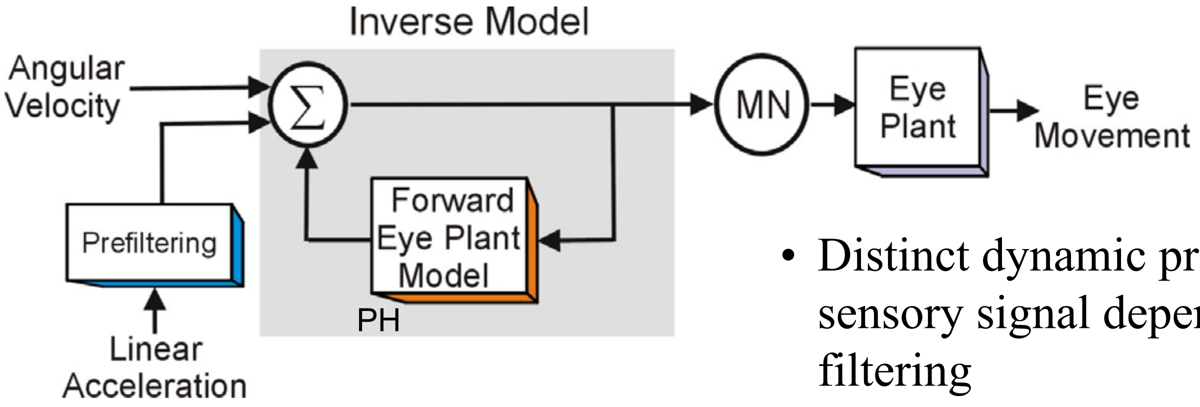
High-pass TVOR due to uncompensated eye plant

$$\dot{E}(s) = -\frac{1}{s}\left[\frac{s}{T_p s+1}\right]s\dot{H}_{lin}(s) = -\frac{s}{T_p s+1}\dot{H}_{lin}(s)$$

Green and Galiana, 1998
Musallam and Tomlinson, 1999

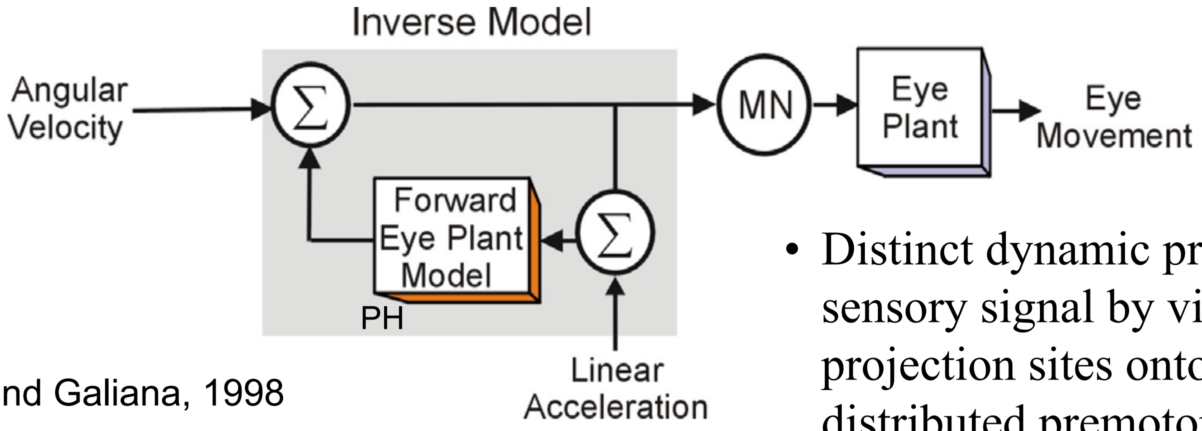
Two potential hypotheses

Common internal model



- Distinct dynamic processing of each sensory signal depends on additional filtering

Distributed dynamic processing

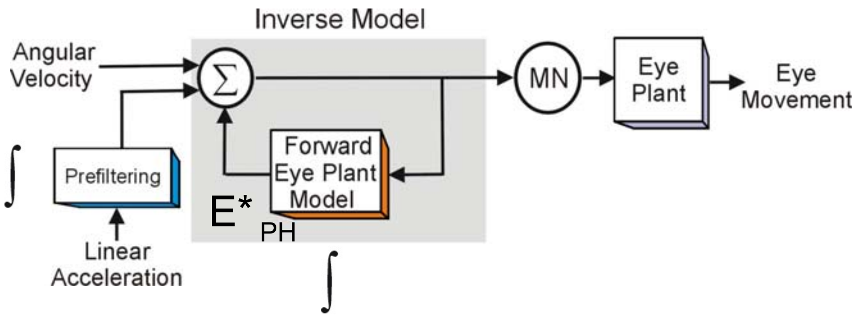


Green and Galiana, 1998

- Distinct dynamic processing of each sensory signal by virtue of different projection sites onto a shared, distributed premotor network

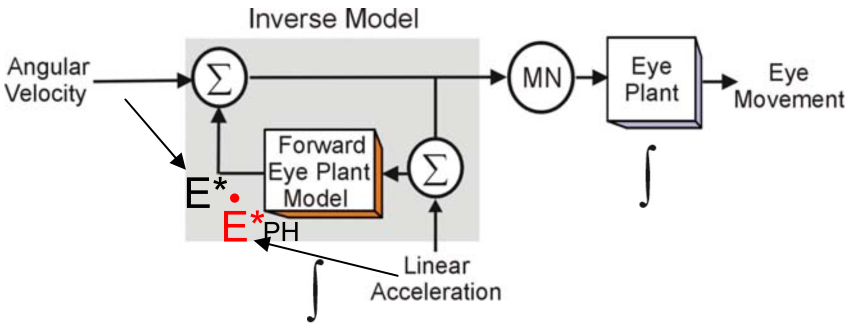
Predictions

Common internal model



- Evidence for a second “neural integration of otolith signals
- Burst-tonic/tonic (BT-T) neurons in the PH should exhibit the same relationship to eye movement during rotation and translation

