

CONTROL

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trust is good
control is better

NOT by Lenin

trust is good
control is better

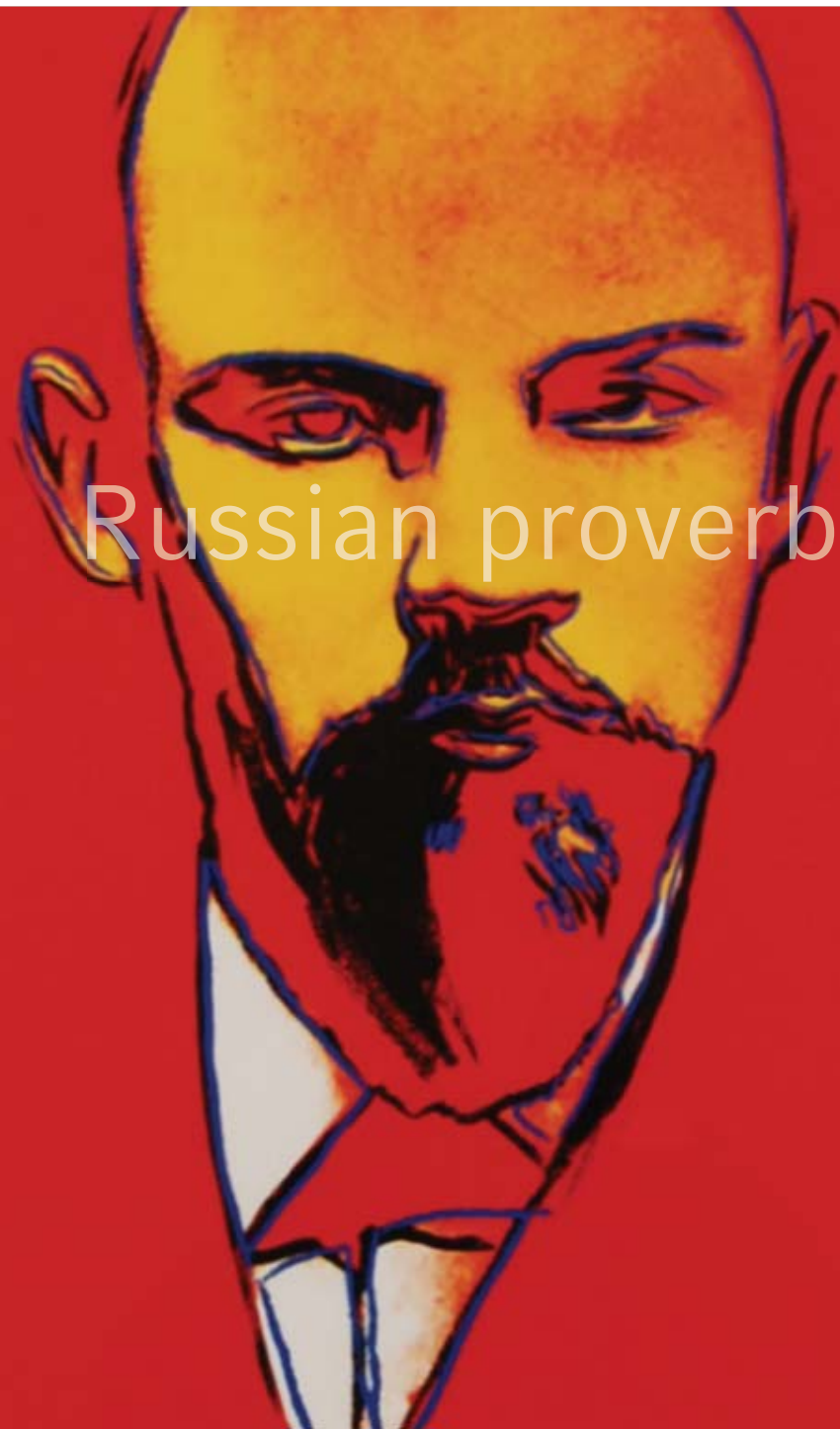
NOT by Lenin

~~trust is good~~
~~control is better~~

trust
but verify

Russian proverb

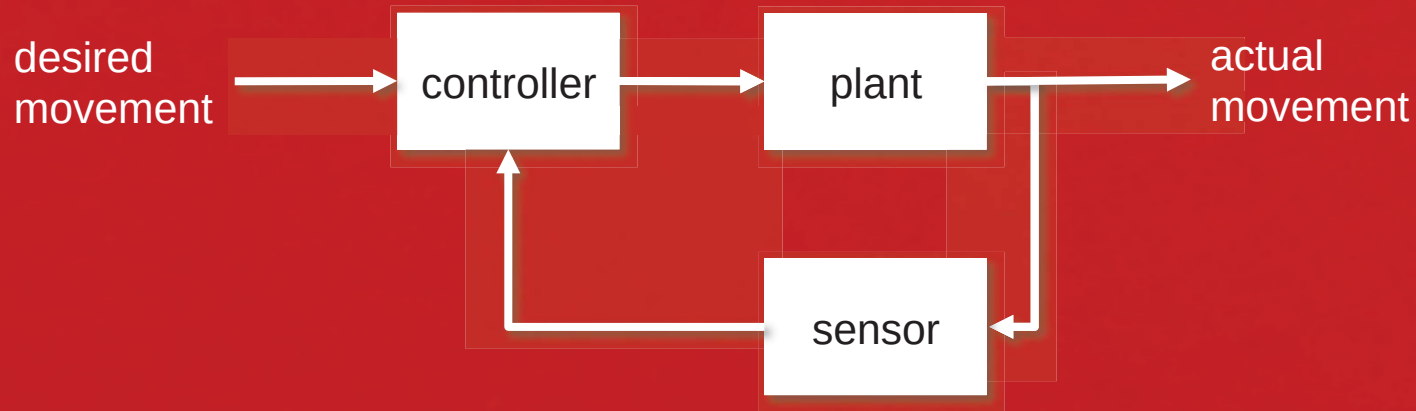
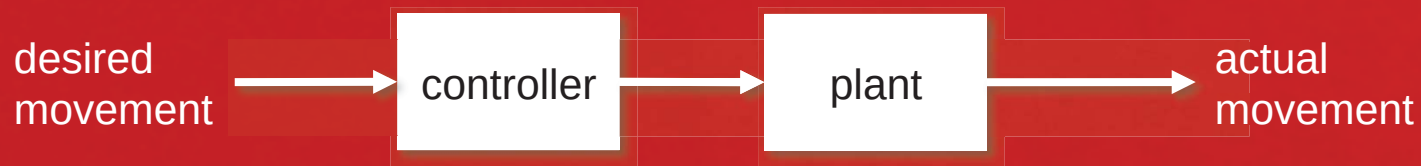
trust
but verify



Russian proverb

trust
but verify

Control



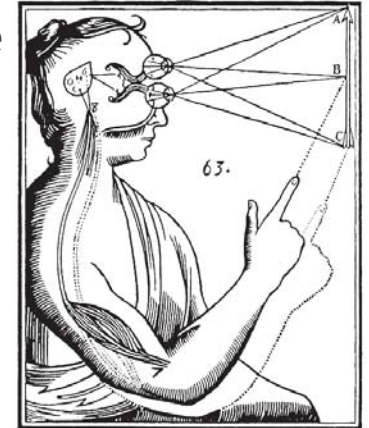
trust ~ feedforward control
verify ~ feedback control

History



... the spirits ... proceed ... into the nerves. Once there ... they have the power to change the shape of the muscles the nerves end up in, and in this way to make all the parts of the body move.

... its muscles and tendons are like the engines and springs used to move them ...



René Descartes (1596-1650), Treatise On The Human Being (posthumous)

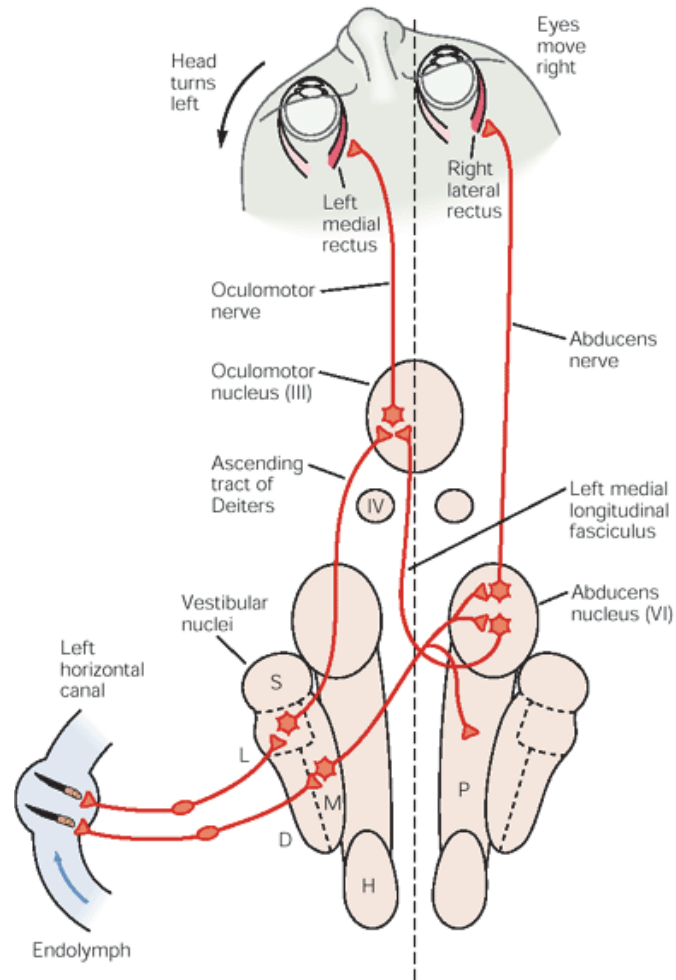


There is the coordination which a reflex action introduces when it makes an effector organ responsive to excitement of a receptor ...

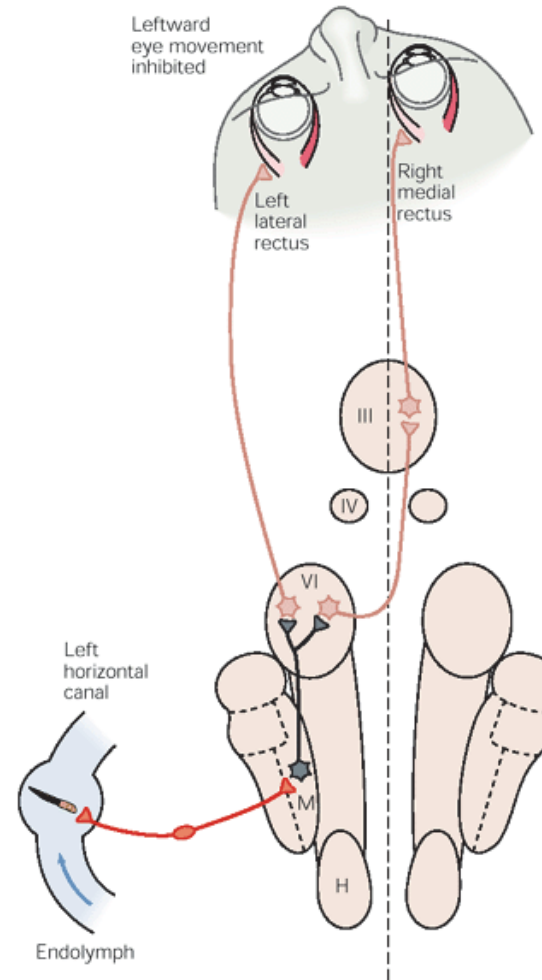
Charles Scott Sherrington (1857-1952), The Integrative Action of the Nervous System (1906)

Feedforward control

A Excitatory connections



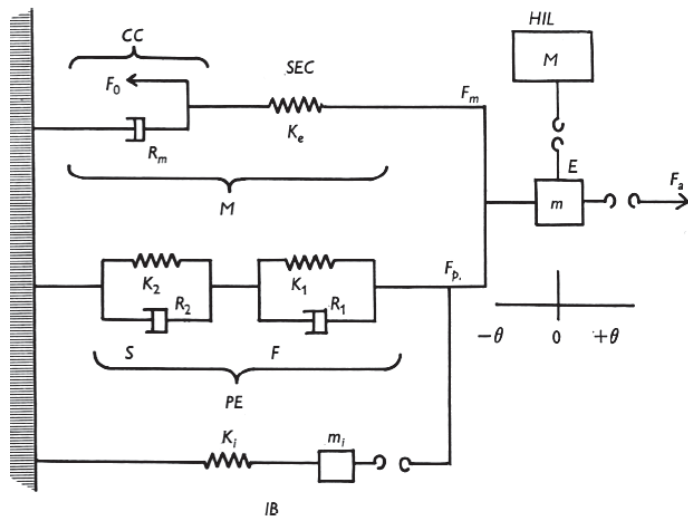
B Inhibitory connections



Kandel et al. Fig. 40-10

The vestibulo-ocular reflex: gaze stabilization

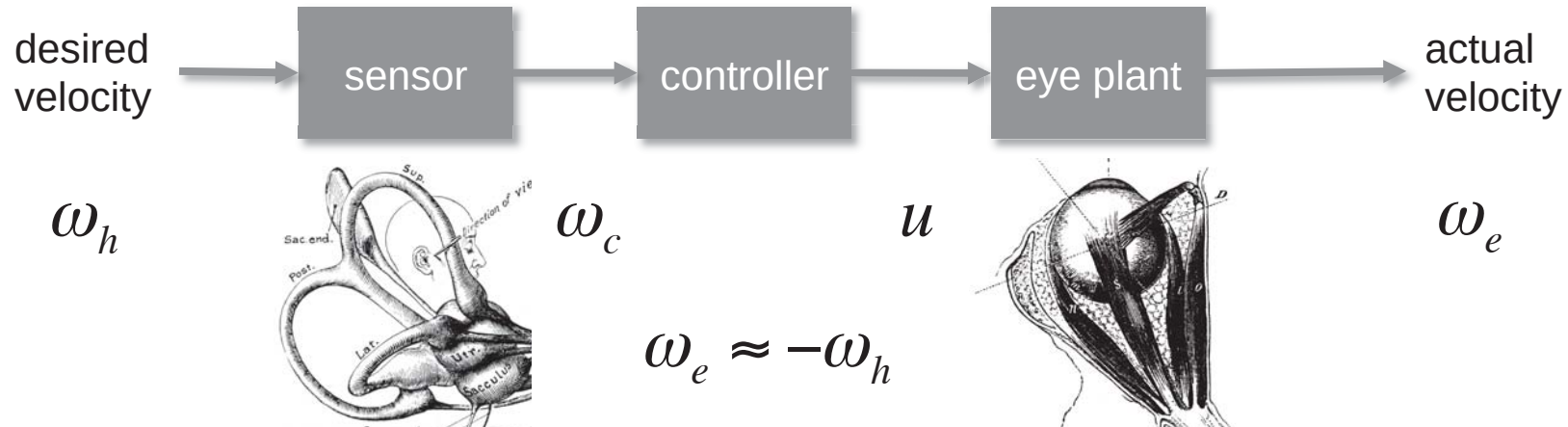
History



The most appropriate discussion is in the form of a theory which accounts at once for all the reported observations. Such a theory is without merit if its predictions are not quantitatively accurate so the schema must be represented by a system of differential equations ...

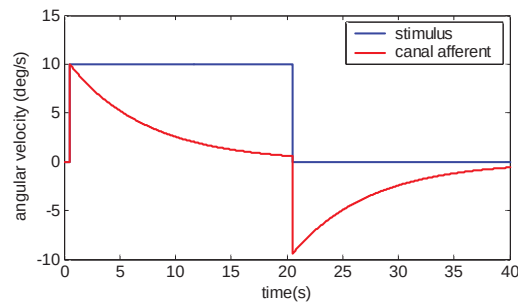
David A. Robinson, The mechanics of human saccadic eye movement (1964)

Feedforward control



$$\omega_c = \frac{\tau_c s}{1 + \tau_c s} \omega_h$$

$$\alpha_e = \frac{1}{1 + \tau_e s} u$$

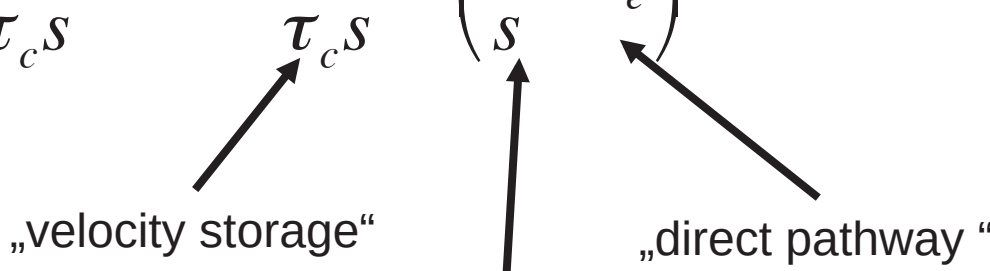


The vestibulo-ocular reflex: what is the task of the controller?

Feedforward control

$$\omega_e = \omega_h \frac{\tau_c s}{1 + \tau_c s} \cdot C(s) \cdot \frac{1}{1 + \tau_e s} \cdot s$$

$$C(s) = -\frac{1 + \tau_e s}{s} \cdot \frac{1 + \tau_c s}{\tau_c s} = -\frac{1 + \tau_c s}{\tau_c s} \cdot \left(\frac{1}{s} + \tau_e \right)$$



„velocity storage“
 „oculomotor integrator“
 „direct pathway“

The controller compensates for sensor and plant dynamics

Feedforward control

$$C(s) = -\frac{1 + \tau_c s}{\tau_c s} \cdot \left(\frac{1}{s} + \tau_e \right)$$

„velocity storage“

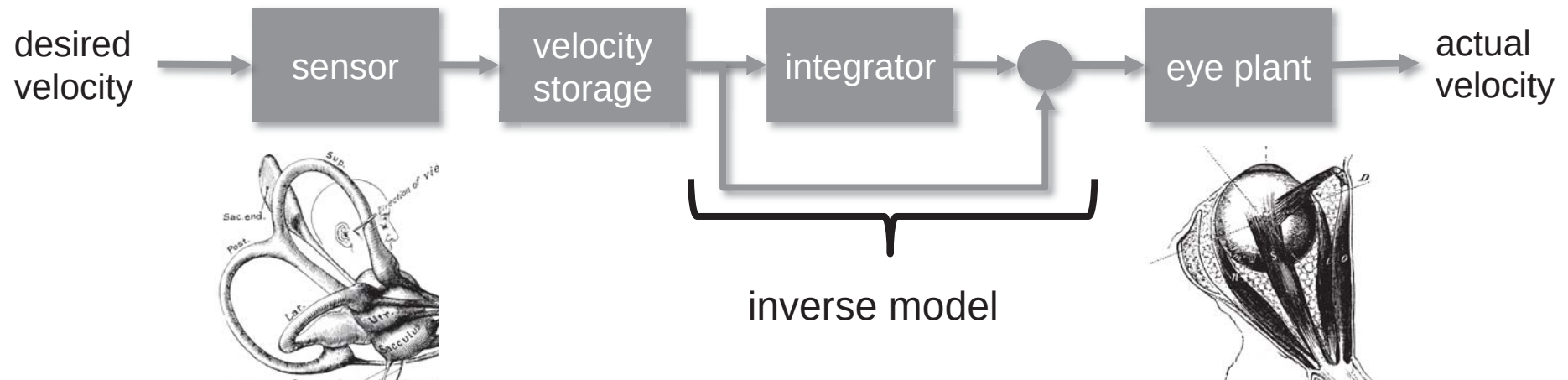
internal inverse model
of sensory processing

„oculomotor integrator and
direct pathway“

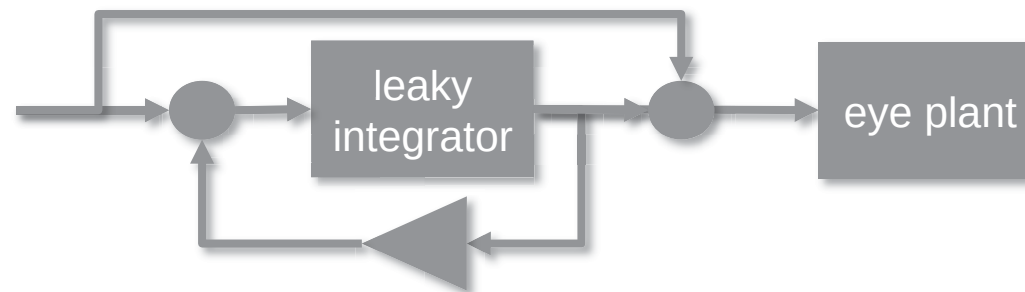
internal inverse model
of motor plant

The controller as internal inverse model

Feedforward control

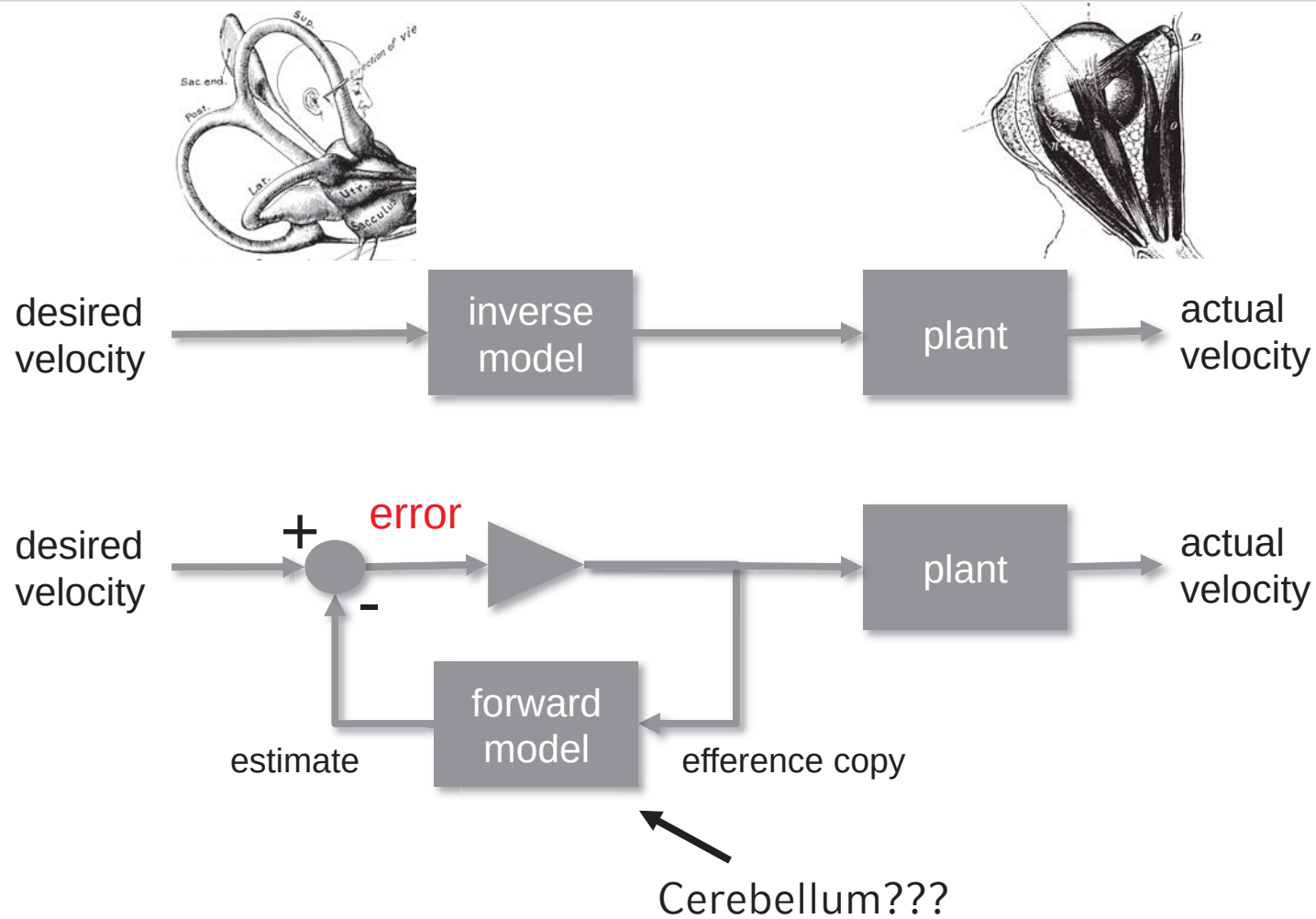


Problem: the inverse model in the brainstem is not perfect, the integrator has a time constant of less than 5 s, the cerebellum improves it to more than 20 s