Distributed dynamic processing

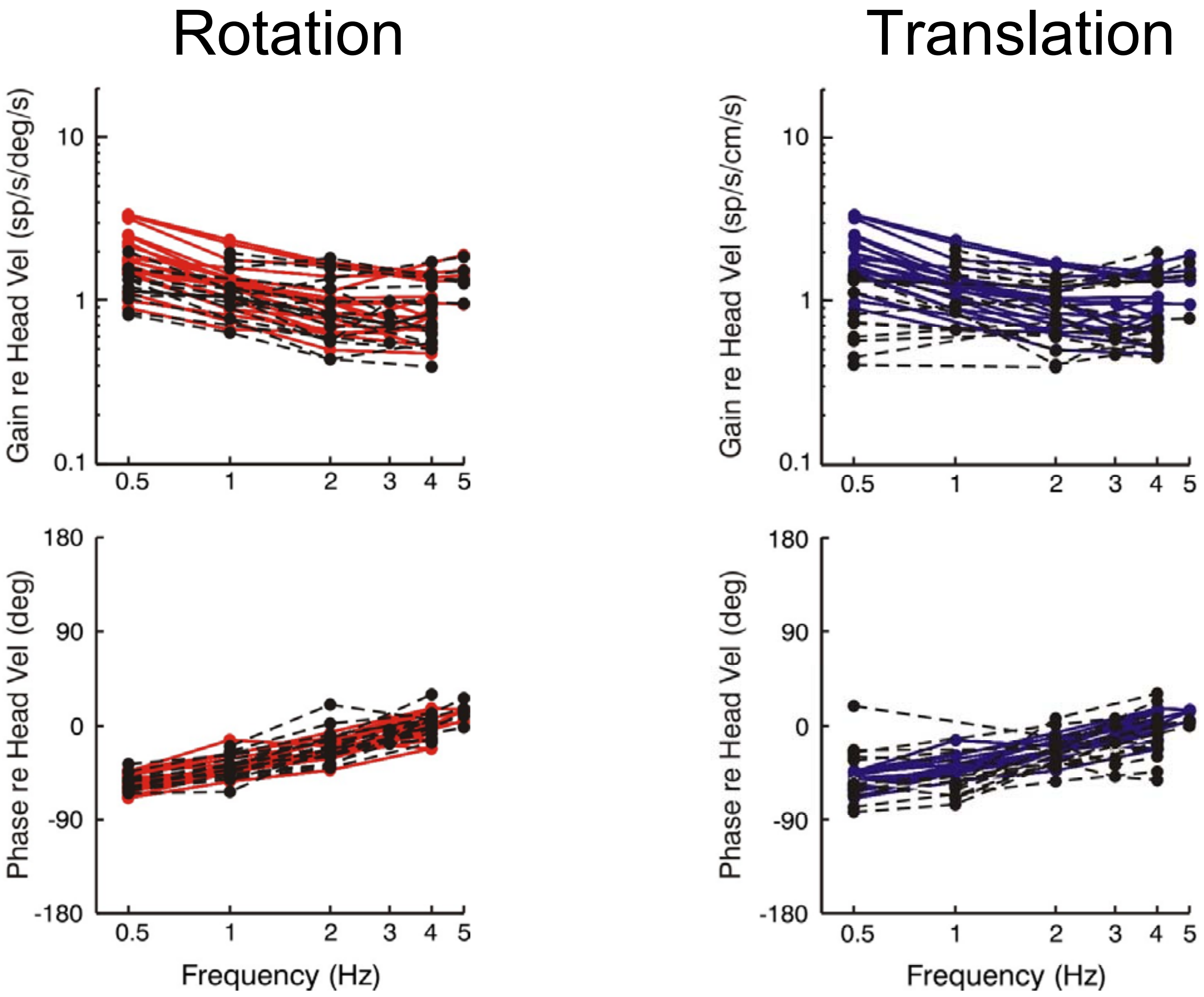


- Evidence for only a single “neural integration” of otolith signals
- Burst-tonic/tonic (BT-T) neurons in the PH should exhibit different relationships to eye movement during rotation and translation

Do PH neurons actually encode a consistent internal estimate?

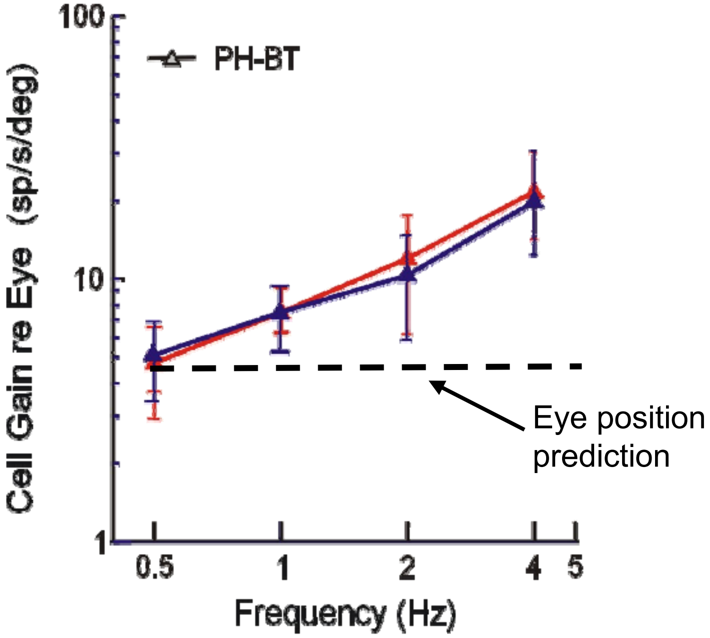
What specifically is estimated?

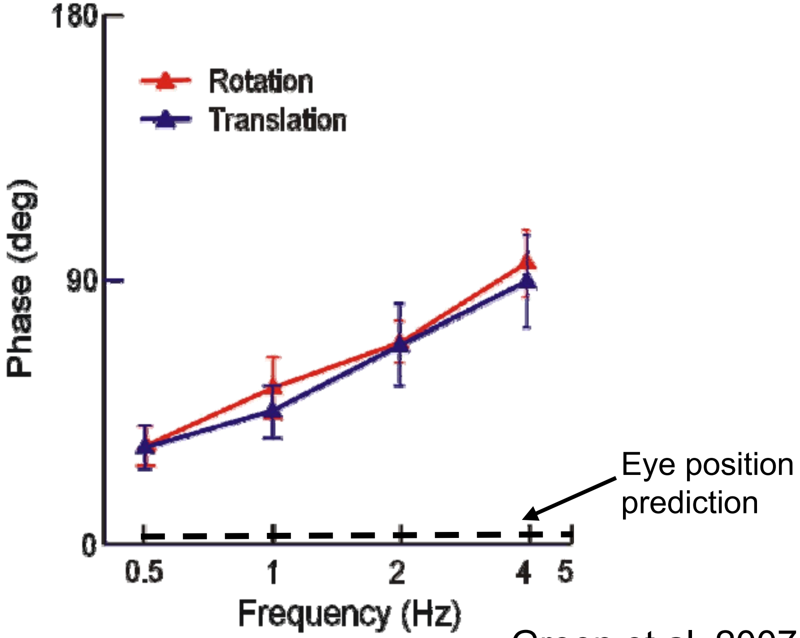
PH translation responses reflect a second neural integration



Green et al, 2007

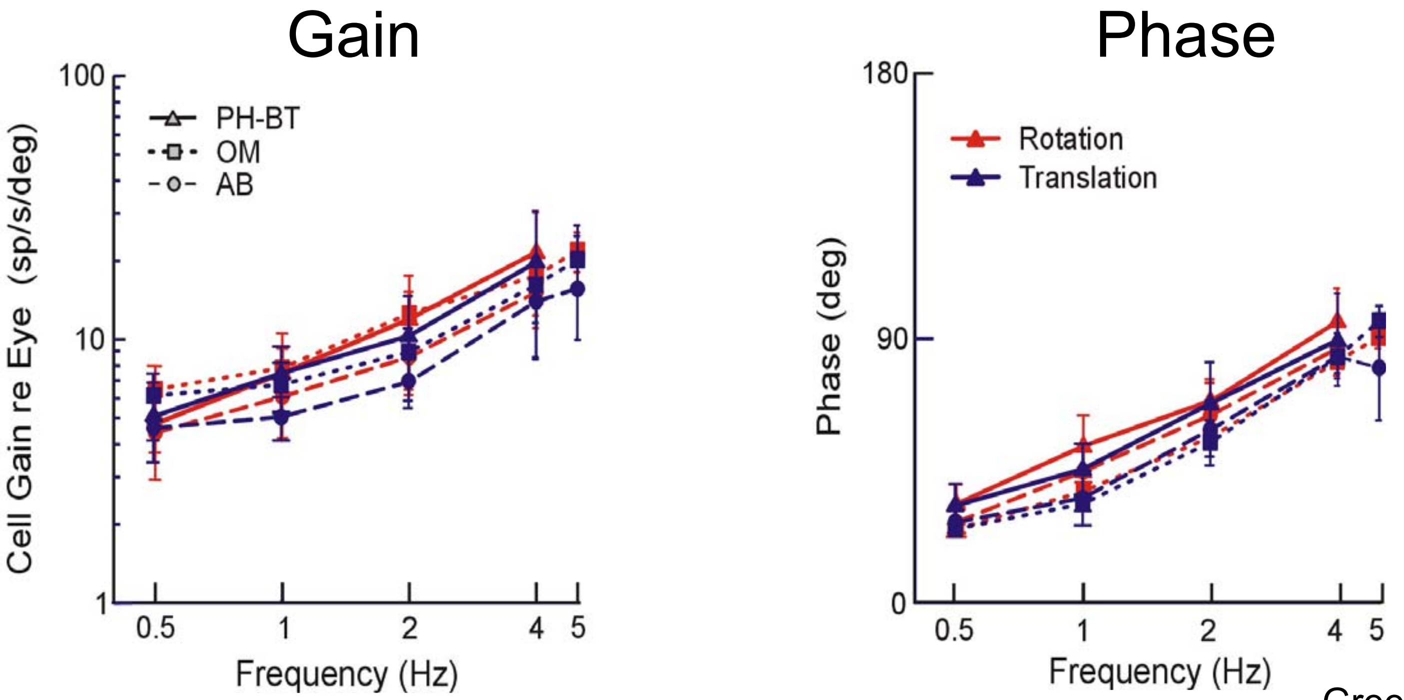
PH neurons encode a consistent internal estimate


Gain


Phase

Green et al, 2007

PH neuron dynamics are identical to those of extraocular motor neurons


Gain

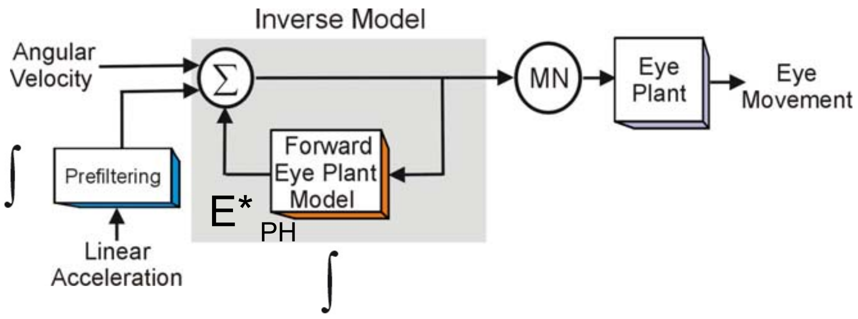
Phase

Green et al, 2007

- PH neurons do not encode either an internal estimate of eye position or a signal that is more “position-like” than that of extraocular motor neurons
- Their dynamics are instead identical to those of extraocular motor neurons suggesting that they encode an *efference copy* of the motor command (i.e., output of inverse model)