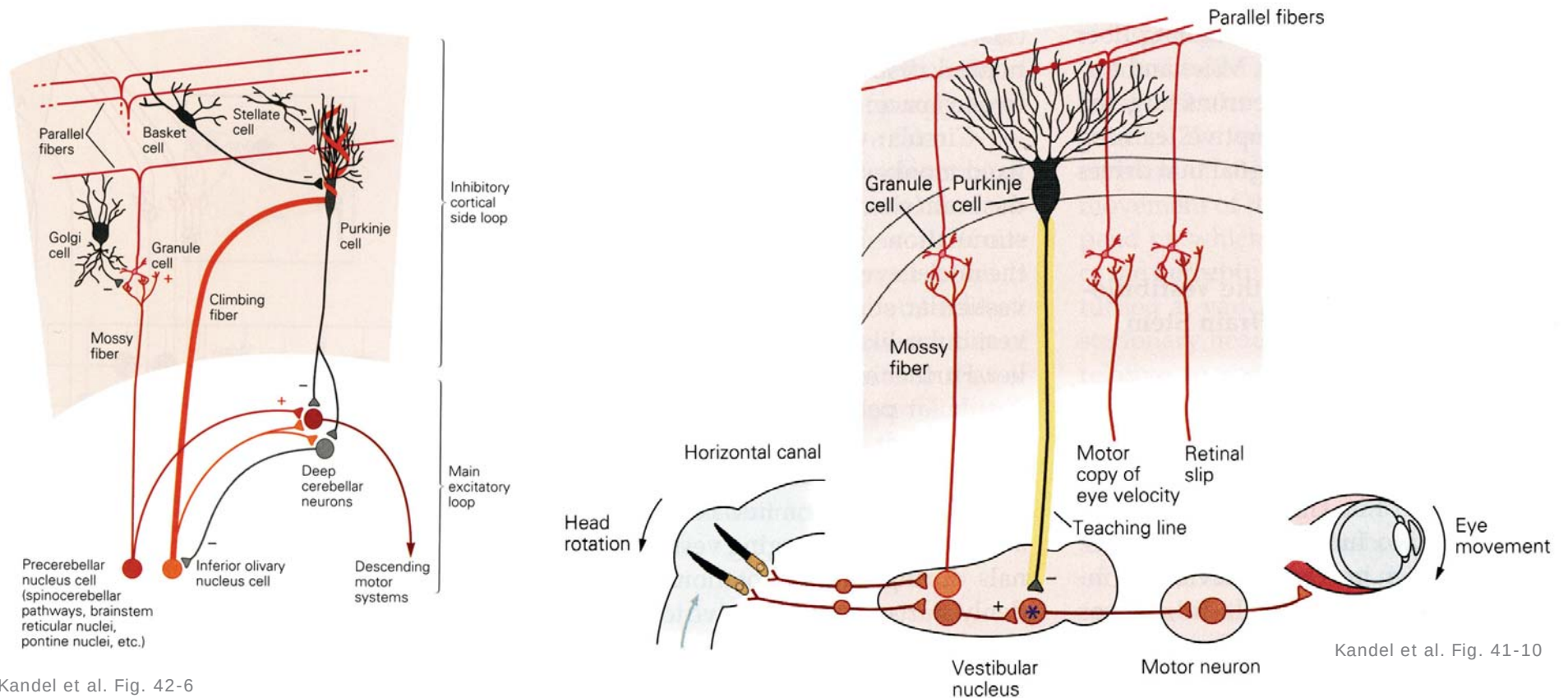
Possible solution: positive feedback (proposed by Zee et al. 1980)

Inverse and forward models



Alternative solution: a negative internal feedback loop with a forward model

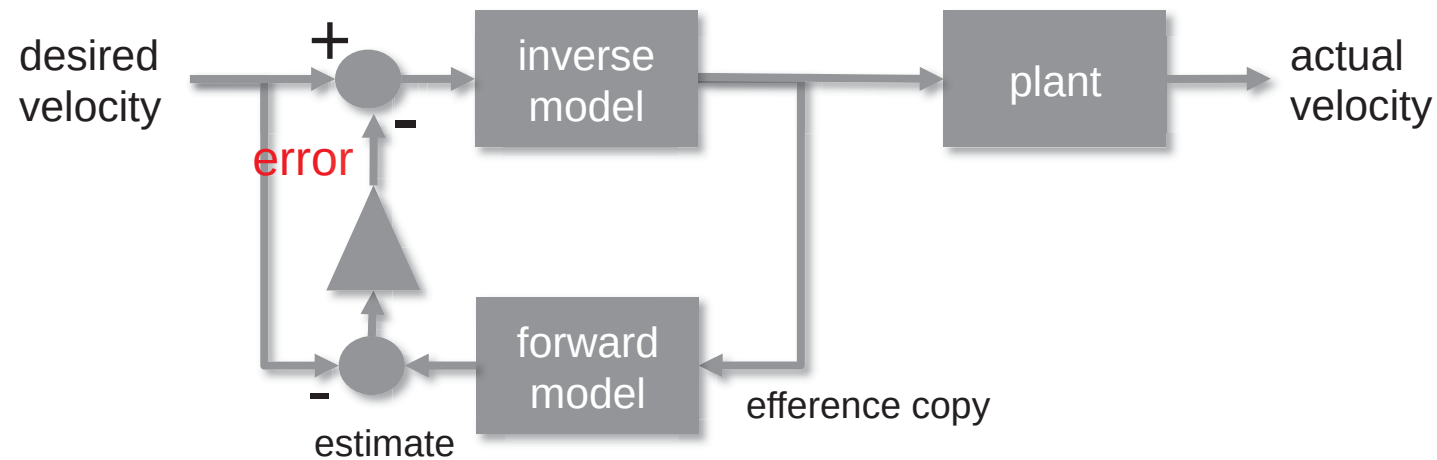
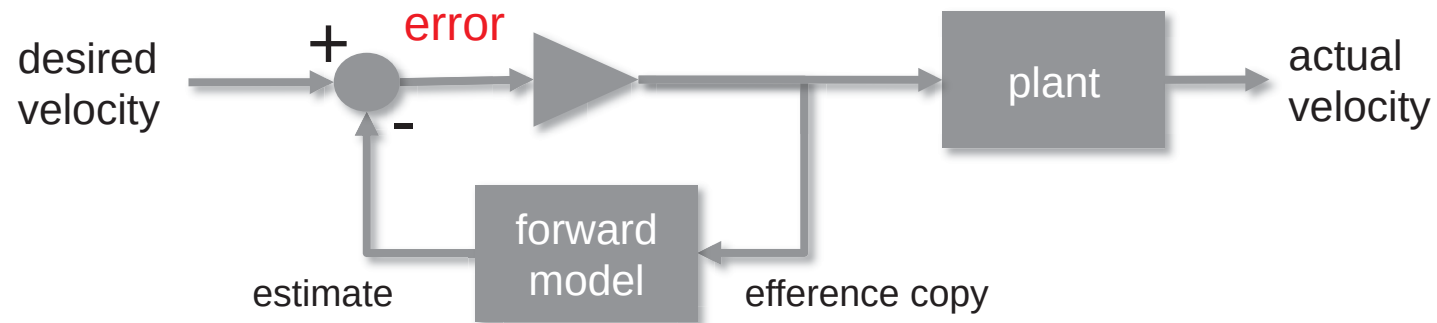
Cerebellar architecture



Kandel et al. Fig. 42-6

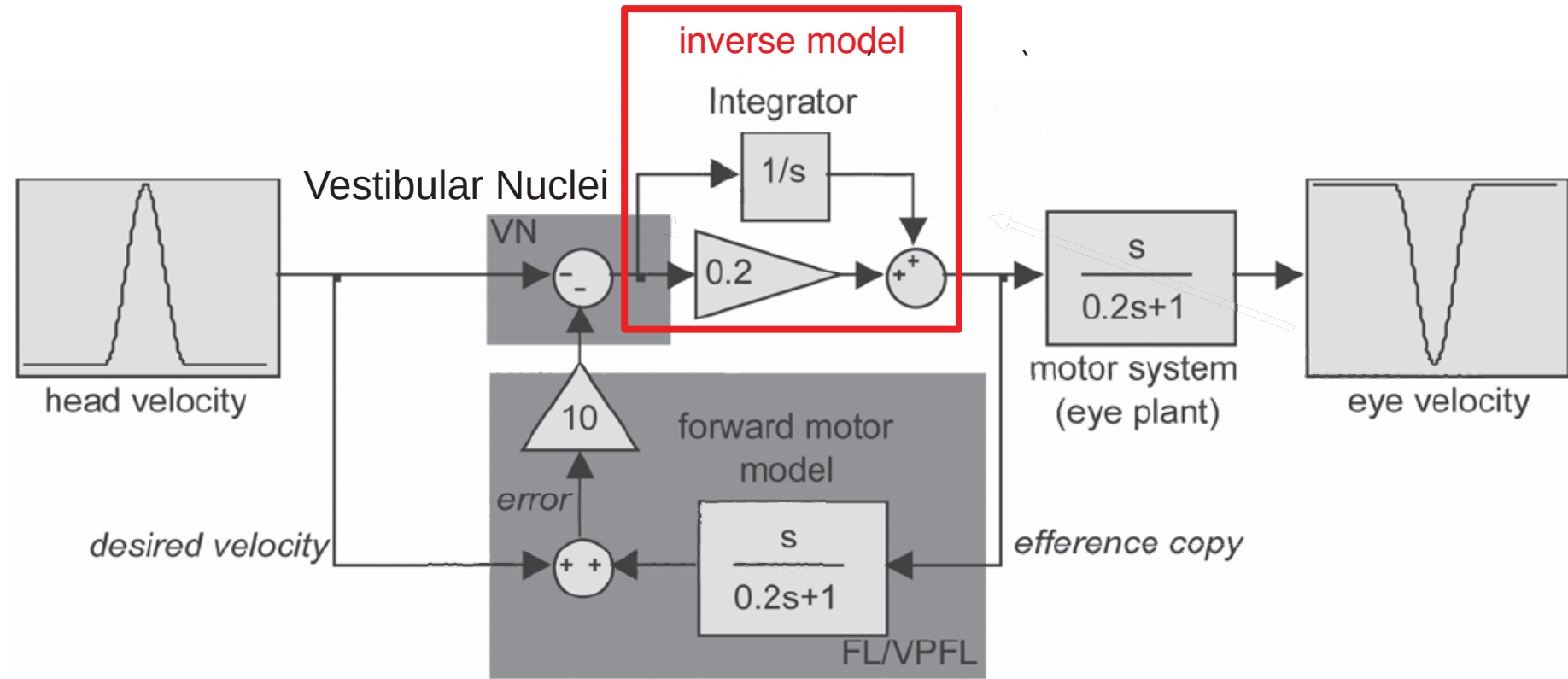
Kandel et al. Fig. 41-10

Inverse and forward models



Reconfigured solution matching cerebellar architecture

Feedforward control using internal models

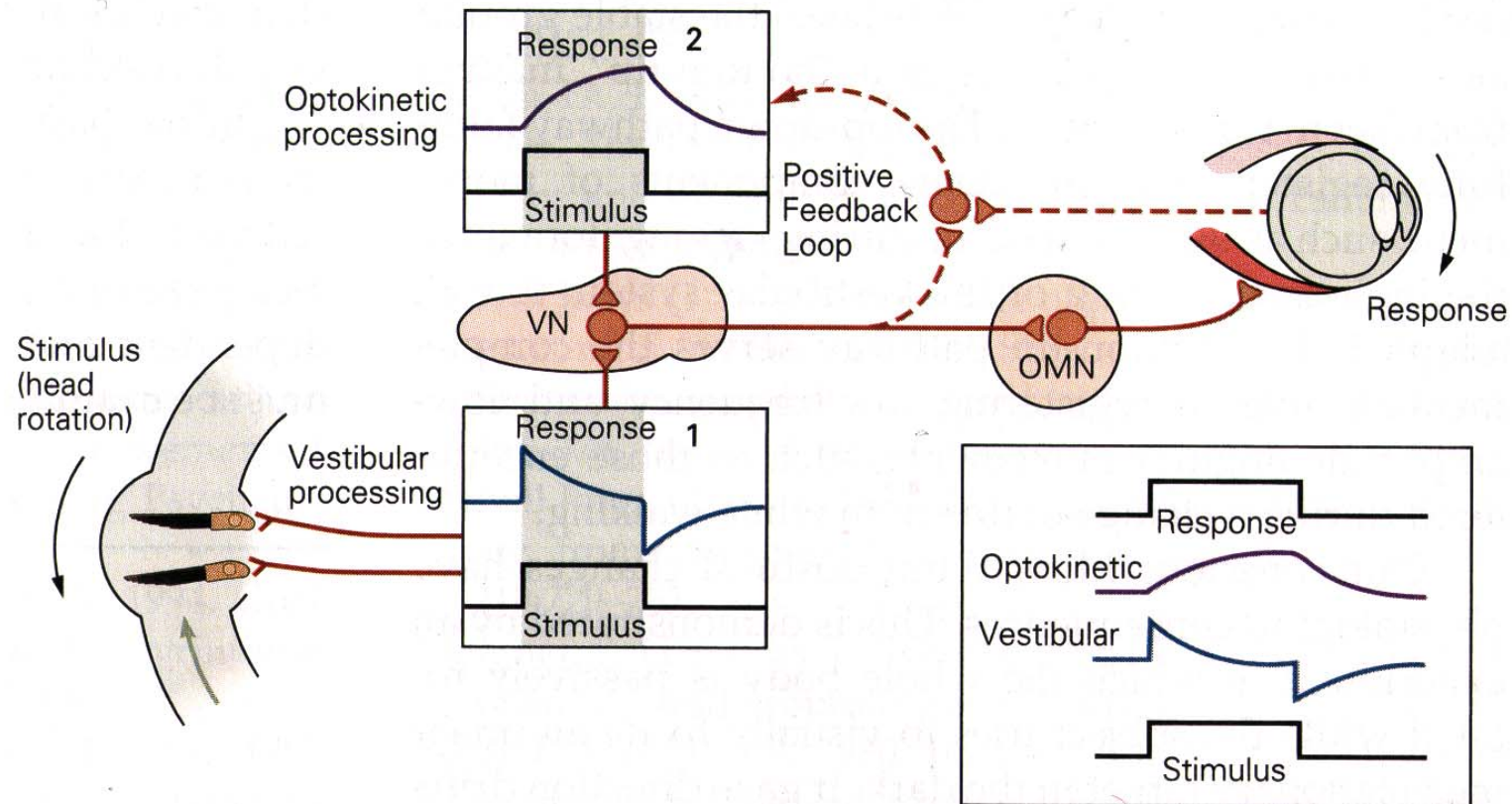


Using the concept of internal models for motor control for ocular motor control

The cerebellum as forward model, comparator, and error feedback

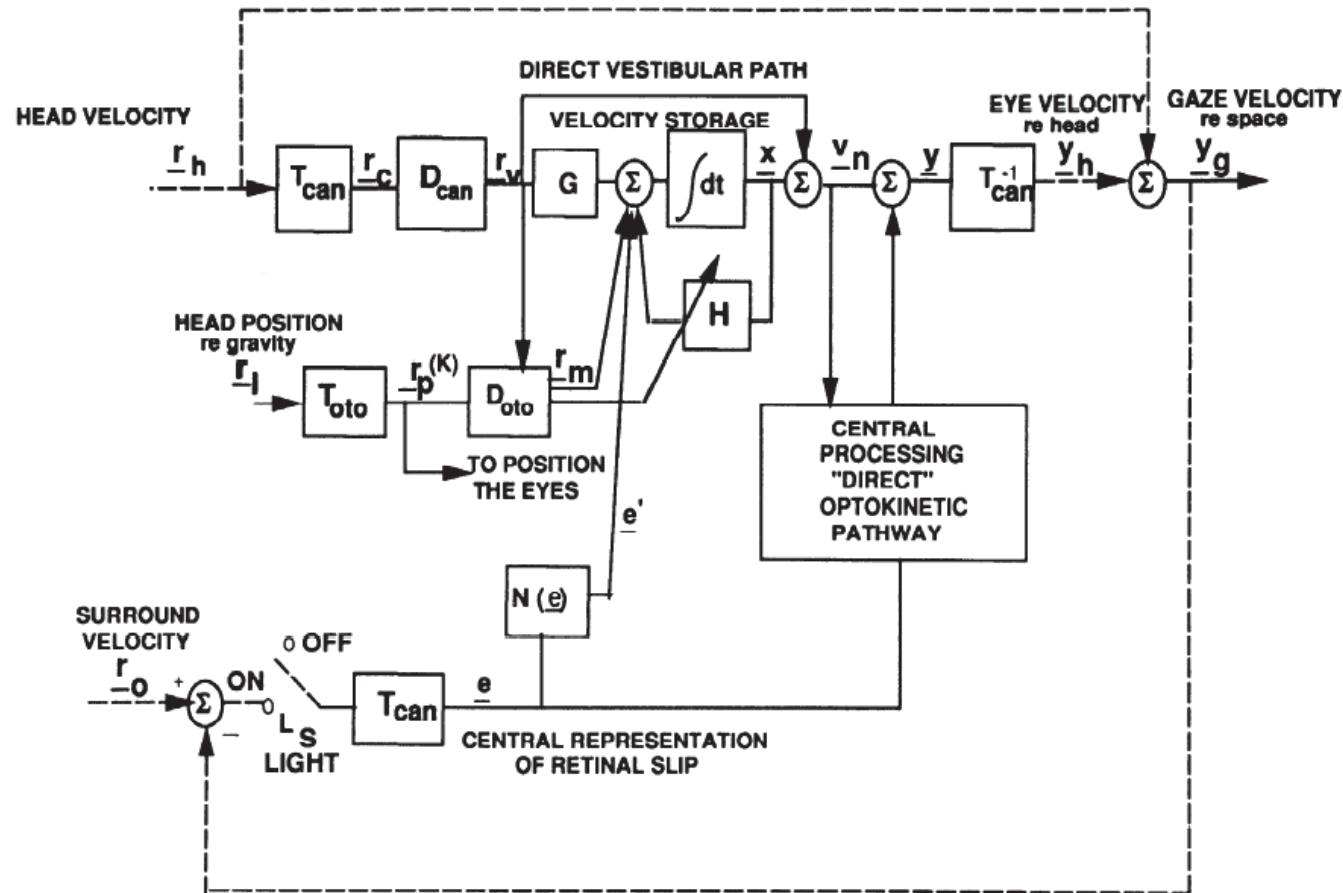
Glasauer S: Cerebellar Contribution to Saccades and Gaze Holding. Ann NY Acad Sci 1004: 206–219 (2003)