Predictions

Common internal model



- Evidence for a second “neural integration of otolith signals
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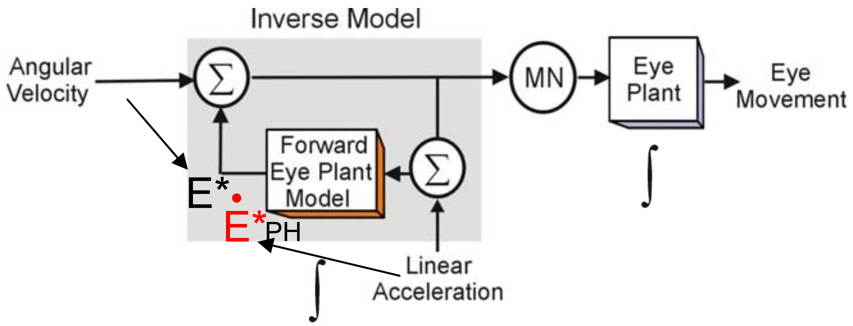
Distributed dynamic processing

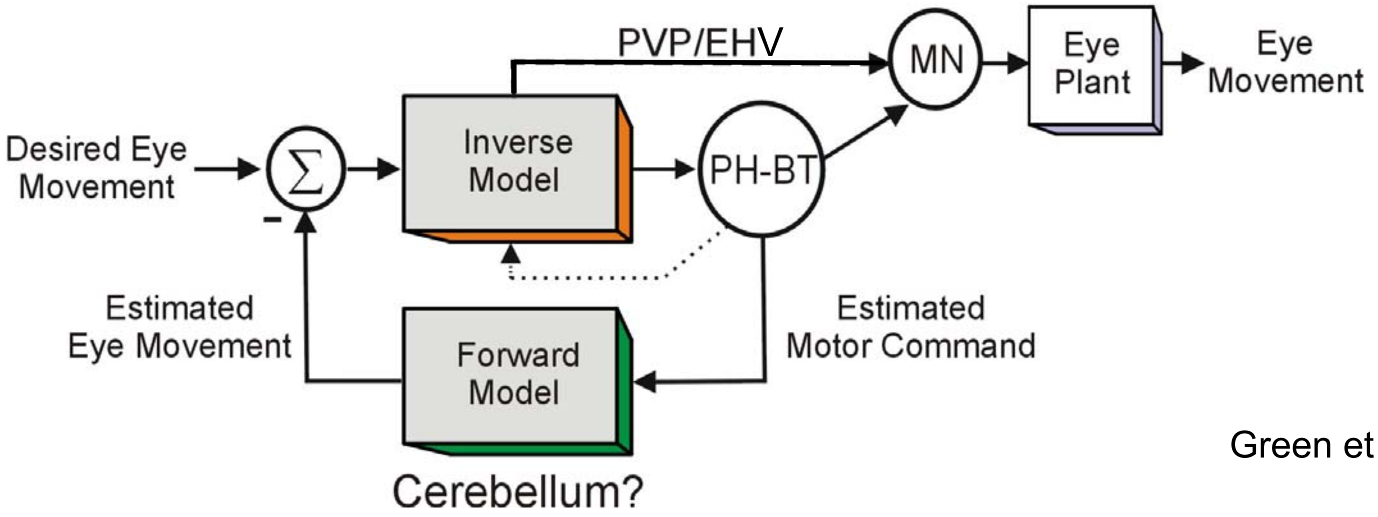


- Evidence for only a single “neural integration” of otolith signals
- Burst-tonic/tonic (BT-T) neurons in the PH should exhibit different relationships to eye movement during rotation and translation

Do PH neurons actually encode a consistent internal estimate? Yes

What specifically is estimated? The motor neural command

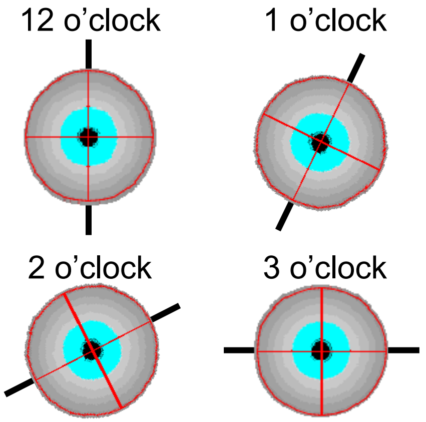
Revised hypothesis for the neural control of eye movements

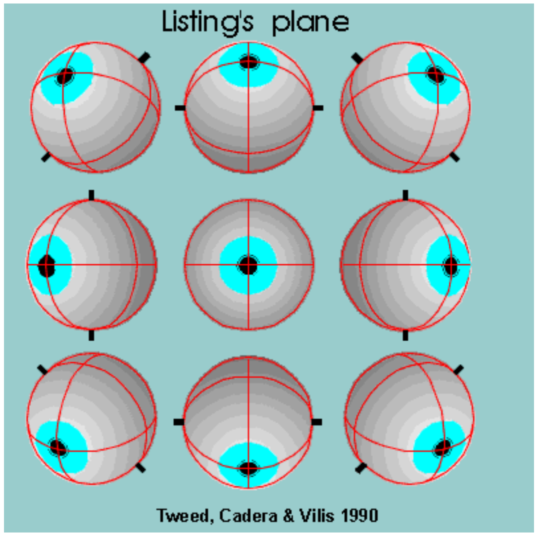


Green et al, 2007

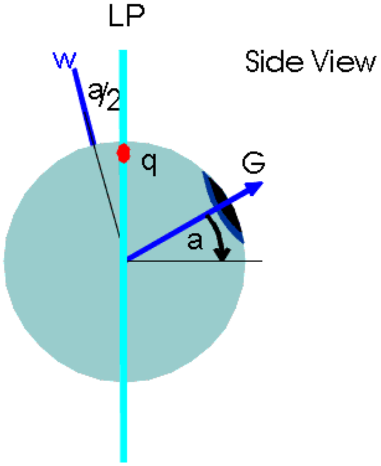
- Theoretical framework consistent with that proposed for limb control (e.g., Miall & Wolpert, 1998; Wolpert & Kawato, 1998; Bhushan & Shadmehr, 1999)
- Forward model is important in the control of eye movement because it has been shown that eye movements do not rely on online proprioceptive feedback
- Forward models have been proposed as an essential component in the control of arm movements because of delays in sensory feedback
- Actual neural correlates for these models are difficult to identify because state estimates are often closely correlated with motor command and sensory signals