Feedforward and feedback control



Vestibulo-ocular and optokinetic reflexes

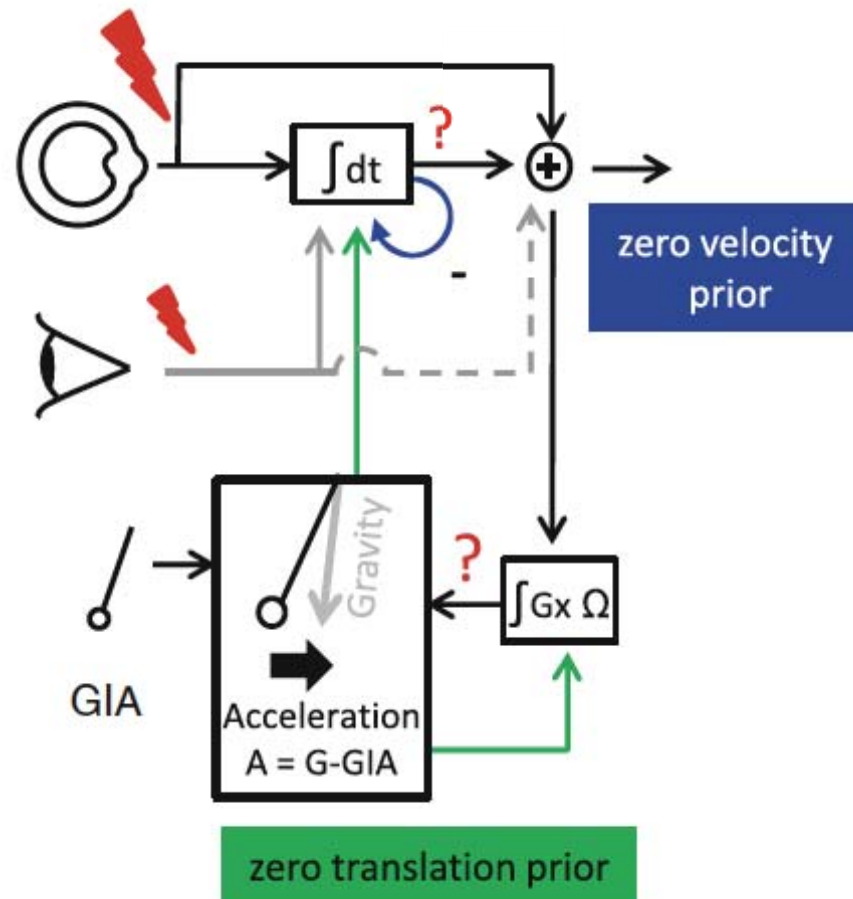
History: the model 20 years ago



Raphan & Sturm, Modeling the Spatiotemporal Organization of Velocity Storage in the Vestibuloocular Reflex by Optokinetic Studies. J Neurophysiol 66, 1991

"Velocity storage"

History: the model (contemporary version)

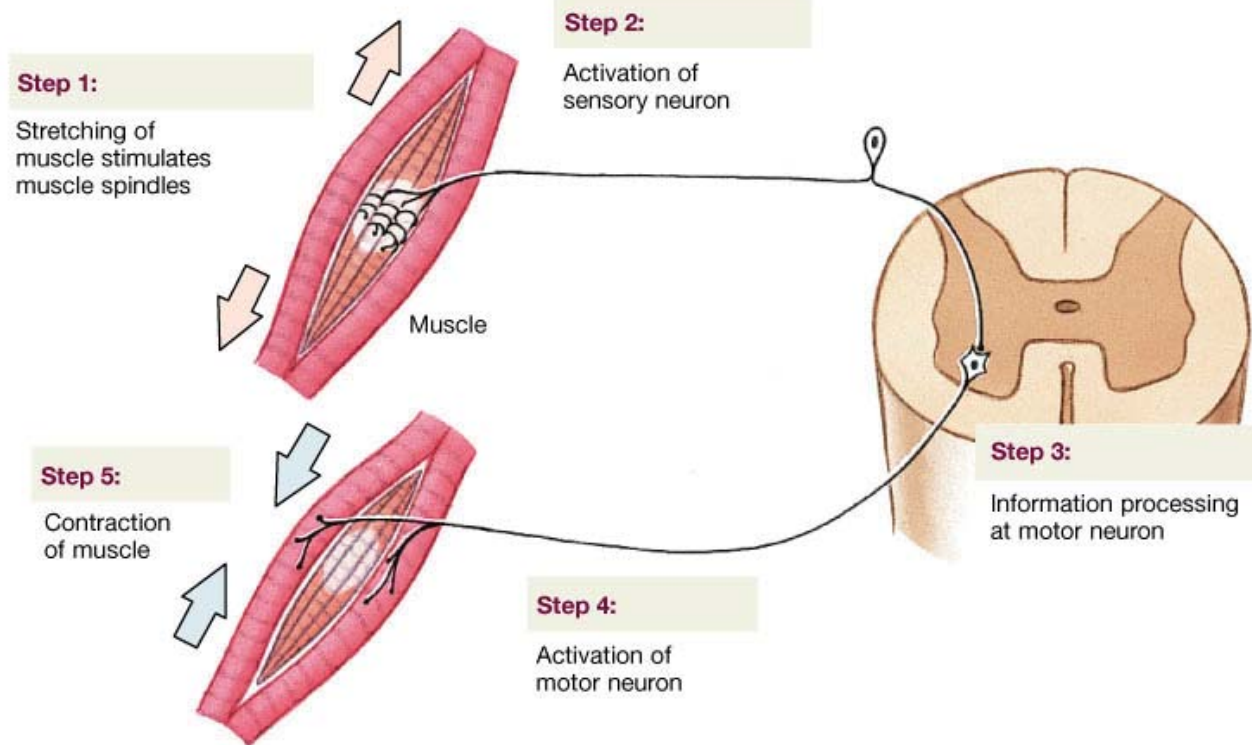
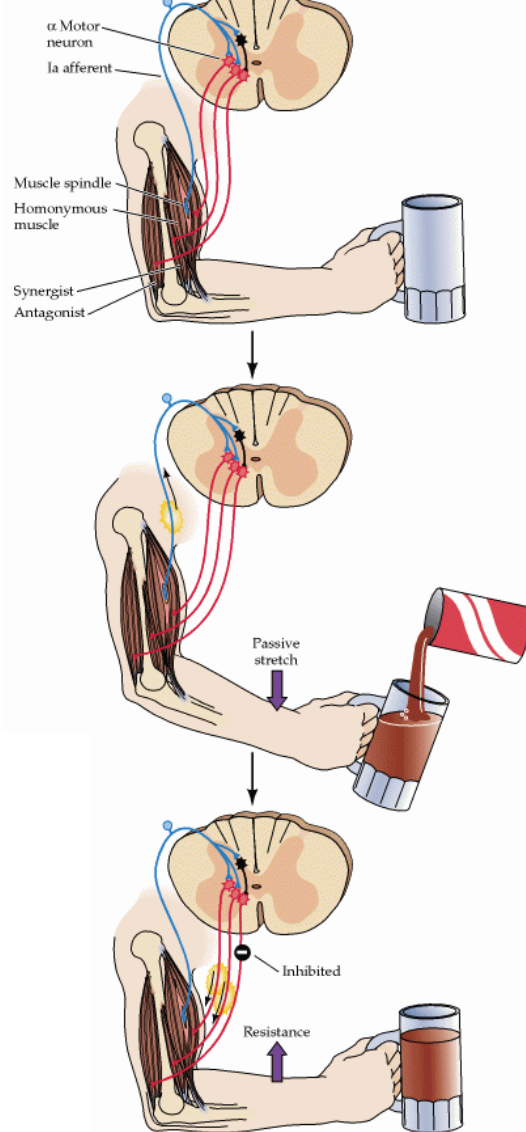


Laurens & Angelaki, The functional significance of velocity storage and its dependence on gravity. Exp Brain Res 210, 2011

Velocity storage 20 years later: "... a central, multisensory rotation estimator ..."

Spinal feedback control

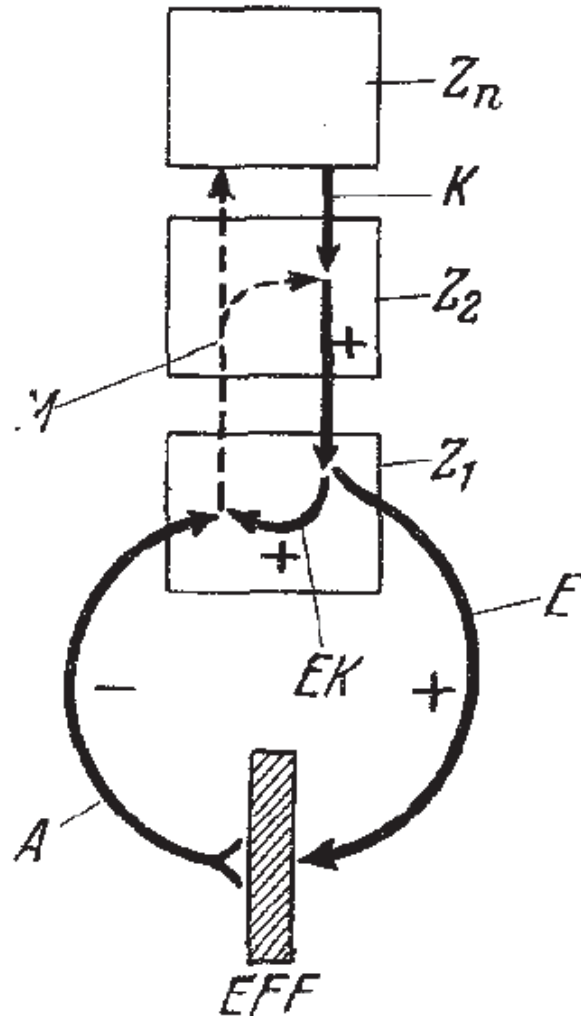
Purves et al. Fig 16.9
(B)



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Stretch reflex and spinal feedback

History

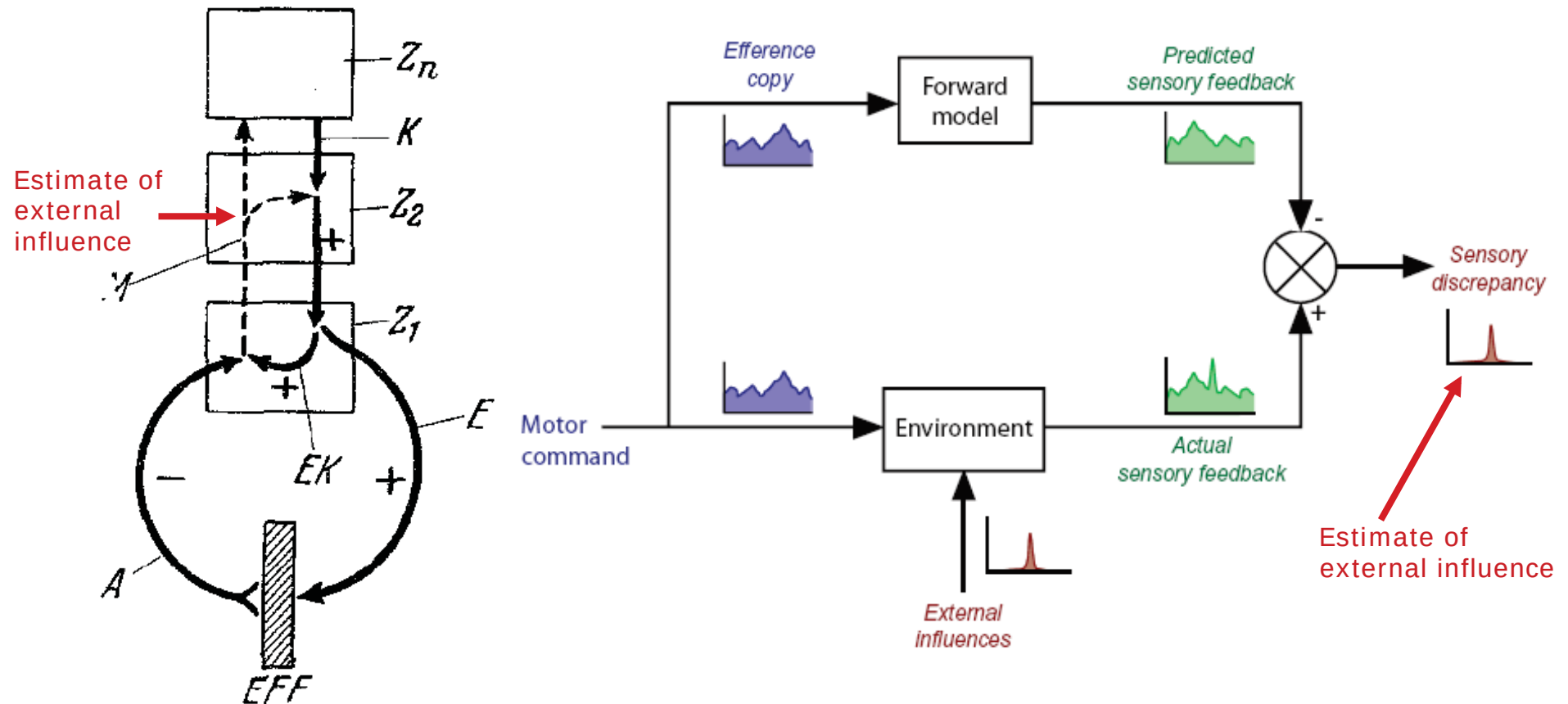


Wir fragen nicht nach der Beziehung zwischen einer gegebenen Afferenz und der durch sie bewirkten Efferenz, also nach dem „Reflex“, sondern gehen *umgekehrt* von der Efferenz aus und fragen: was geschieht im ZNS mit der von dieser Efferenz über die Effektoren und Rezeptoren verursachten Afferenz, die wir die „*Reafferenz*“ nennen wollen?

... das *Auge* unterscheidet eigene und Umweltbewegungen zwar nicht, aber das *Tier* ... unterscheidet sie *wohl*.

Erich von Holst & Horst Mittelstaedt, *Das Reafferenzprinzip* (1950)

Reafferrence principle



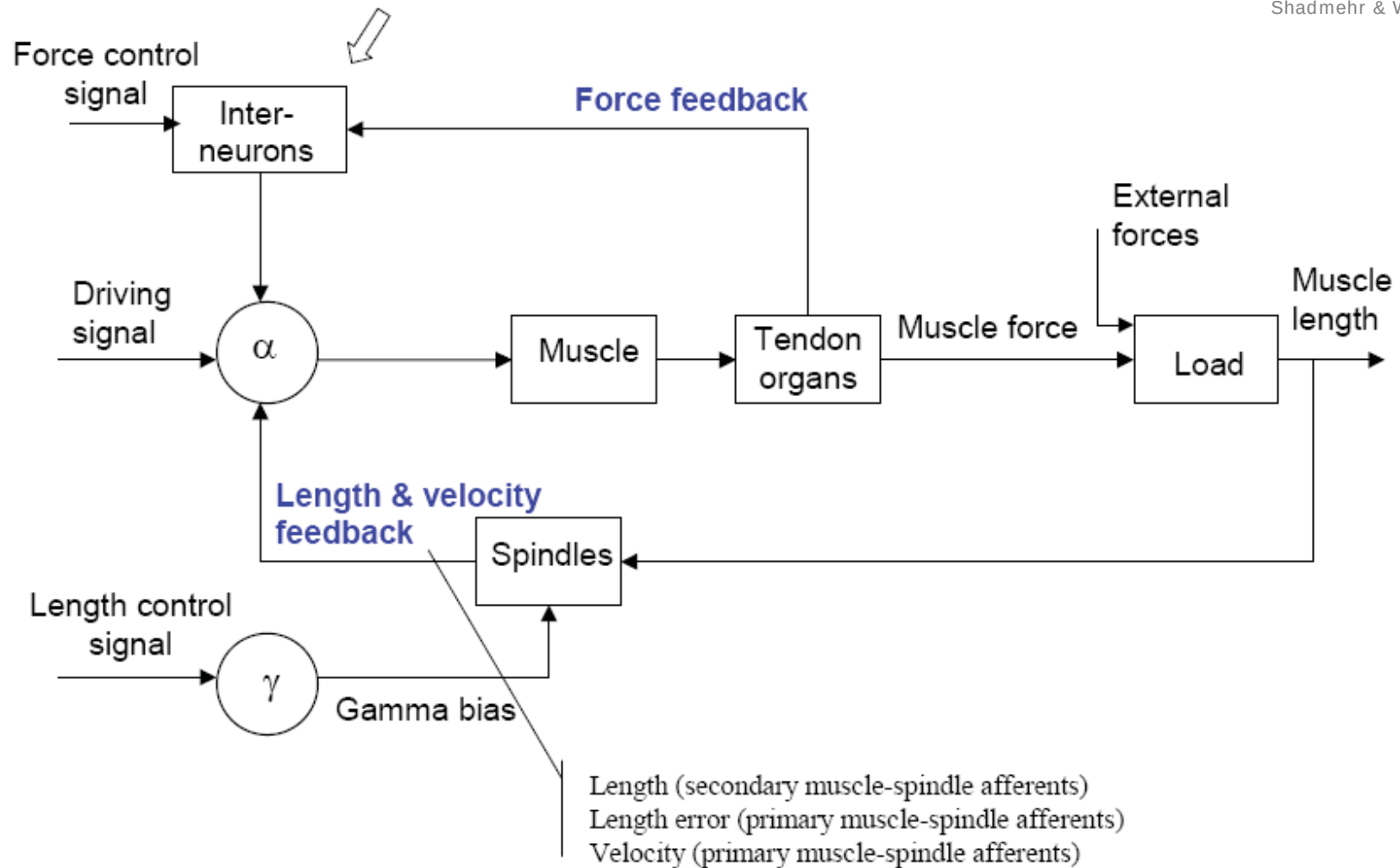
von Holst & Mittelstaedt 1950

Bays & Wolpert 2007

Efference copy is used to distinguish self-generated sensory input (reafference) from external perturbations

Spinal feedback control

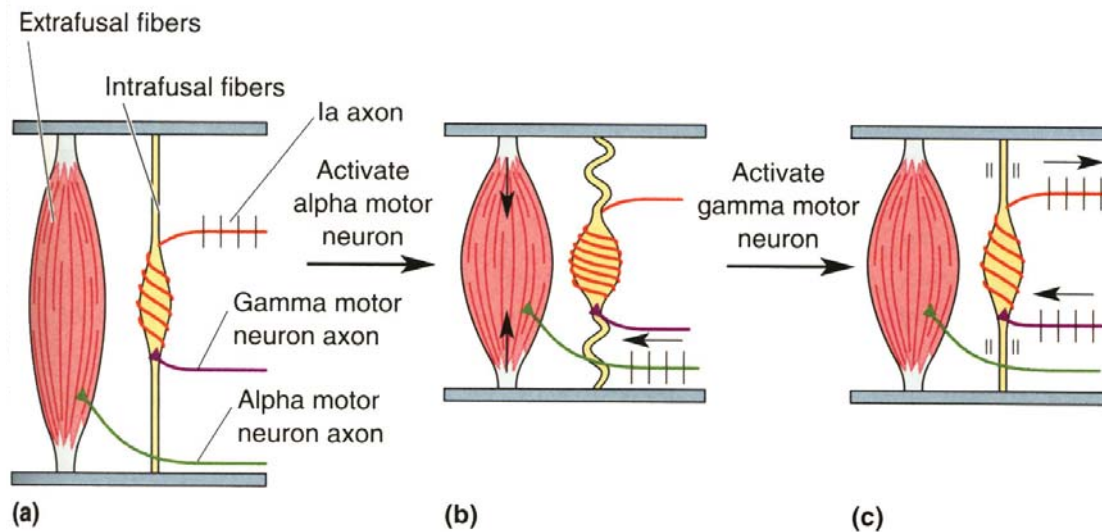
Shadmehr & Wise 2005



The local spinal feedback control circuit

Spinal feedback control

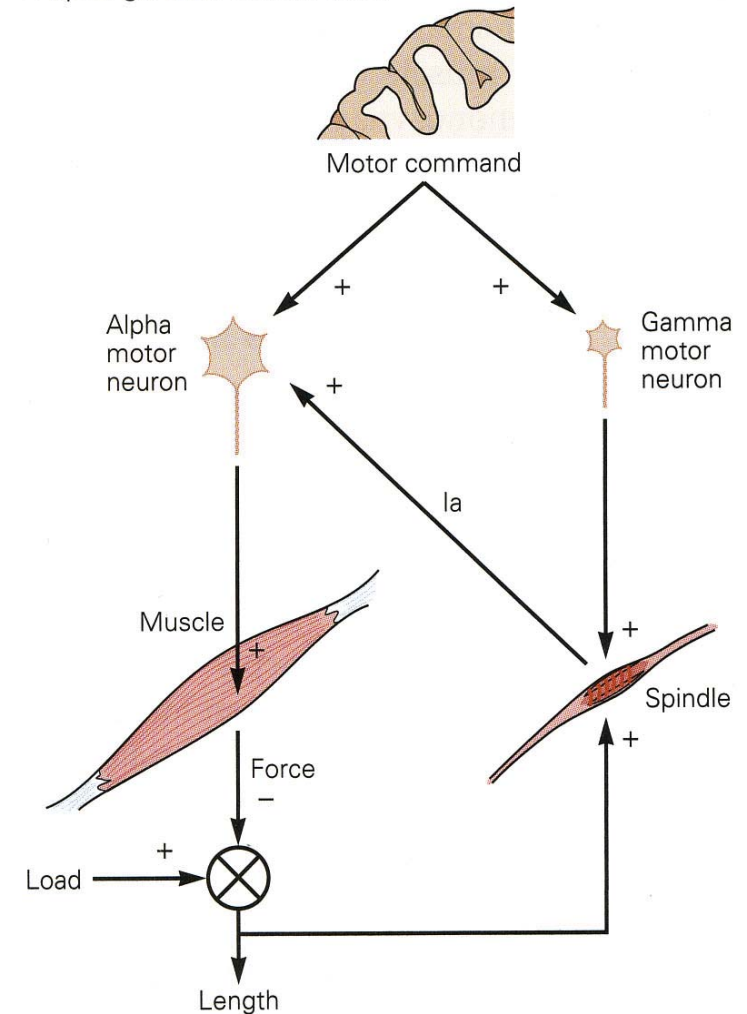
Bear et al. Fig 13.19



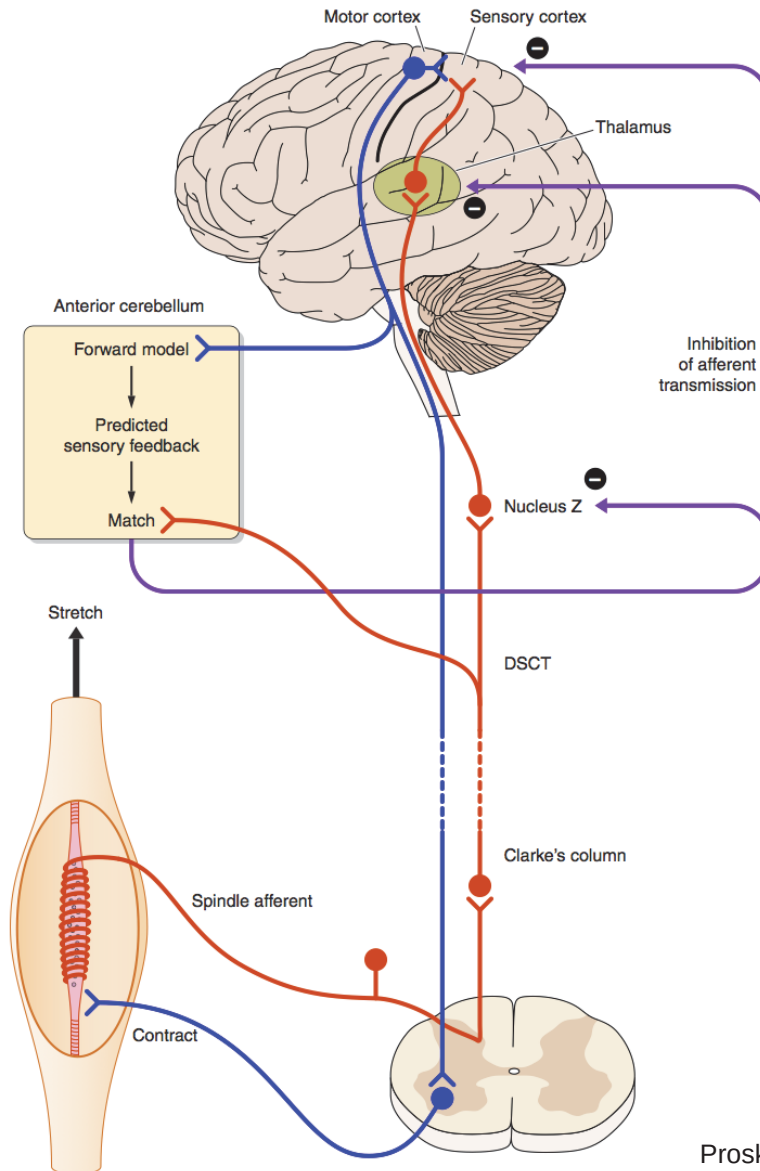
Alpha-gamma co-activation

Kandel et al. Fig 36-12

Alpha-gamma coactivation



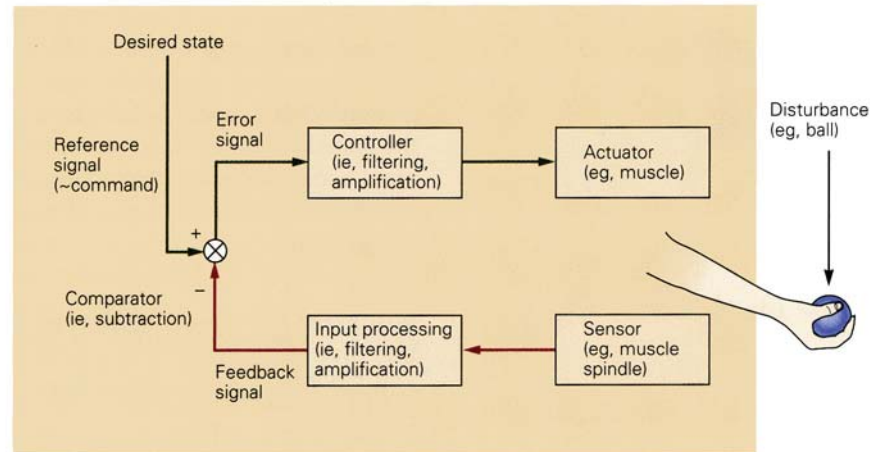
Proprioception and efference copy



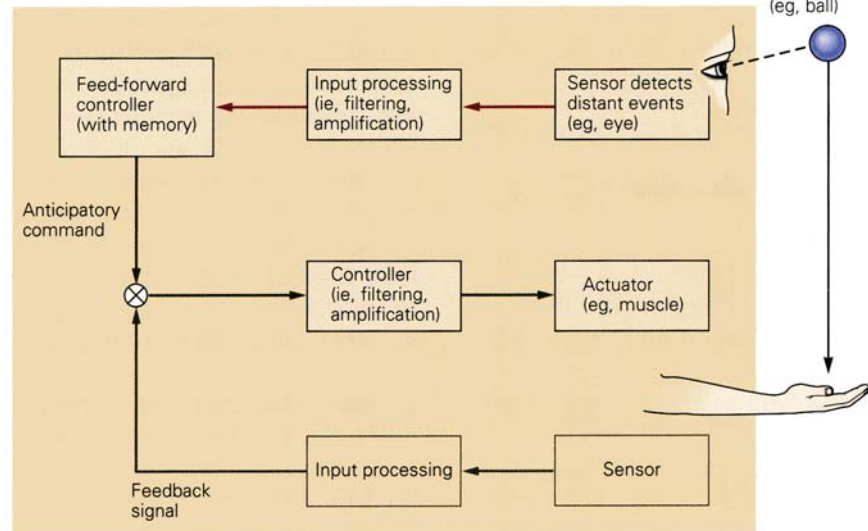
Possible mechanism for how the brain distinguishes between impulses coming from muscle spindles that are generated by muscle stretch (exafference) or by fusimotor activity (reafference)

Combined Control

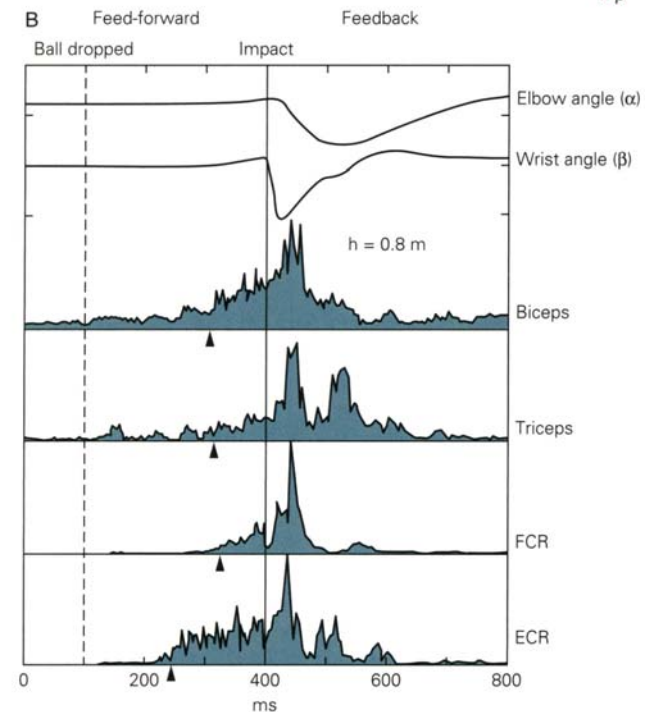
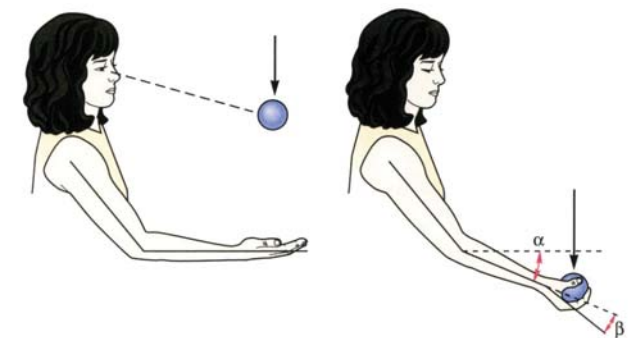
A Feedback control: command specifies desired state



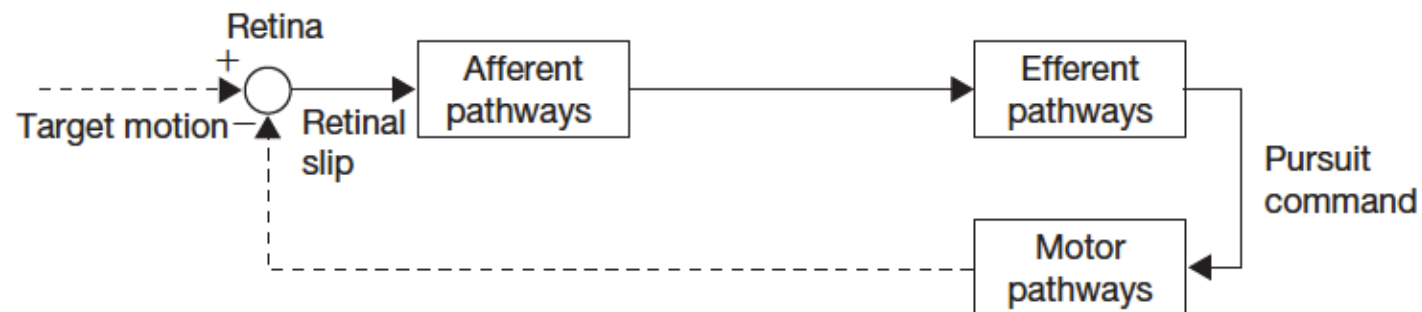
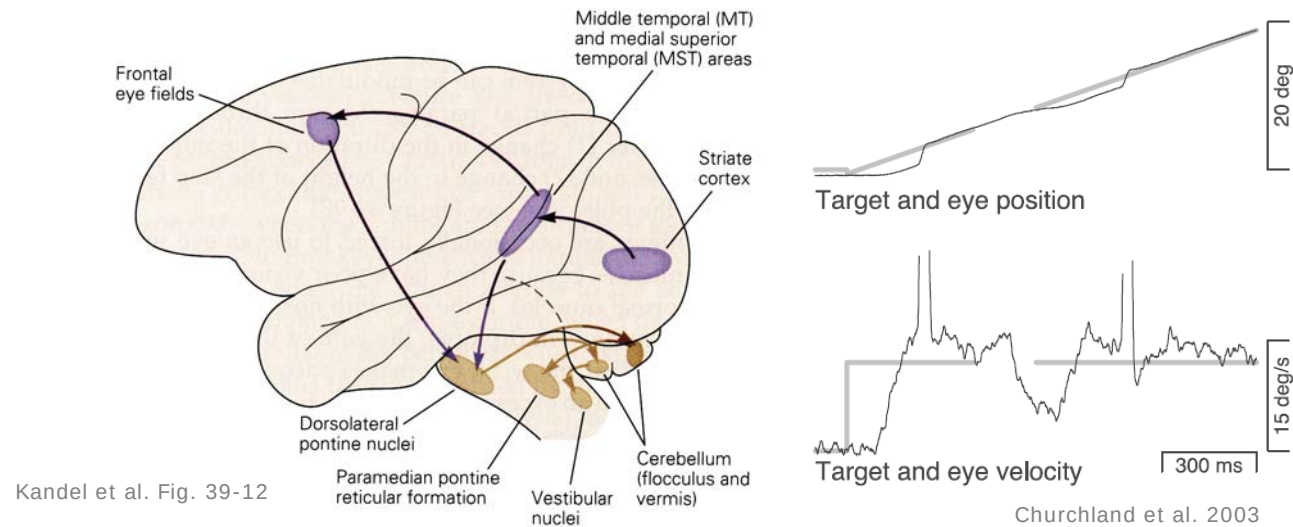
B Feed-forward control: command specifies response



A Feed-forward Feedback



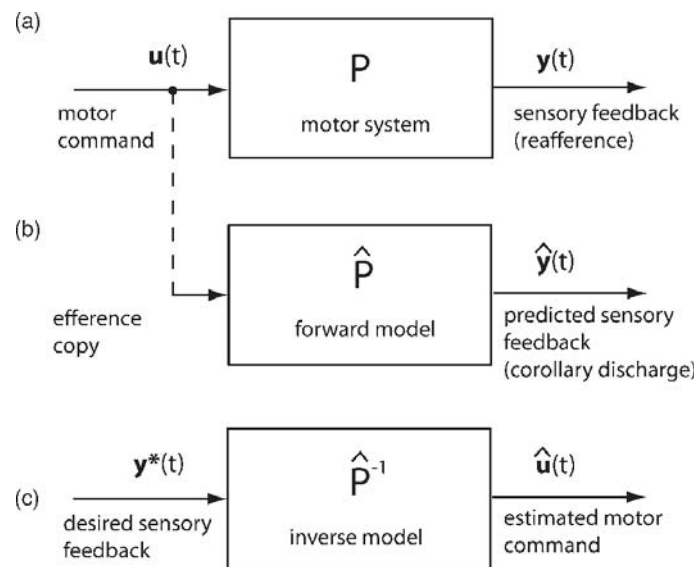
Feedback Control: Smooth Pursuit



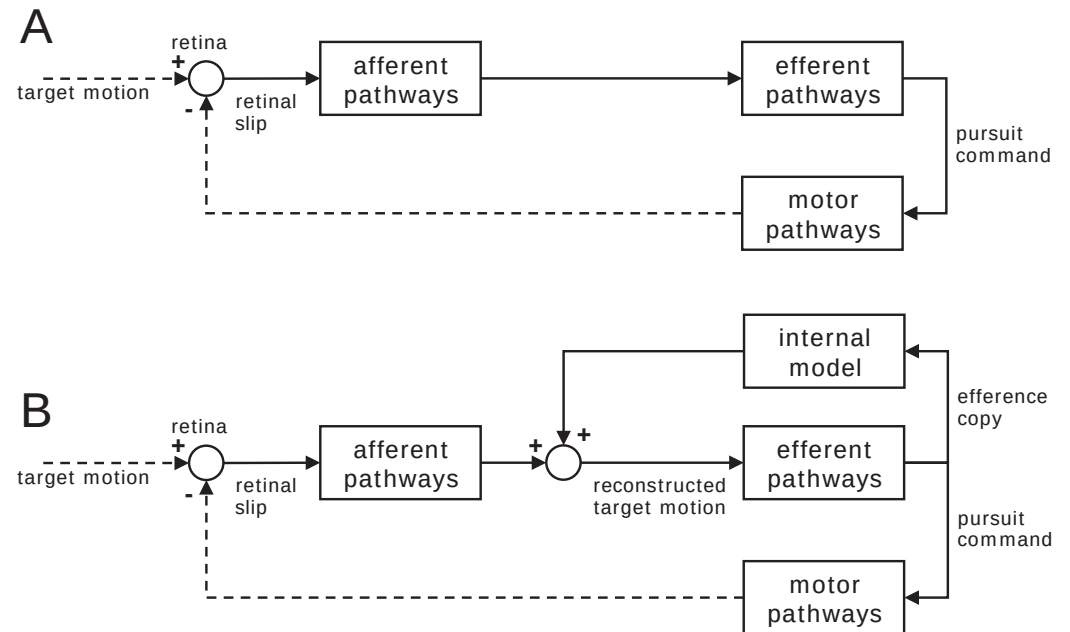
Glasauer 2007 after Lisberger 1987

Following a target by smooth pursuit

Internal models



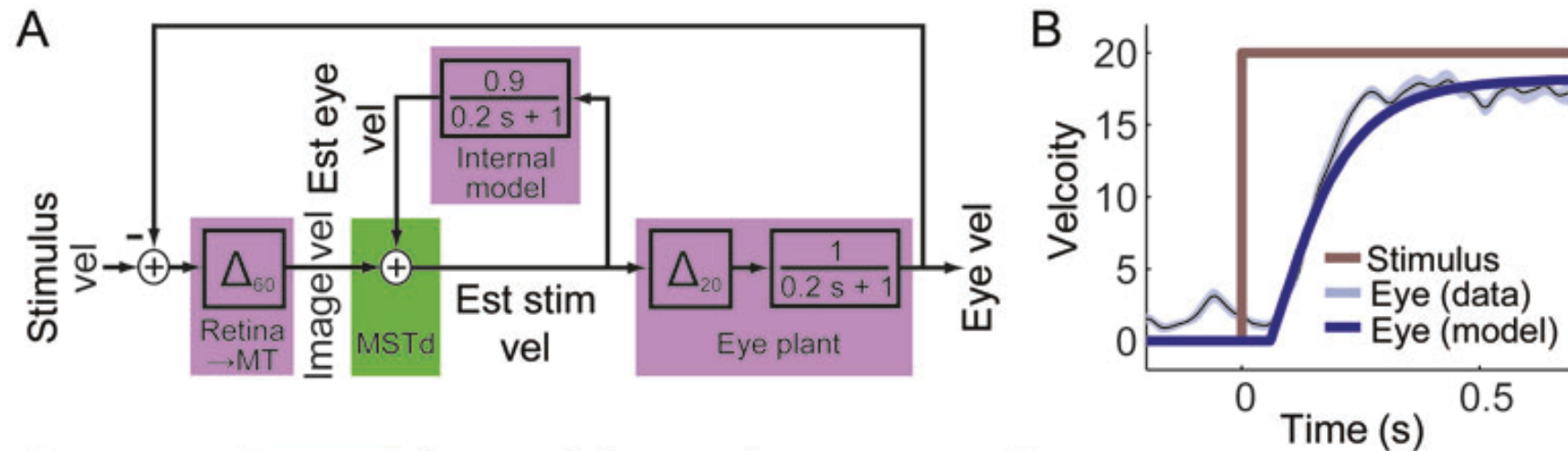
Davidson & Wolpert 2005



Glasauer 2007 after Lisberger 1998

Forward and inverse models

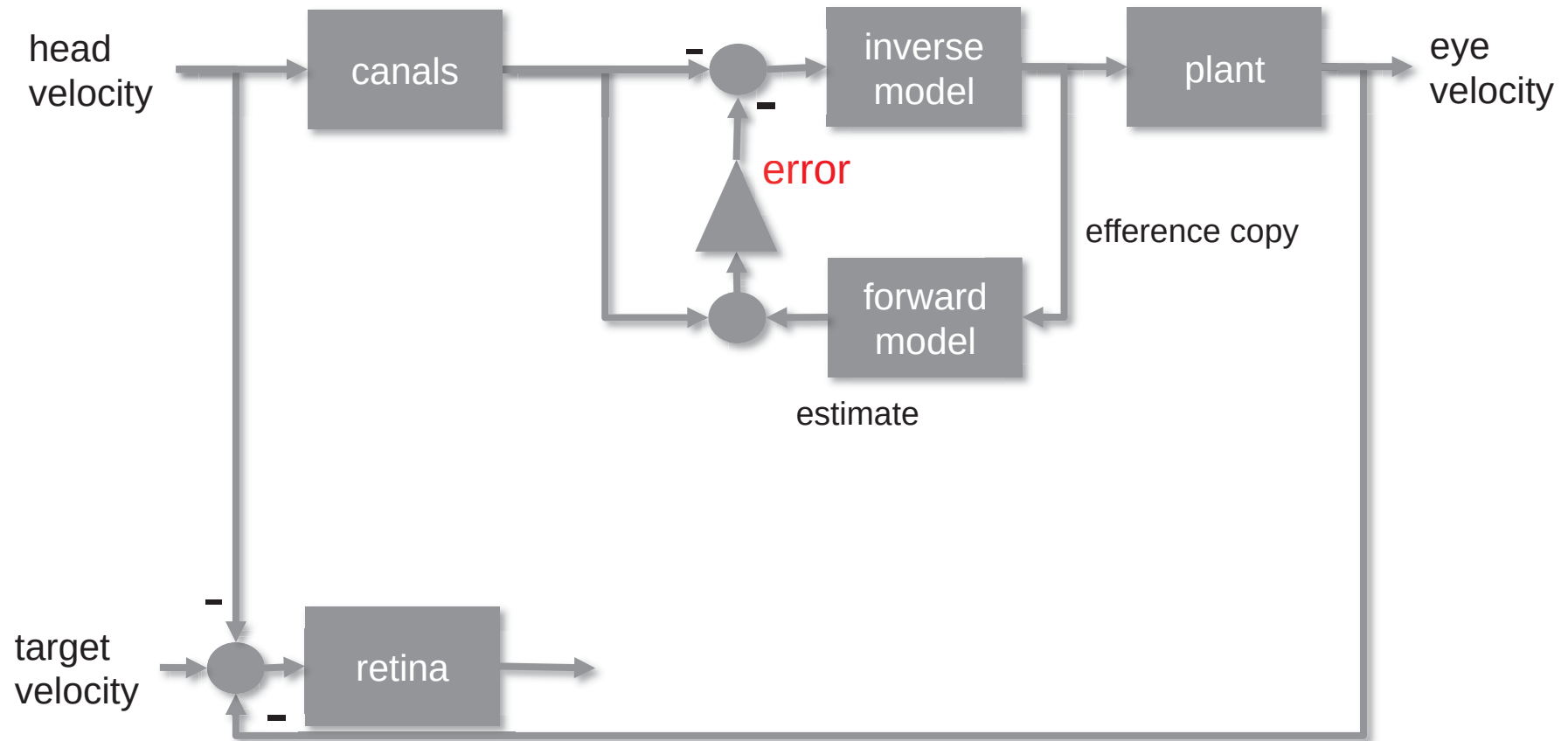
Feedback Control: Smooth Pursuit



Brostek et al. Cereb Cortex 2014

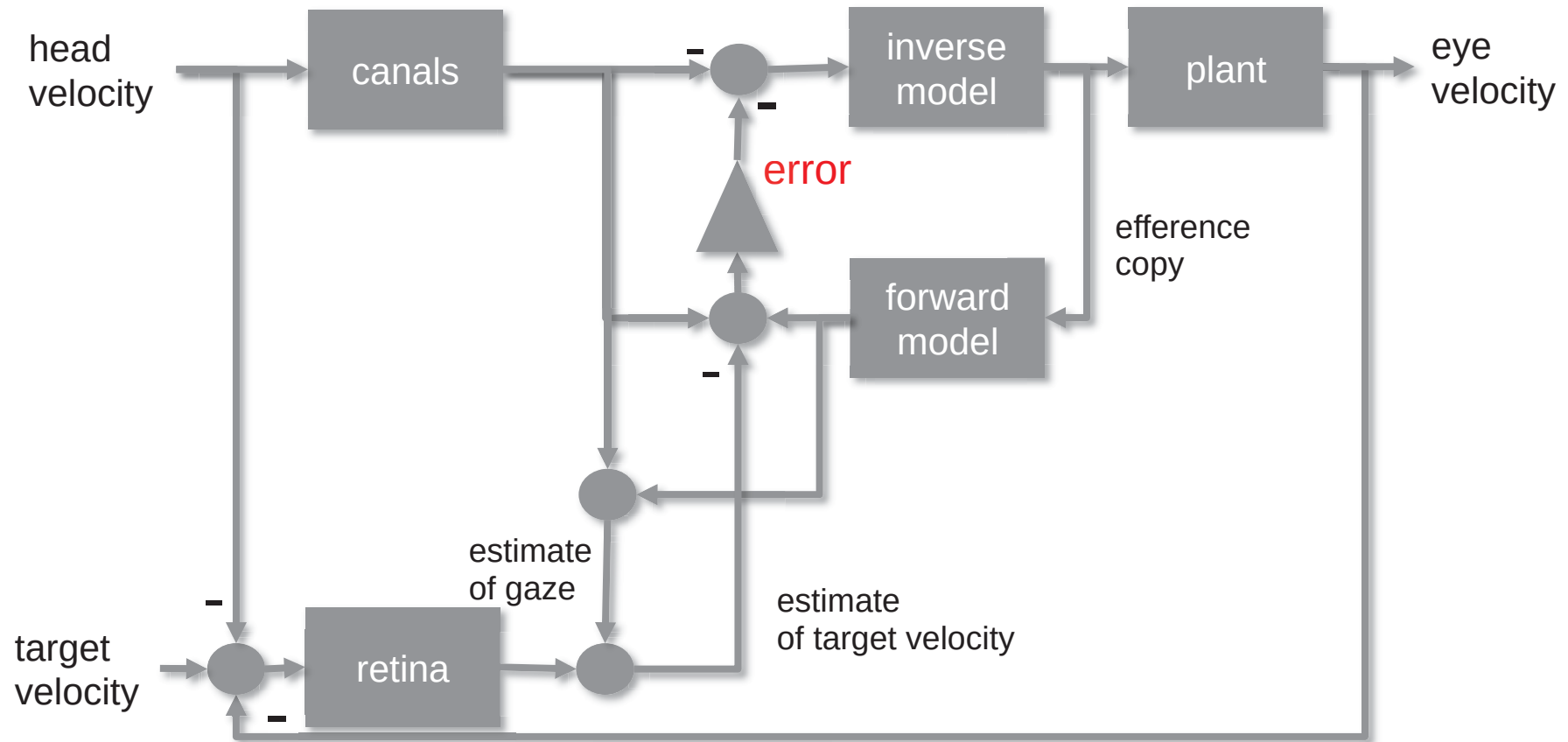
The internal forward model allows estimating an external variable and overcoming the problem of temporal delays in feedback control

Closing the loop



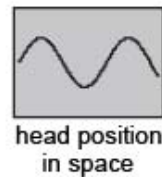
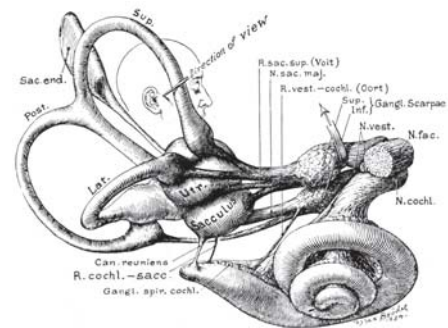
How to follow the target?