Neural correlates for inverse and forward models from 3-D kinematics




Listing's plane

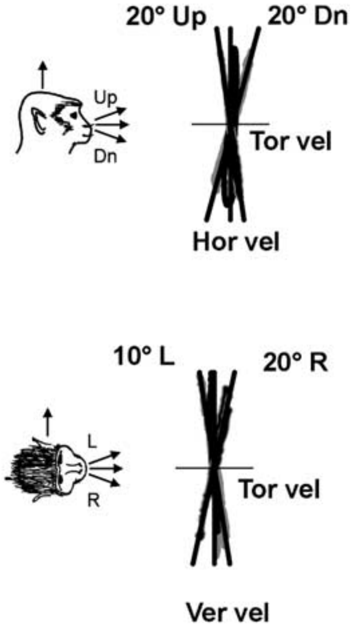
Tweed, Cadera & Vilis 1990



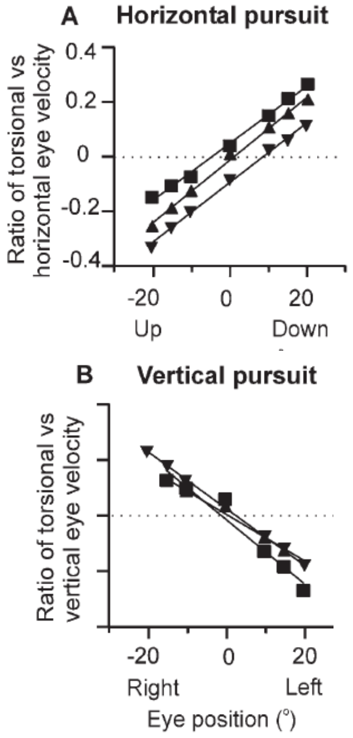
- In theory, the eye can assume an infinite number of torsional positions for any gaze direction.
- In reality, the orientation when looking in a given direction is always the same (Donder's law)
- These orientations can be reached by rotating the eye from a primary reference position about axes that lie in a plane perpendicular to line of sight in primary orientation (Listing's law)
- If the eye starts from a position deviated away from primary position, the eye rotates about an axis that tilts out of Listing's plane by half the angle by which gaze is deviated away from primary position (half-angle rule) → holds for saccades and pursuit

Neural correlates for inverse and forward models from 3-D kinematics

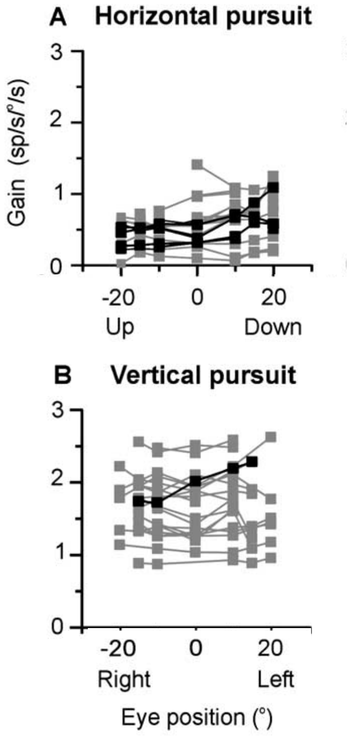
To what extent is Listing's law implemented neurally vs. mechanically through the active control of connective-tissue "sleeves" or "pulleys" which direct the paths of the muscles?



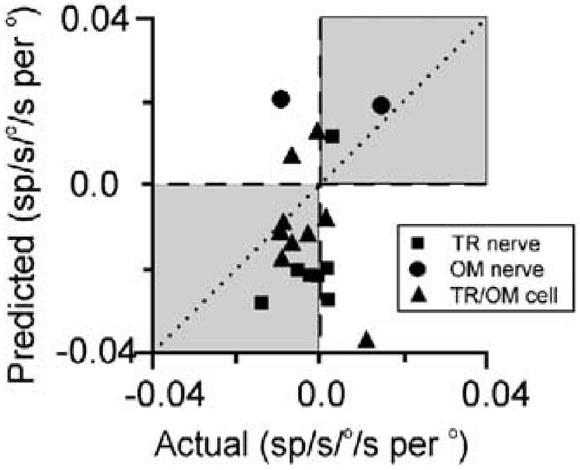
Eye Movement



Motor Neuron Activity



Comparison with prediction based on torsion sensitivity during head rotation



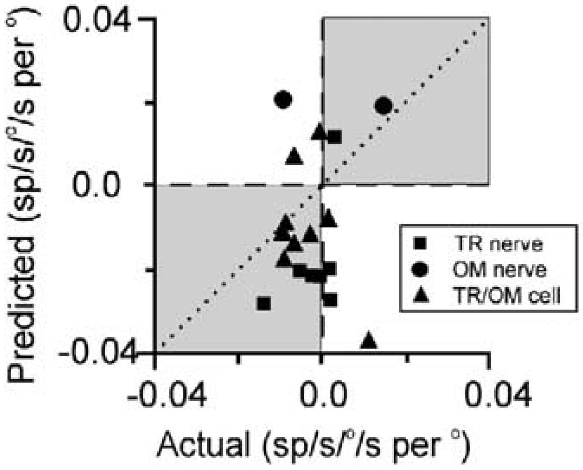
Ghasia and Angelaki, 2005

- Motor neural firing rates do not reflect the torsional velocity component associated with the "half-angle rule" suggesting a role for the mechanical properties of the eye in generating kinematically appropriate eye movements.

Neural correlates for inverse and forward models from 3-D kinematics

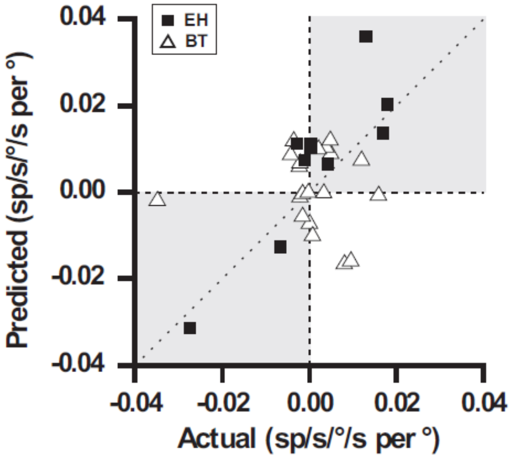
- If PH-BT cells encode an efference copy of the motor command (output of an inverse model) then like motor neurons they should not reflect signals consistent with the “half-angle” rule.
- In contrast, neurons which encode an internal estimate of actual eye movement (output of a forward model) should encode signals consistent with the “half-angle” rule.