Closing the loop



Use internal estimates!

Ocular motor circuitry model



head position

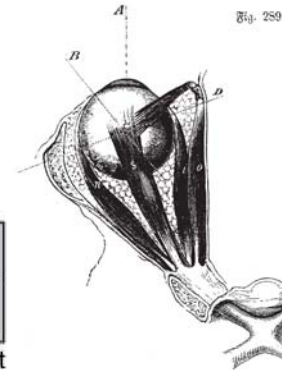
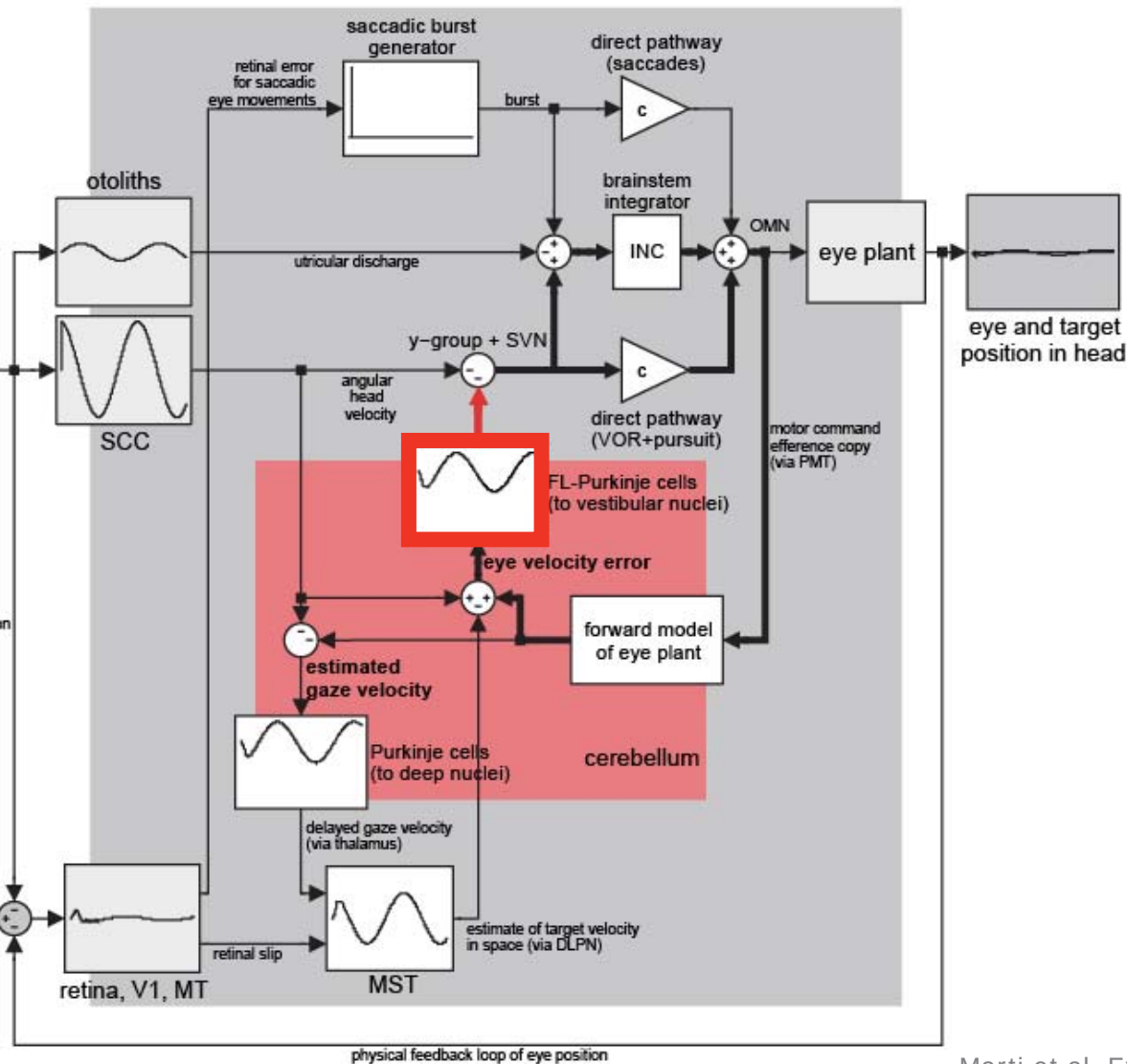
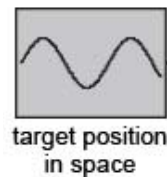
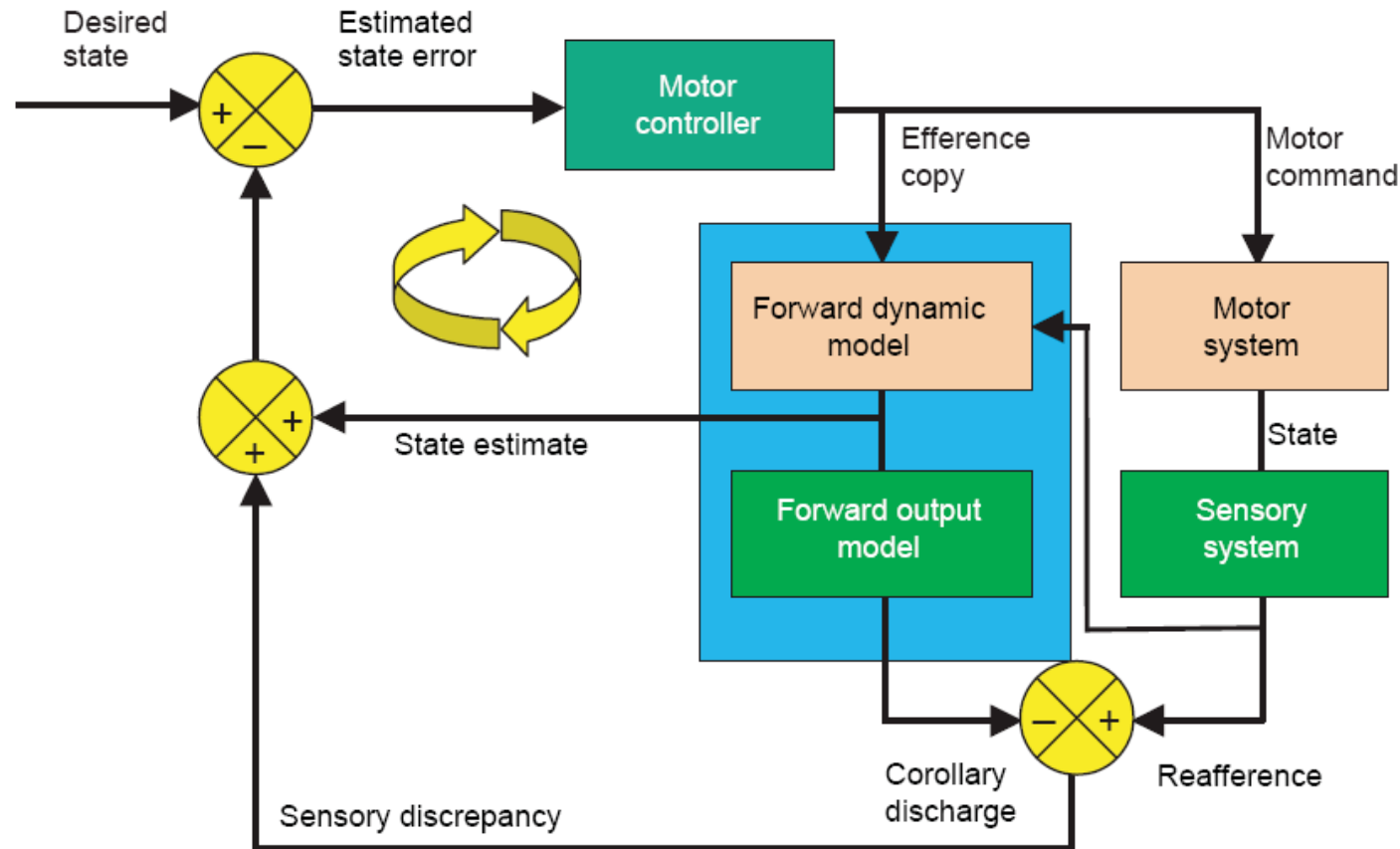


Fig. 259

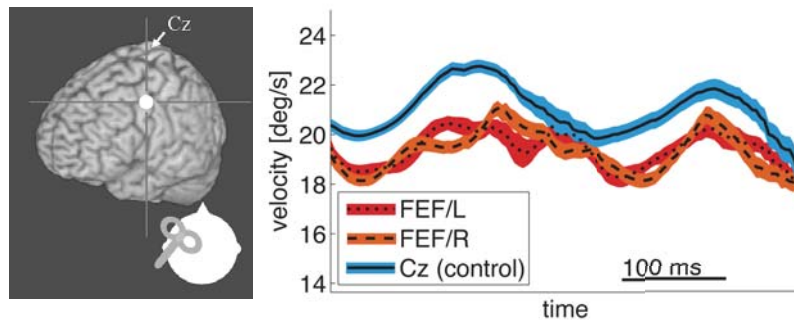
Feedback Control: Smith Predictor

Wolpert, Miall, Kawato 1998

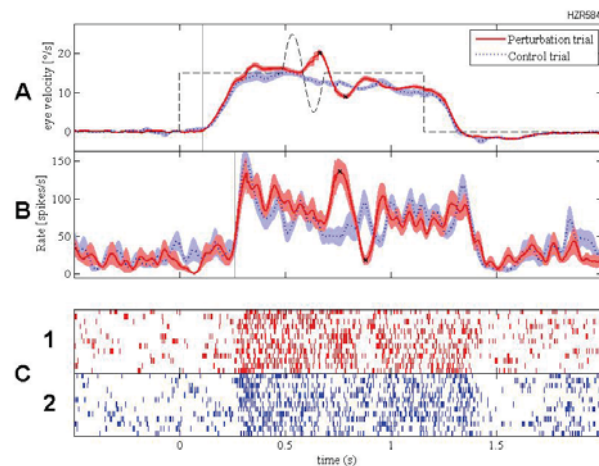


The internal forward model allows estimating an external variable and overcoming the problem of temporal delays in feedback control

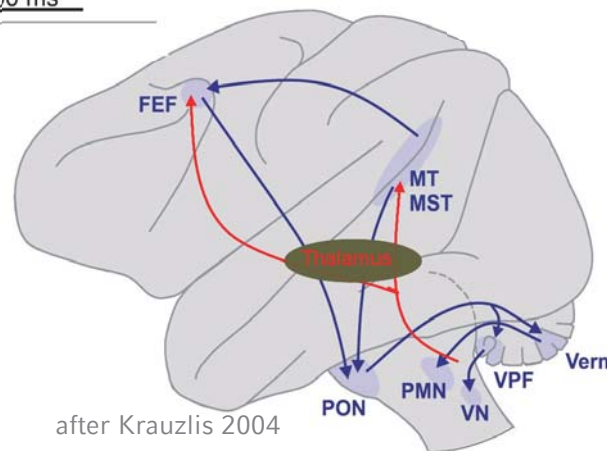
Cortical Control of Smooth Pursuit



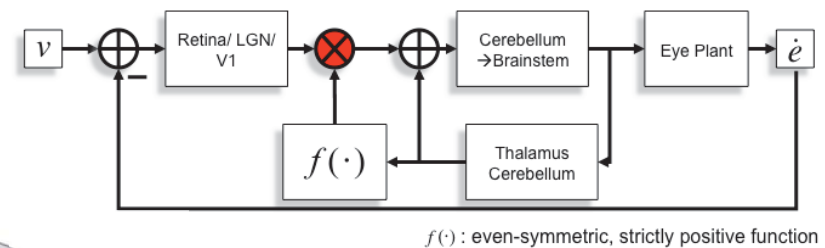
Nuding et al. Cereb Cortex, 2009



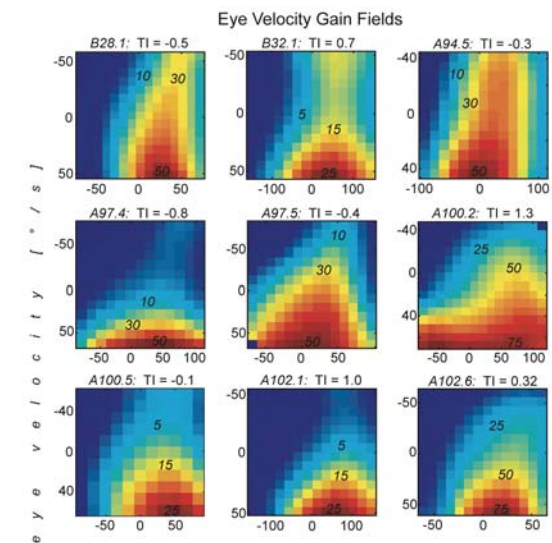
Ono et al. J Neurophysiol, 2010



$$\tau \cdot \ddot{e} = (v - \dot{e}) \cdot (c + m|\dot{e}|)$$



Nuding et al. J Neurophysiol, 2008



Brostek et al. Cerebral Cortex, 2014

Investigating the gain control mechanism (see Lisberger 2010 for review)
Non-linear feedback and multi-dimensional tuning curves

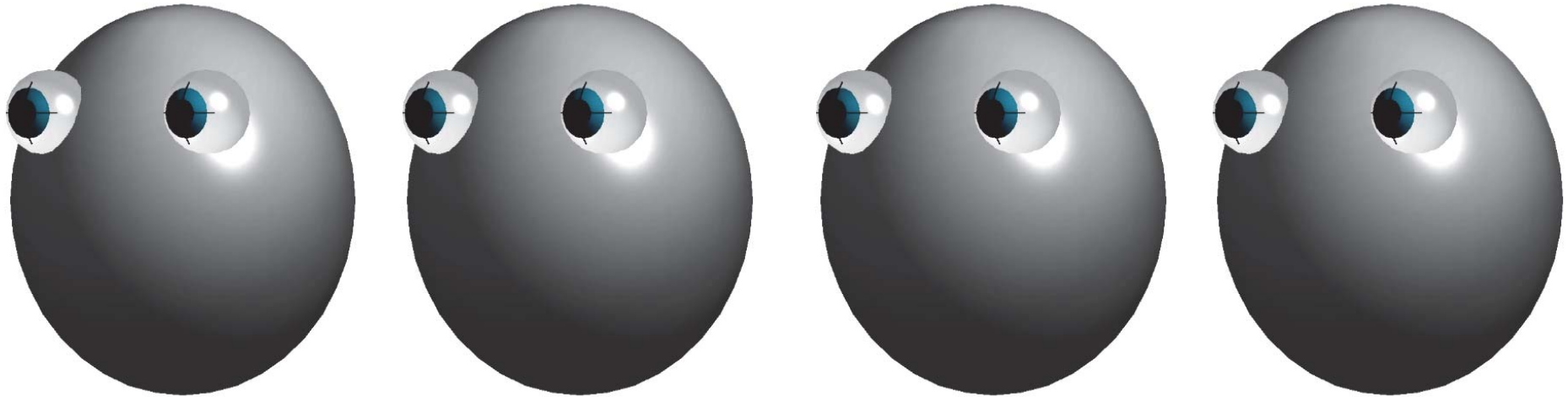
History



Coordination is overcoming excessive degrees of freedom of our movement organs, that is, turning the movement organs into controllable systems.

Nikolai Alexandrowitsch Bernstein (1896-1966)

Gaze shift



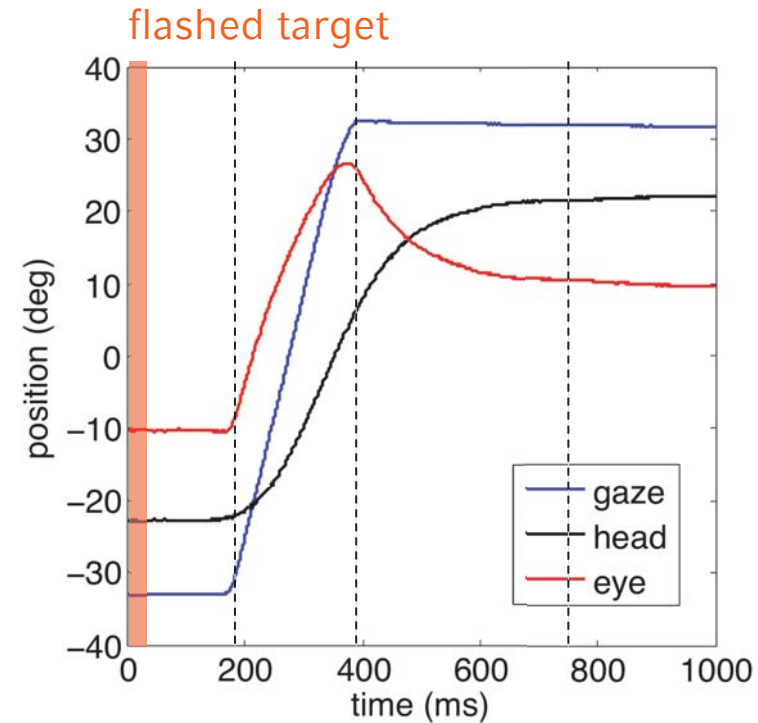
Natural goal-directed gaze shifts involve eye *and* head movements.

Indefinitely many eye-head movements (different combinations of eye and head, different durations and velocity profiles) may yield the same gaze shift amplitude.

Combined eye-head gaze shift

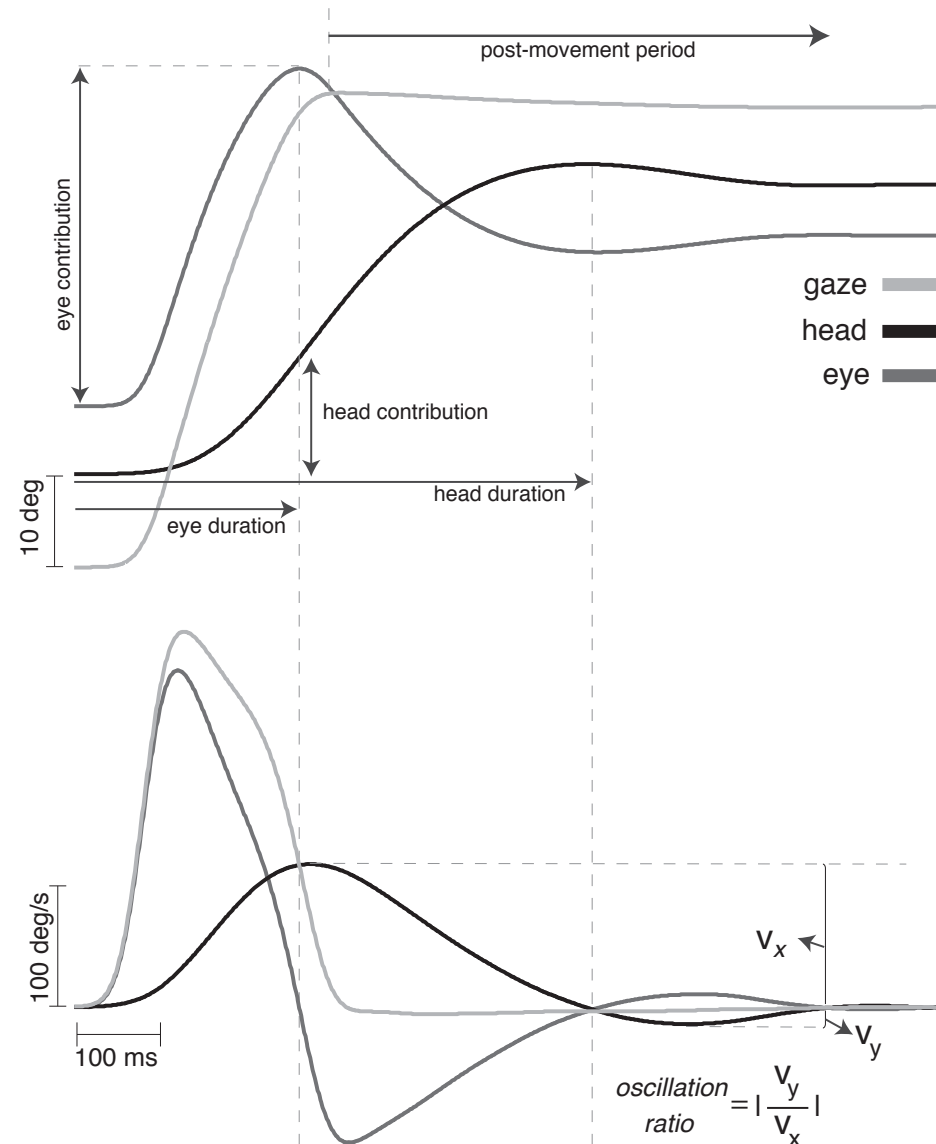


Slow motion (10x)

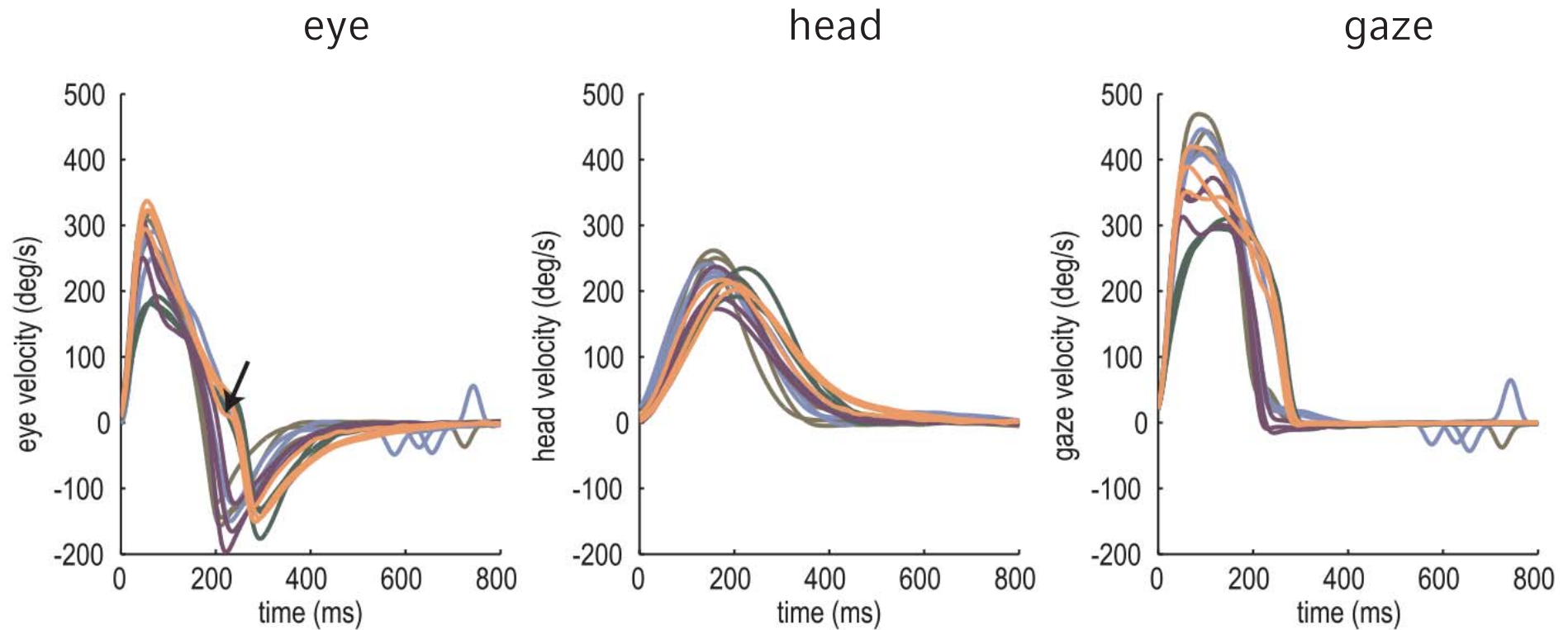


A typical movement to a flashed target (no visual feedback)

Phases of movement

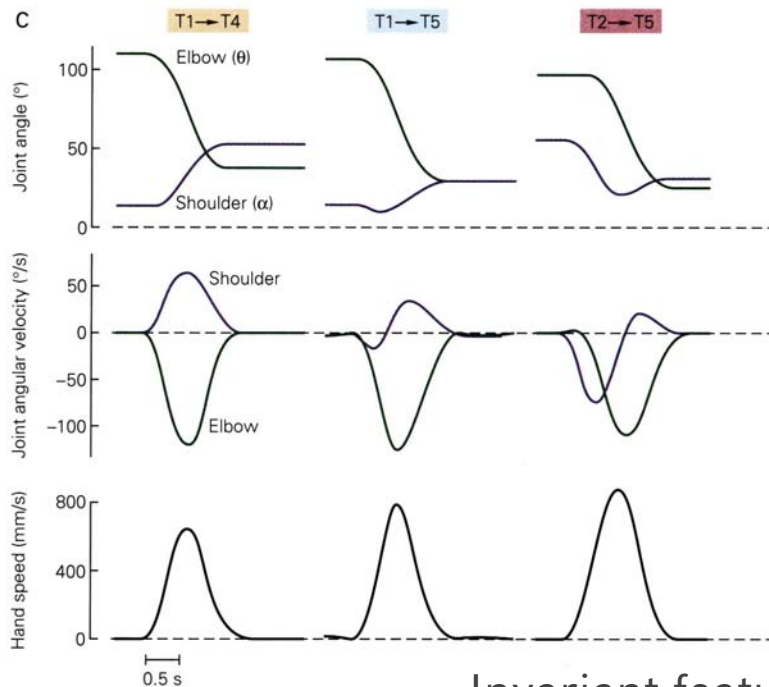
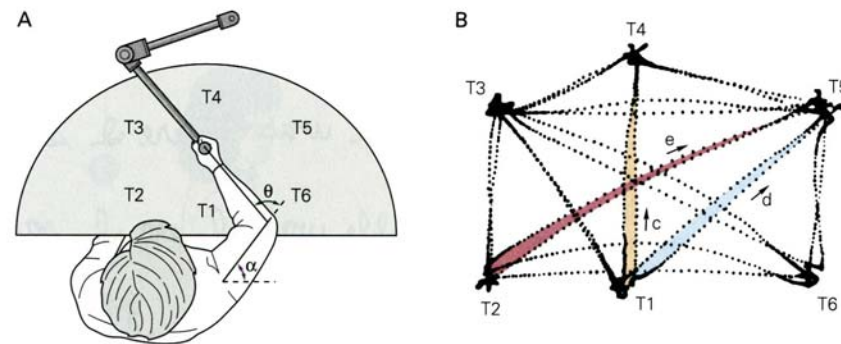


Stereotypical movements

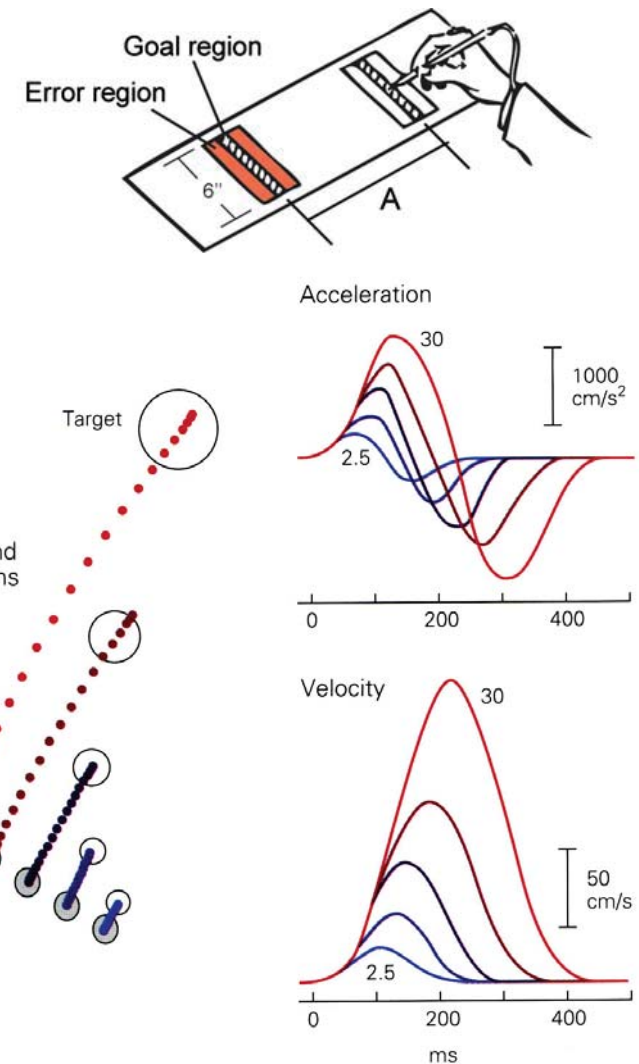


Observation: stereotypical movements
⇒ the choice of movement is optimized

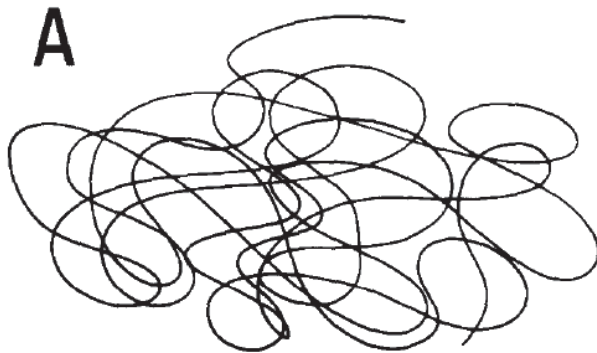
Movements



Invariant features and motor programs



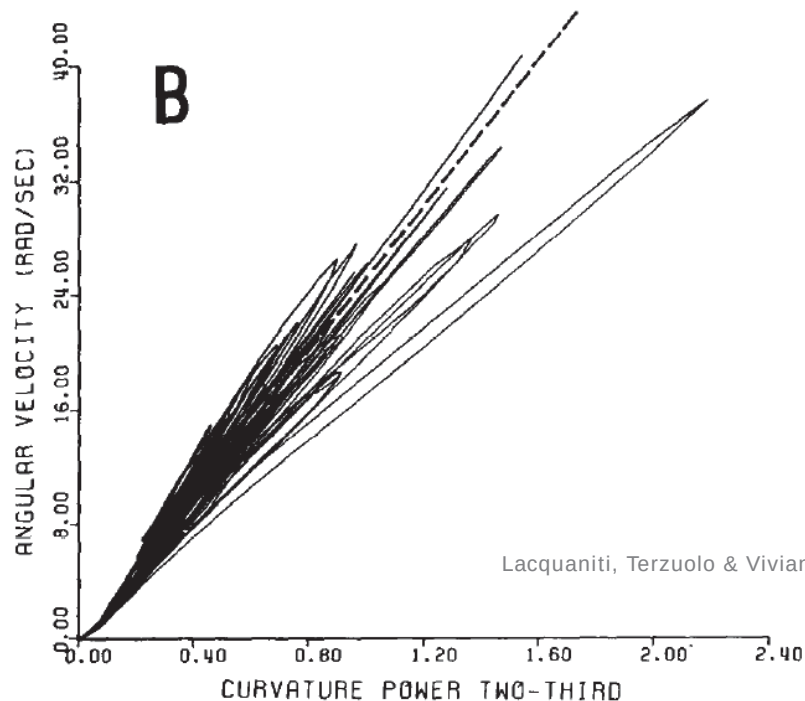
Curvature and Velocity



$$V(t) = k \cdot g(R(t)) = k \cdot R(t)^{1/3}$$

With $\omega(t) = V(t)/R(t)$
and $C(t) = 1/R(t)$

$$\omega(t) = k \cdot f(C(t)) = k \cdot C(t)^{2/3}$$

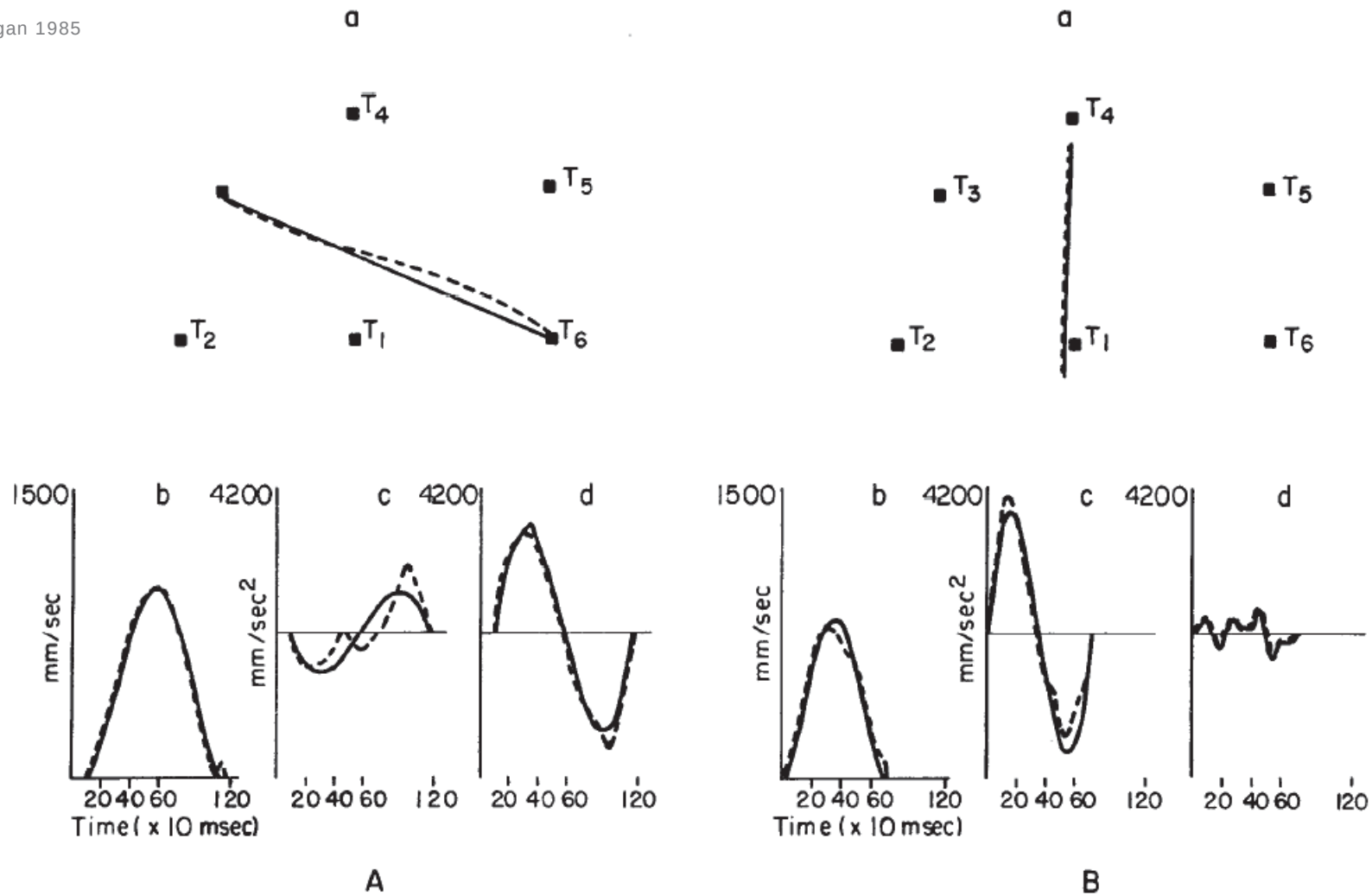


V: tangential velocity
R: instantaneous radius
 ω : angular velocity
C: curvature

The two-third power law

Trajectories and profiles

Flash & Hogan 1985

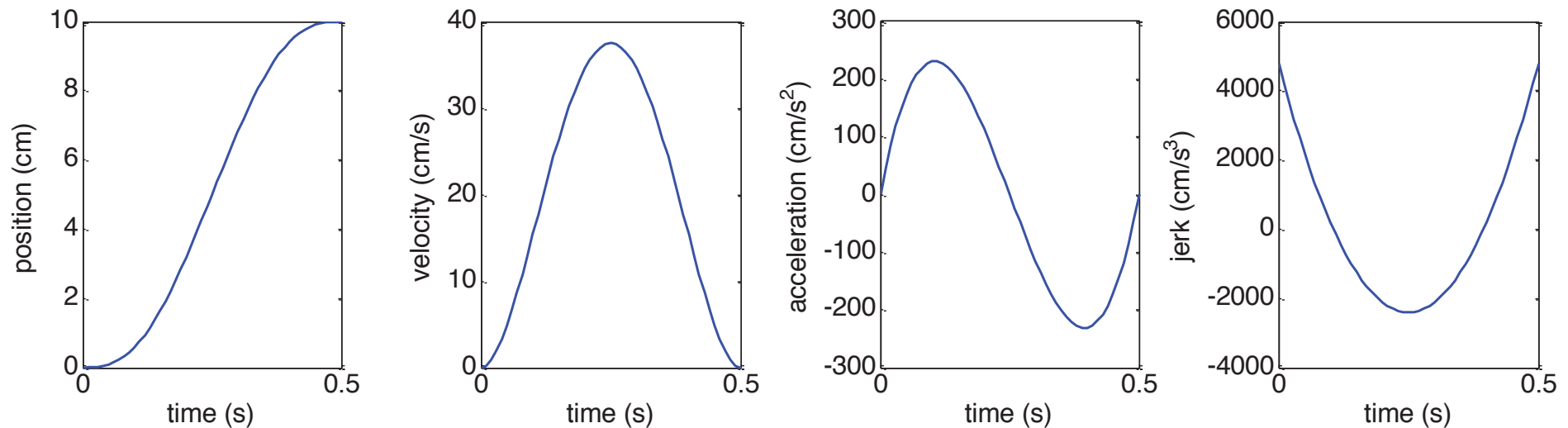


Trajectories are straight lines, velocity profiles are bell-shaped

Minimum-jerk model

Find the function $x(t)$ that **minimizes the cost** $H(x(t)) = \frac{1}{2} \int_{t=0}^{0.5} \ddot{x}^2 dt$

General solution $x(t) = \sum_{i=0}^5 a_i \cdot t^i$ $\dot{x}(t) = \sum_{i=1}^5 i \cdot a_i \cdot t^{i-1}$ etc.