Extraocular Motor Neurons



Ghasia and Angelaki, 2005

Premotor Neurons

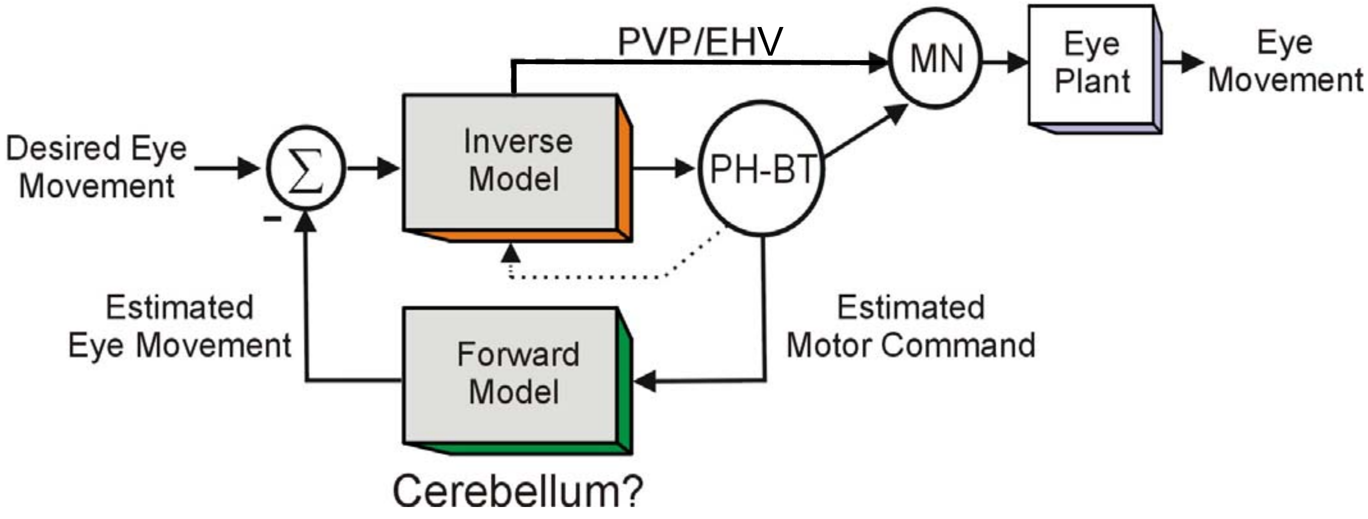


Ghasia er al., 2008

- PH-BT cell activities are consistent with encoding the output of an inverse model
- Eye-head-velocity cell activities reflect the “half-angle” rule

  → these signals might reflect the output of a forward model in the cerebellum

Revised hypothesis for the neural control of eye movements



- Remains to be confirmed through investigations of neural activity in the cerebellum
- The forward model is an essential component of controllers based on state-feedback

→ State estimators or observers

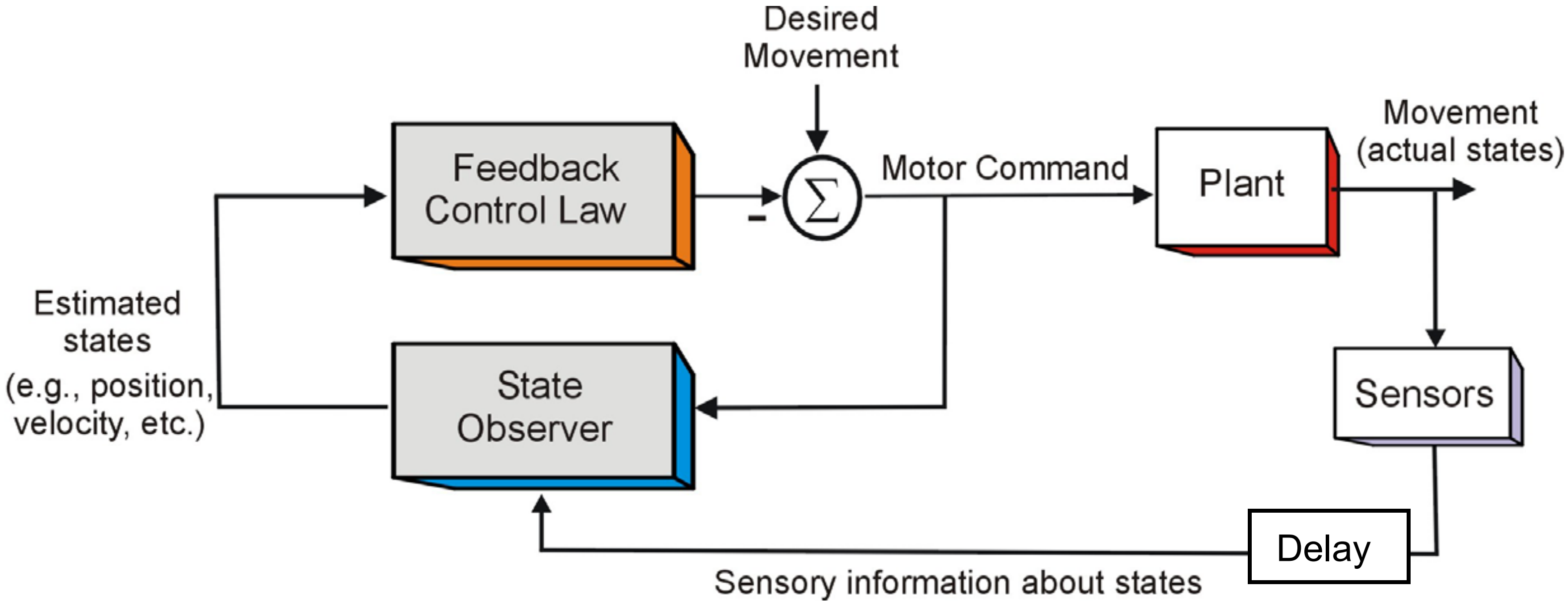
→ Control rule based on a weighted combination of state estimates