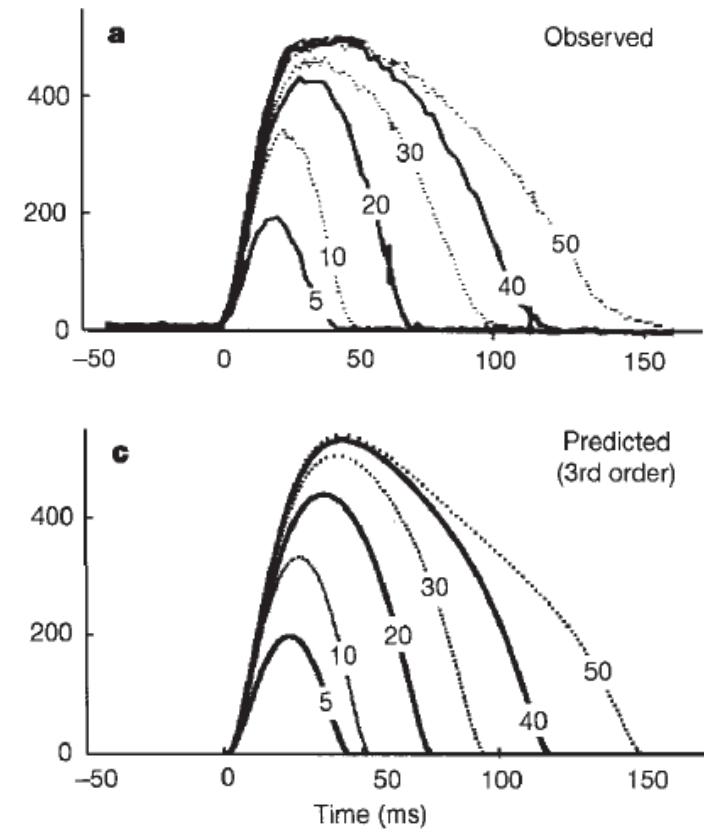
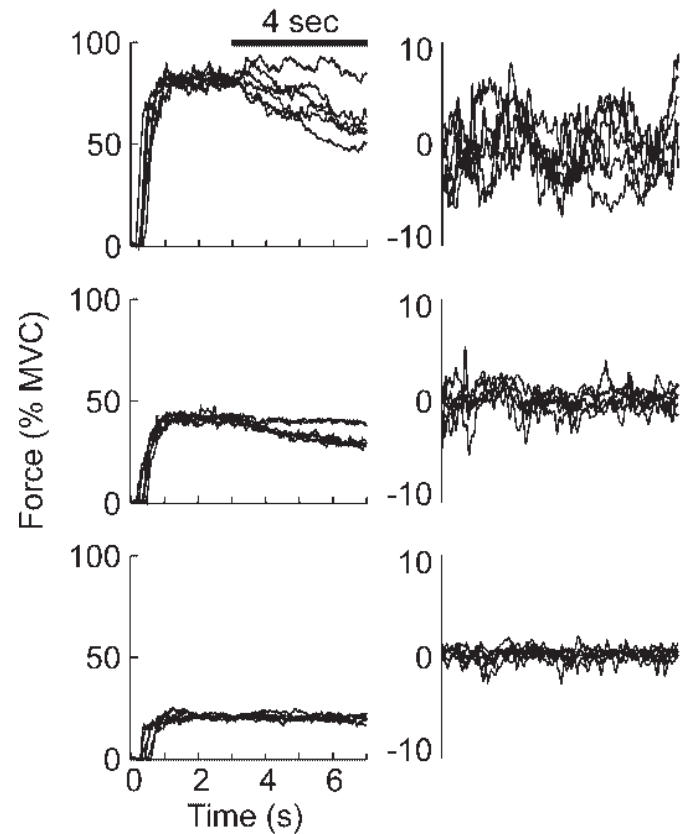
Symmetric velocity profiles, straight trajectories (Flash & Hogan 1985)

Minimum-variance model

Körding & Wolpert 2006

Jones, Hamilton, Wolpert 2002

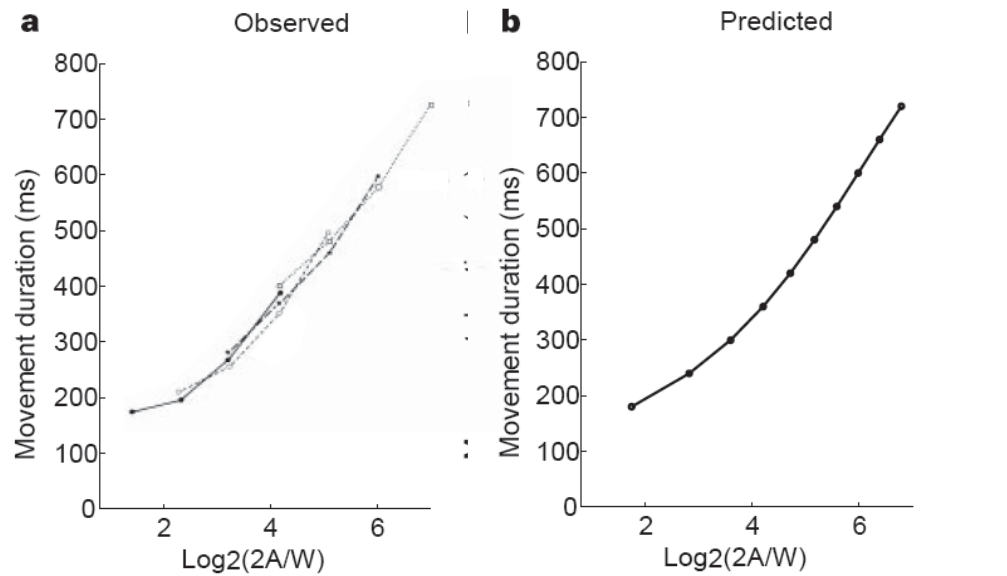
Harris & Wolpert 1998



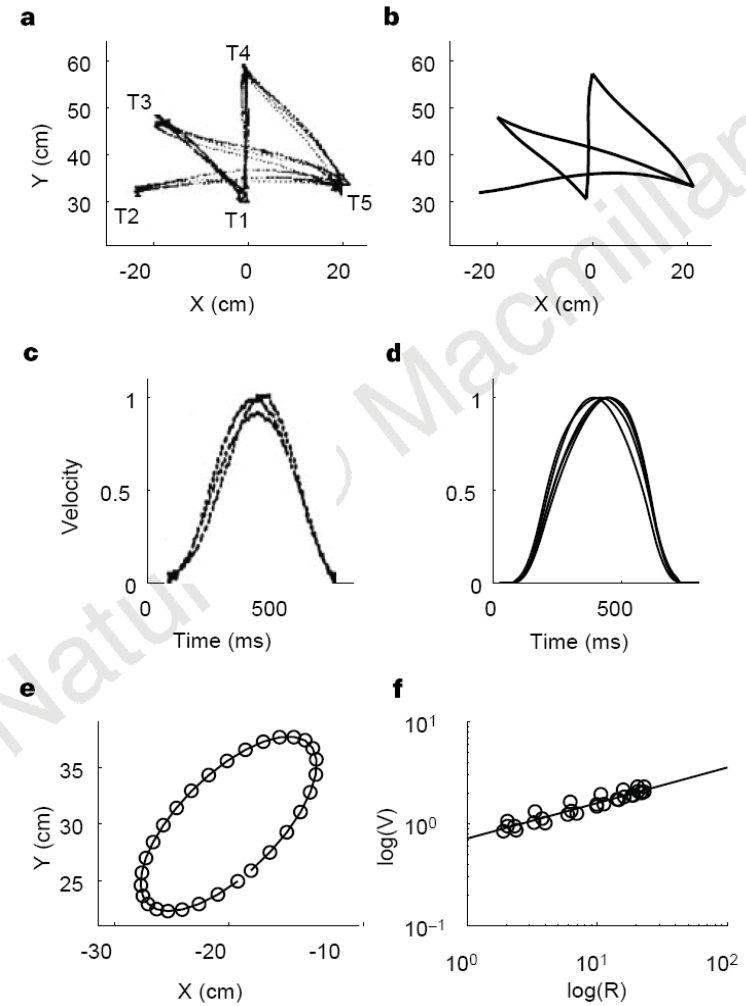
neural commands: signal-dependent noise

minimize the total positional variance during the immediate post-movement period
total movement duration is pre-fixed

Minimum-variance model

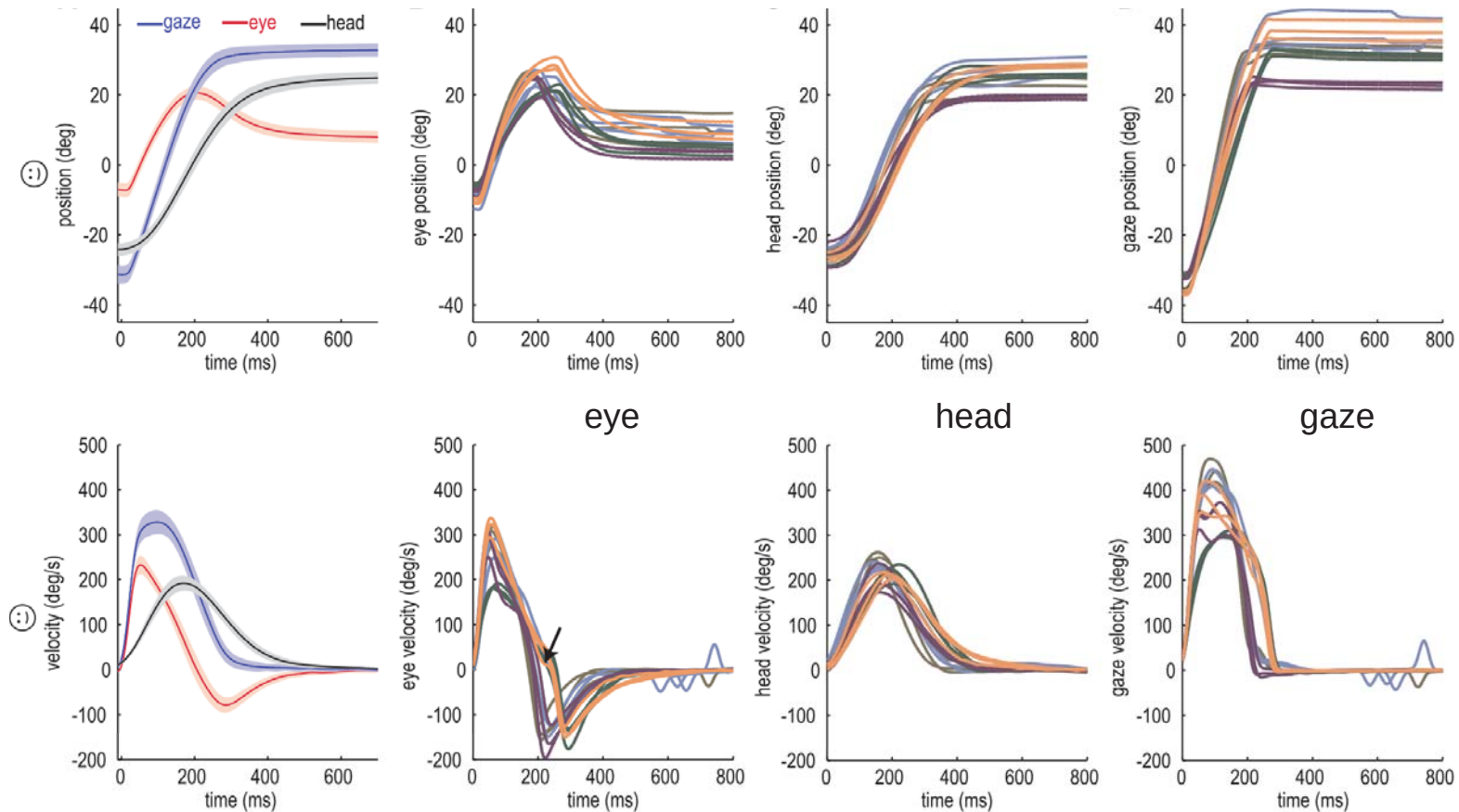


Harris & Wolpert 1998



explains Fitts' law, arm movements during pointing, and the 2/3 power law

Stereotypical movements



Question: if the choice is optimal, what is the criterion?



Optimization criteria

Possible optimization criteria

Minimum jerk

(Flash & Hogan 1985)

Minimum time

(Enderle & Wolfe 1987)

Minimum torque-change

(Uno, Kawato, Suzuki 1989)

Minimum effort

(e.g., Kardamakis & Moschovakis 2009)

Minimum variance

(Harris & Wolpert 1998)

Constrained minimum-time

(Tanaka, Krakauer, Quian 2006)

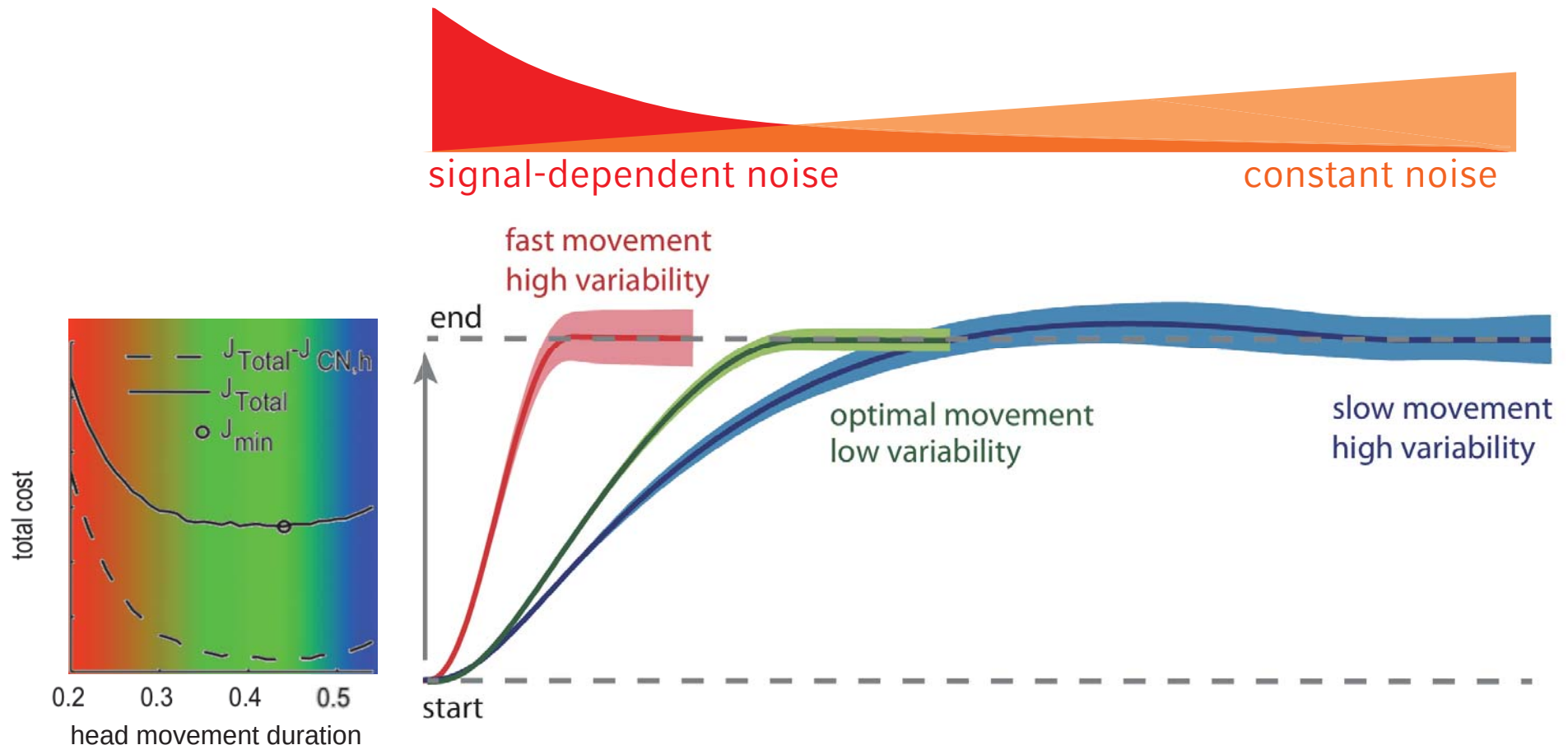
Reward discounting

(Shadmehr et al. 2010)

Minimum consequence of motor noise

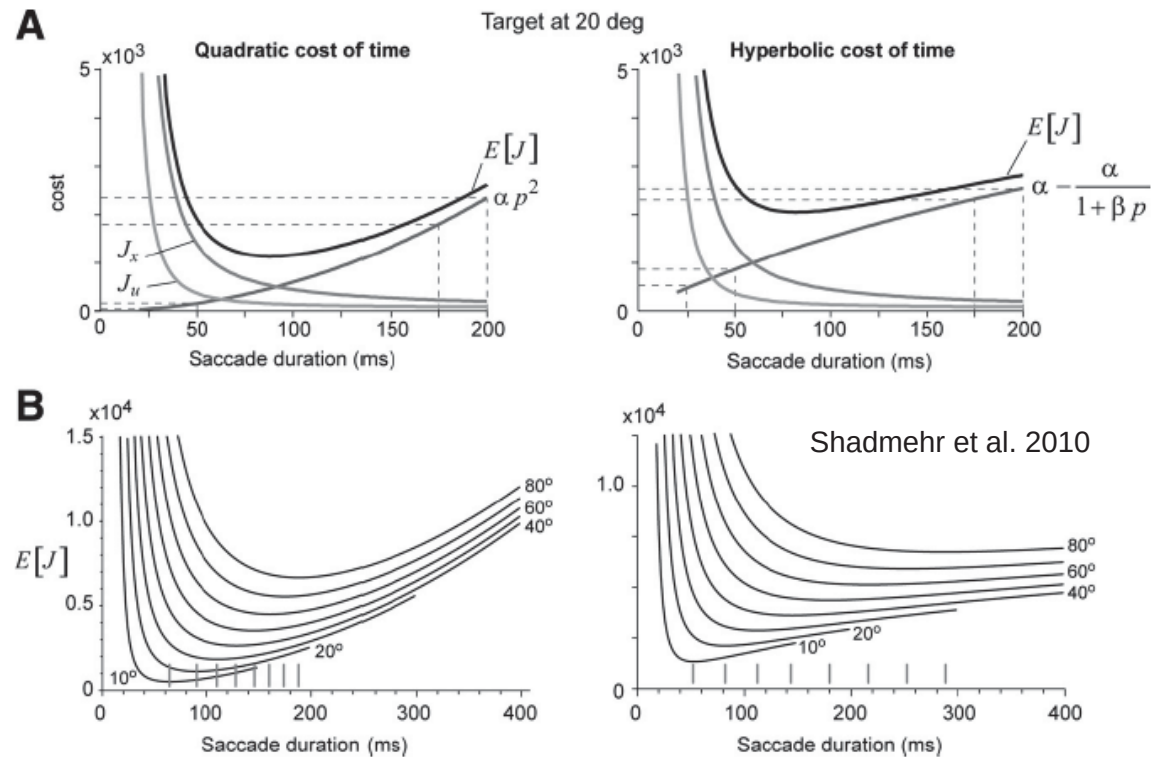
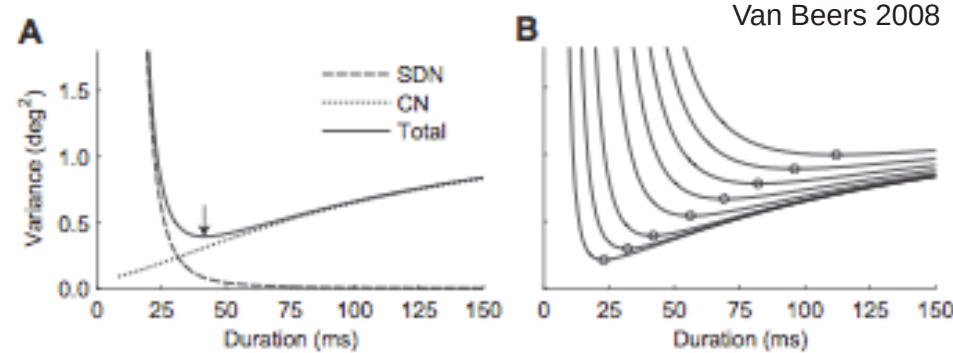
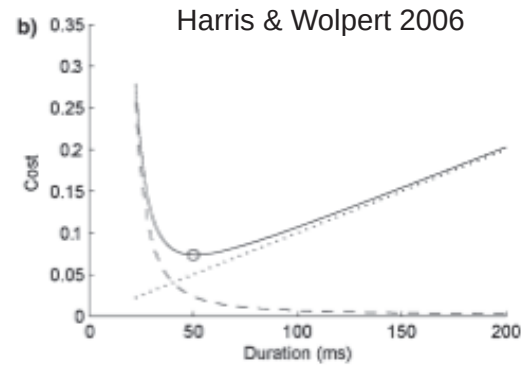
(van Beers 2008)

Minimizing the consequence of noise

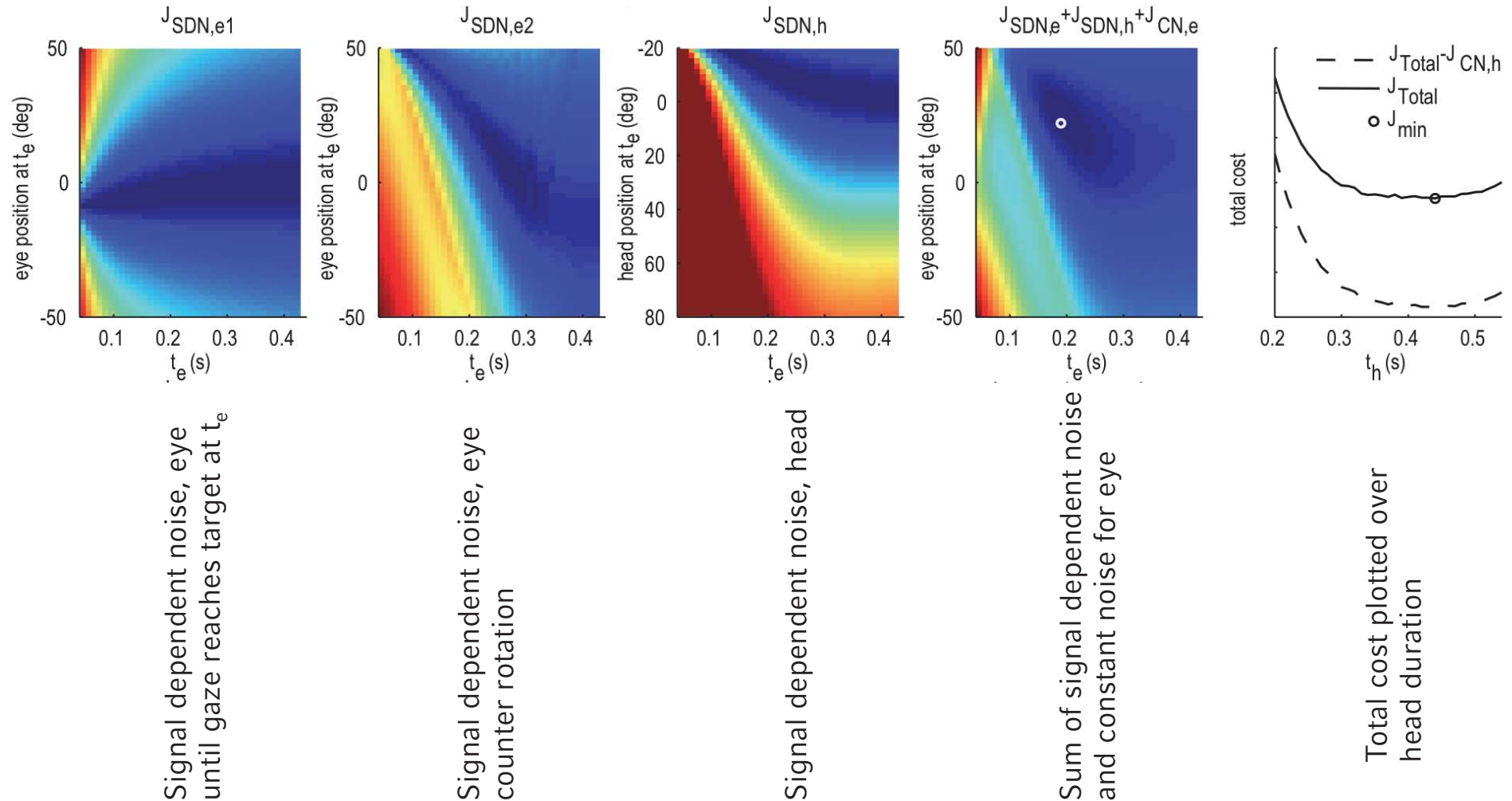


The mix of signal-dependent and constant motor noise explains the optimal movement duration and the shape of the trajectory