Control based on state estimation

$$\frac{d^2 y(t)}{dt^2} = -\frac{K}{M} y(t) - \frac{B}{M}\frac{dy}{dt} + \frac{1}{M} f(t)$$

state vector

$$\begin{bmatrix} \dot{x}_1(t) \\ \dot{x}_2(t) \end{bmatrix} = \begin{bmatrix} 0 & 1 \\ -K/M & -B/M \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix} + \begin{bmatrix} 0 \\ 1/M \end{bmatrix} f(t)$$



Control based on state estimation

$$\frac{d^2 y(t)}{dt^2} = -\frac{K}{M} y(t) - \frac{B}{M}\frac{dy}{dt} + \frac{1}{M} f(t)$$

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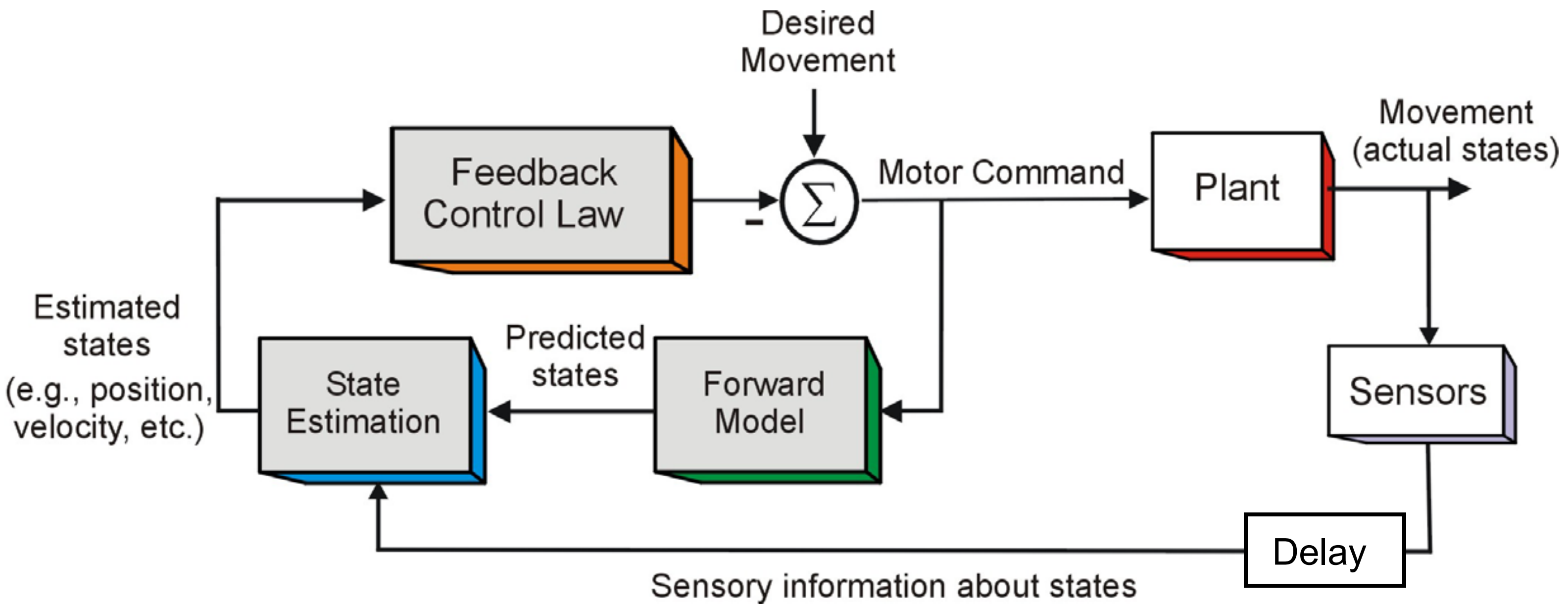
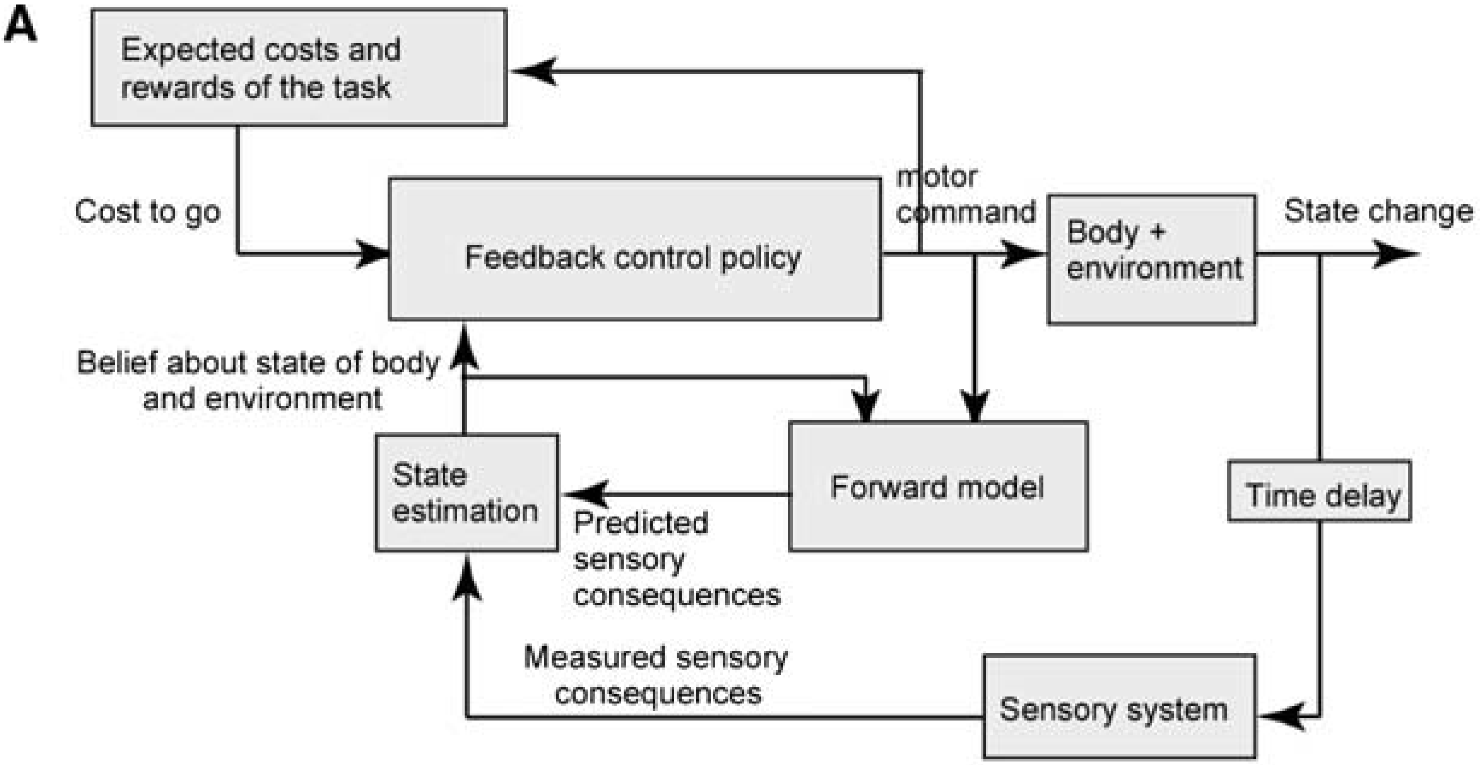
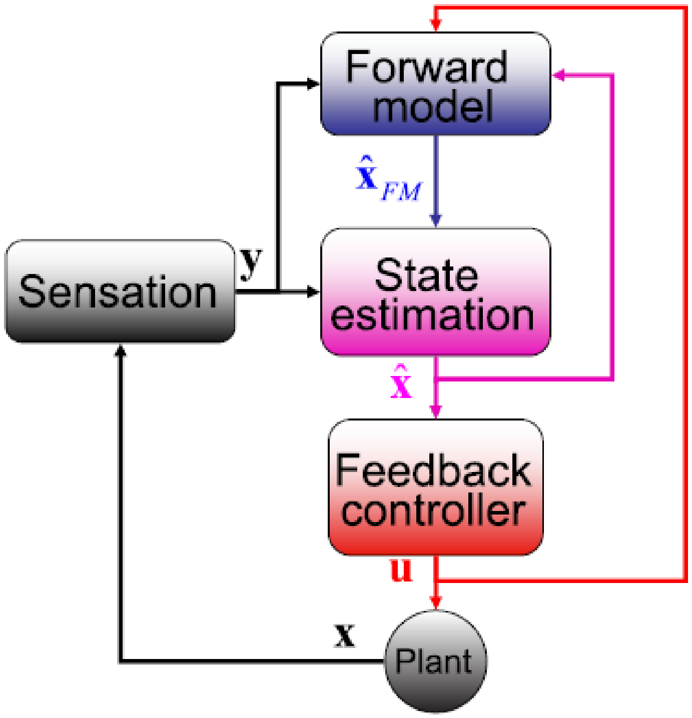


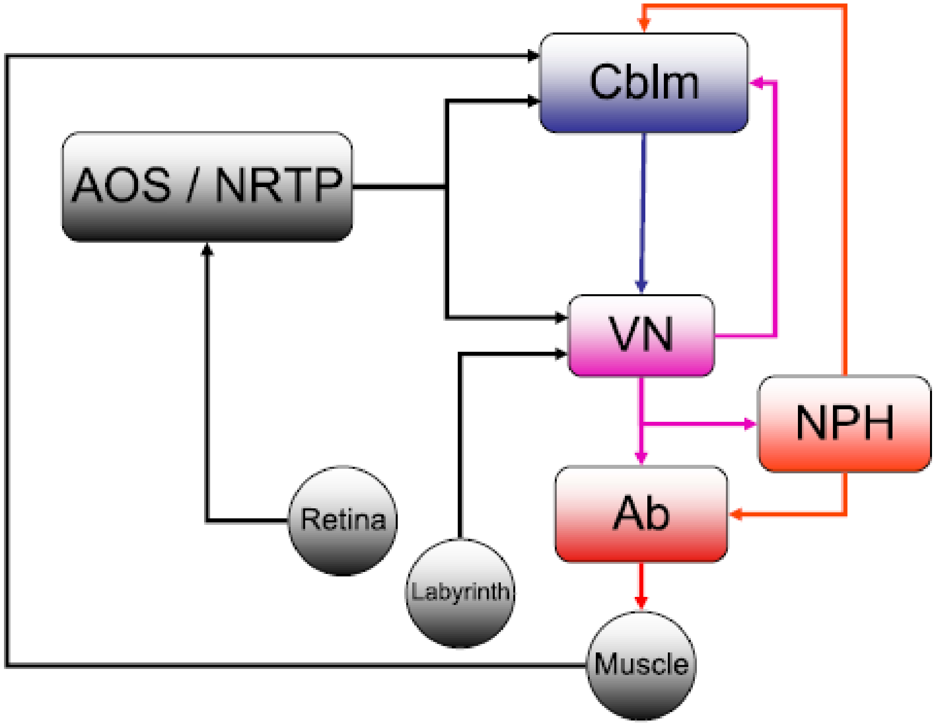
Computational framework for limb control



Shadmehr and Krakauer, 2008

Model for state estimation in compensatory eye movements





Frens and Donchin, 2009

What have we learned about the oculomotor system by using computational approaches?

Many things!!!

- What fundamental computations need to be performed
- How such computations might be implemented neurally
- How to test the role of different cell populations in these computations
- How the topology of the premotor circuitry contributes to motor control
- Role of internal estimates in the control of eye movement