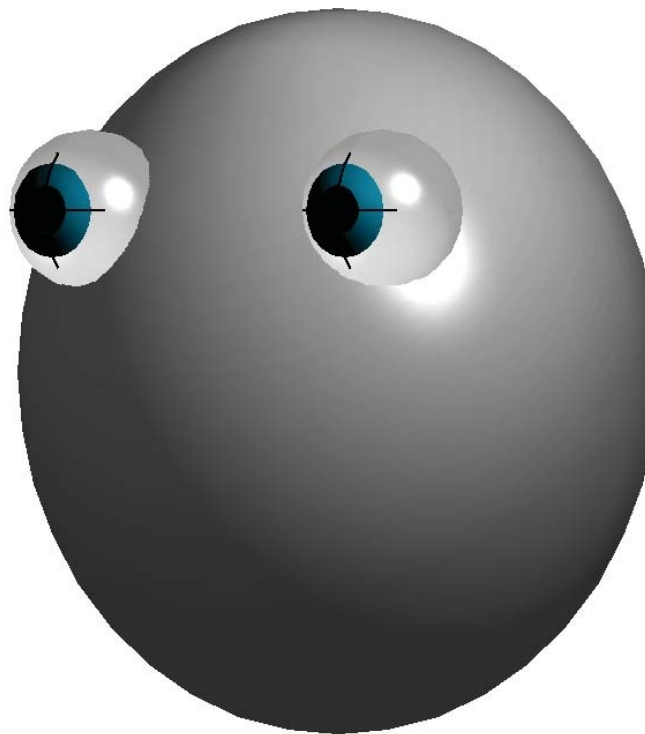
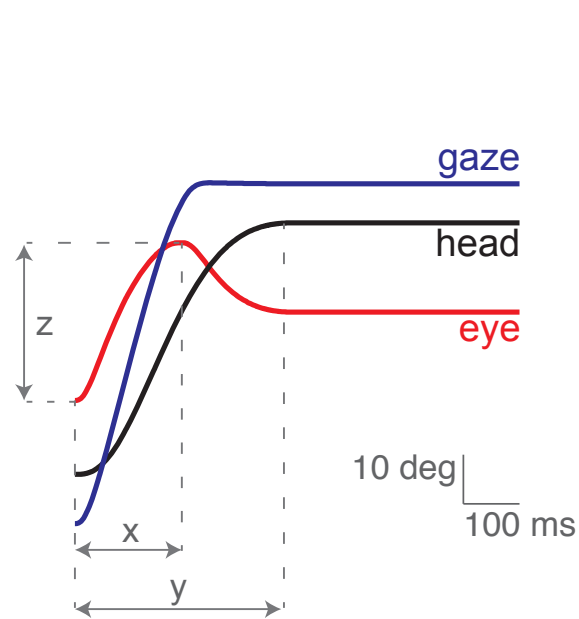
Optimization criteria



Optimization: cost-to-go surfaces



Simulation

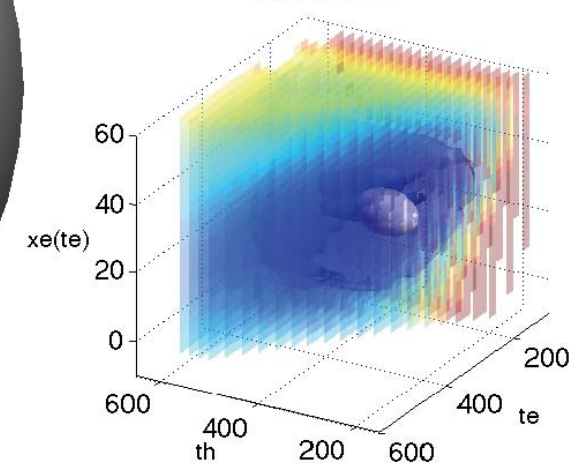


t=0 ms

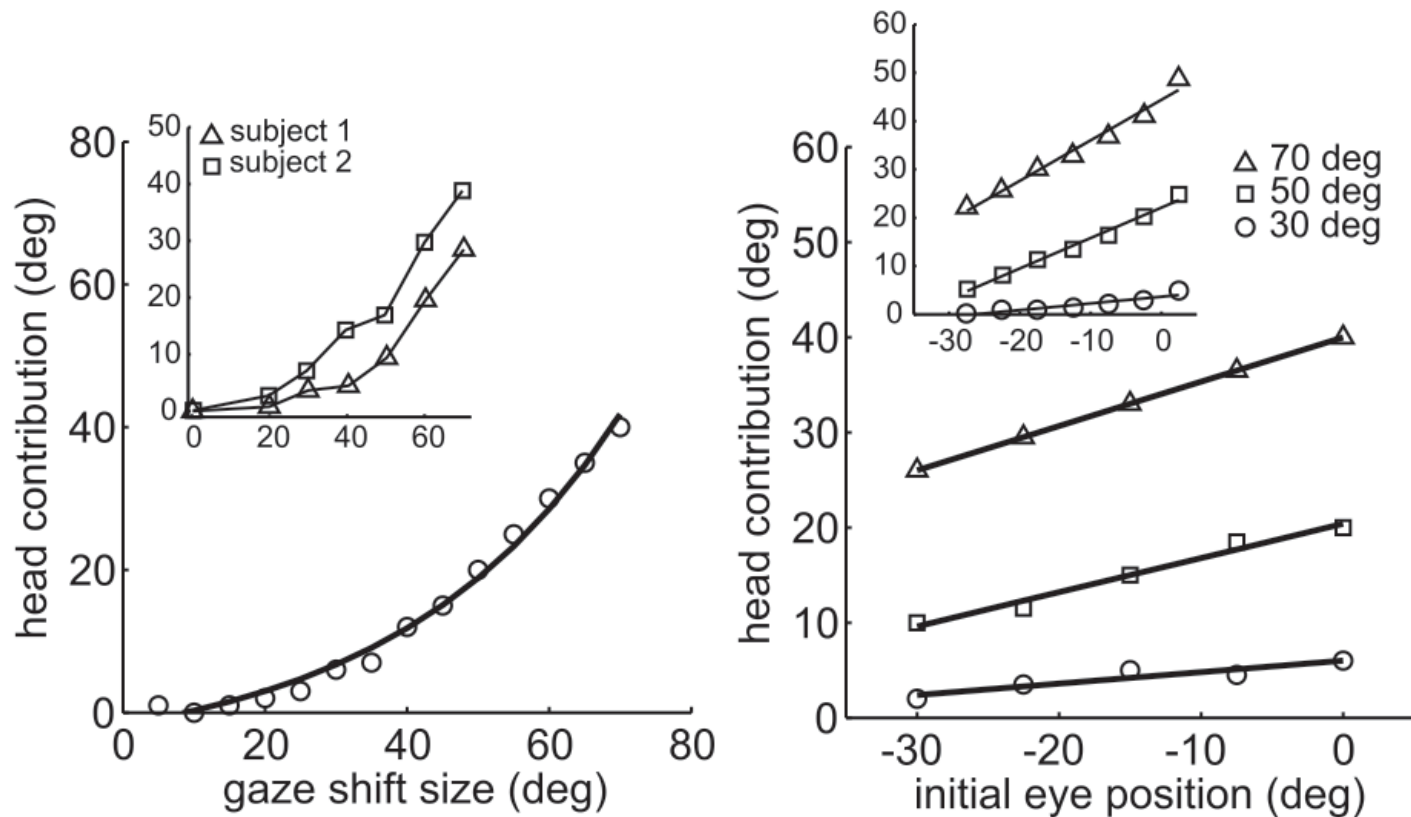
Horizontal Movement Traces



Cost Volume



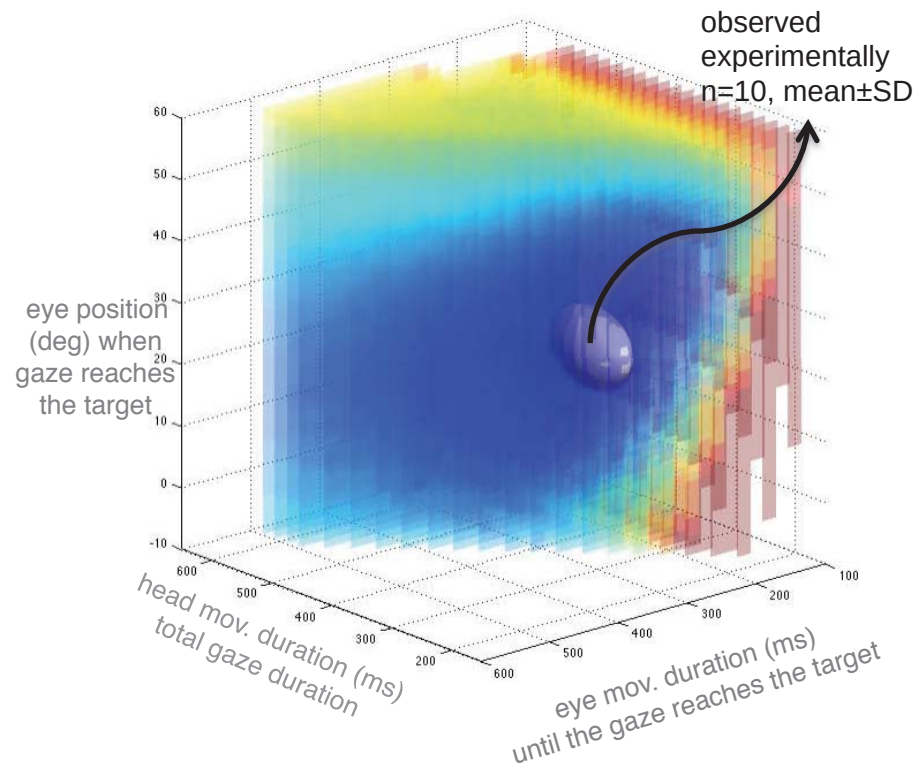
Head contribution



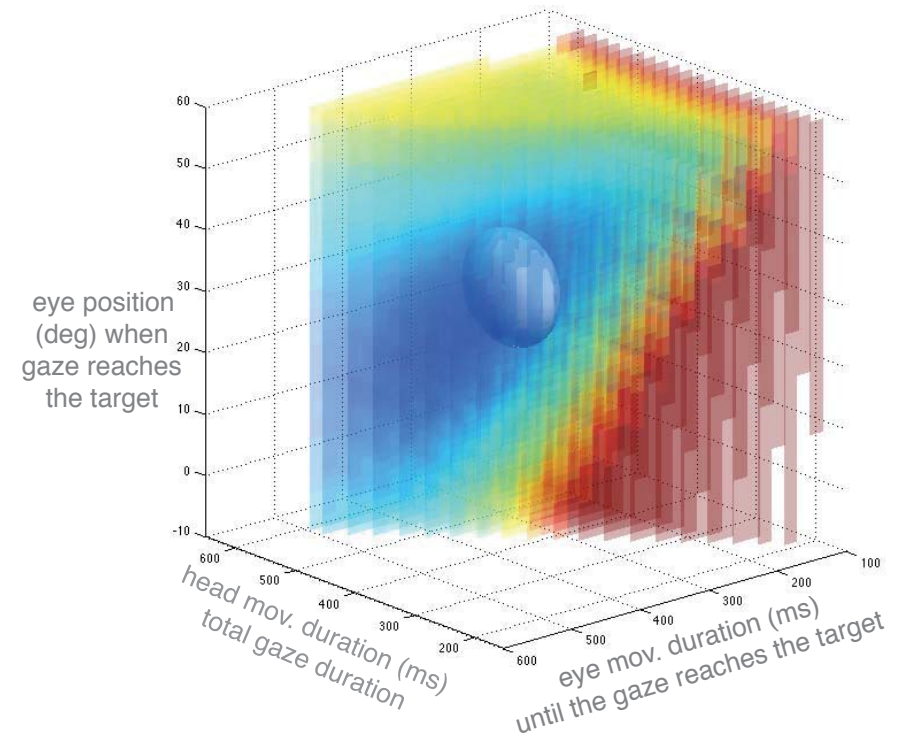
Minimizing the consequences of signal-dependent and constant motor noise explains the features of normal eye-head gaze shifts

Altering head dynamics

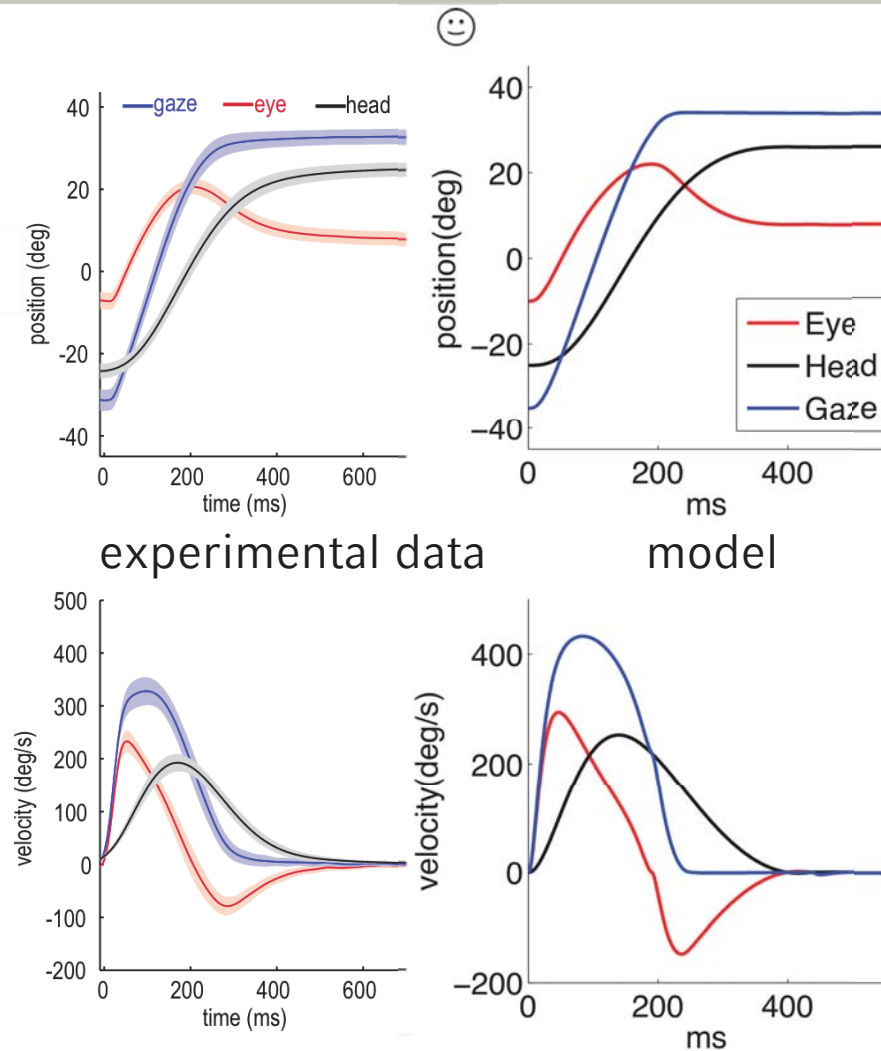
natural condition



increased
head moment of inertia



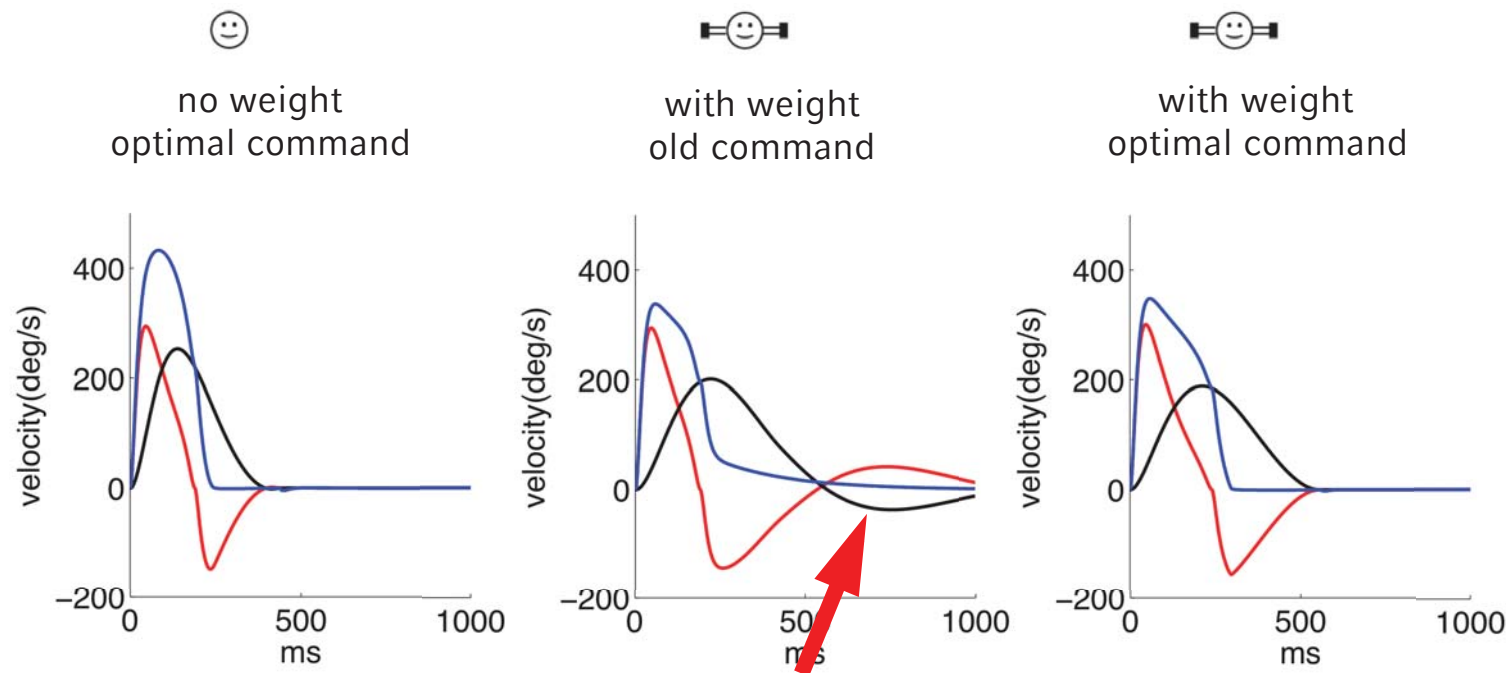
Changing head plant inertia



Model simulates eye-head gaze shifts with increased head moment of inertia.

Saglam M, Lehen N, Glasauer S: Optimal control of natural eye-head movements minimizes the impact of noise. J Neurosci 2011

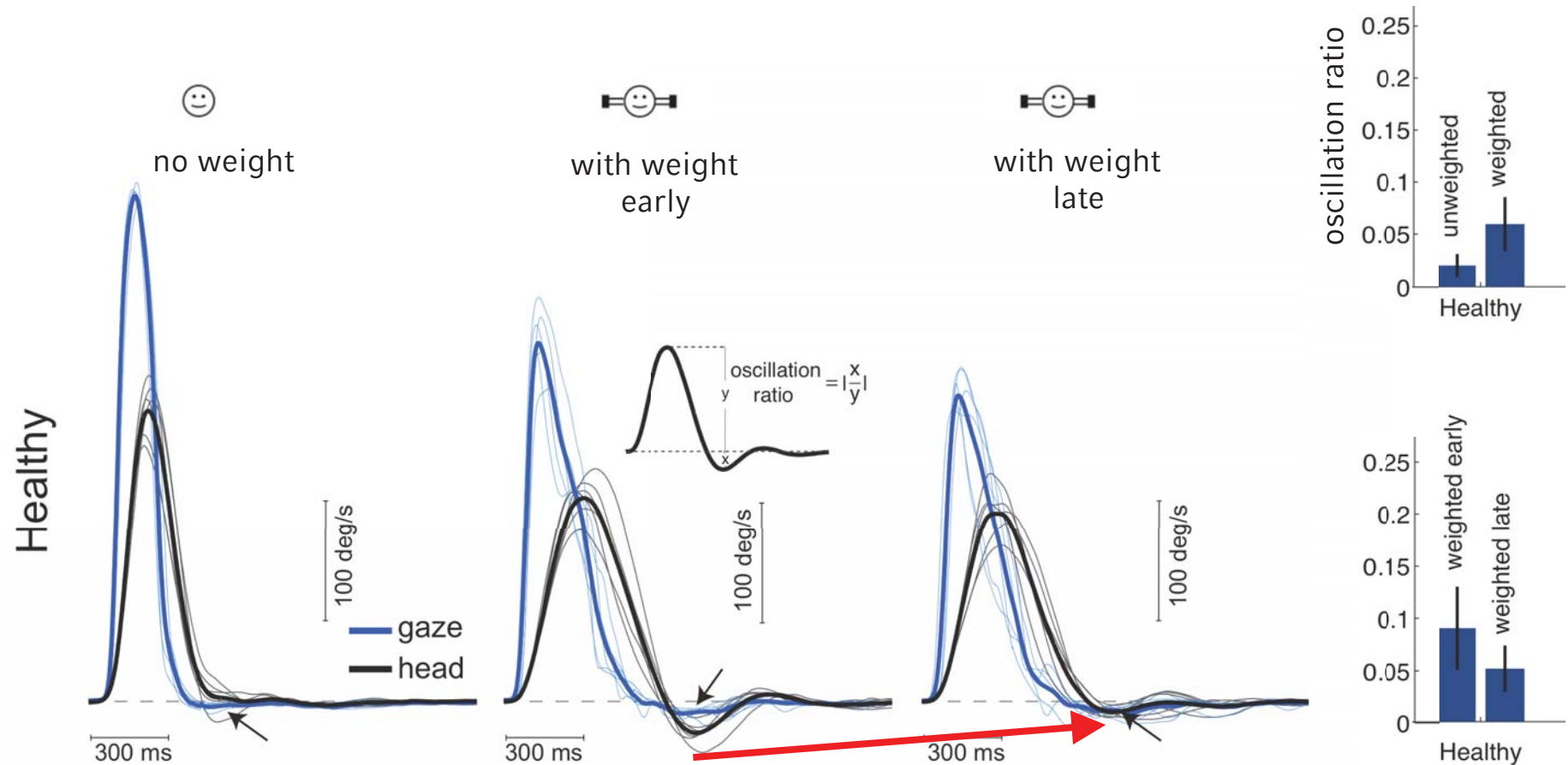
Adapting to changes of head plant inertia



Unmodified head command leads to major **head oscillations**

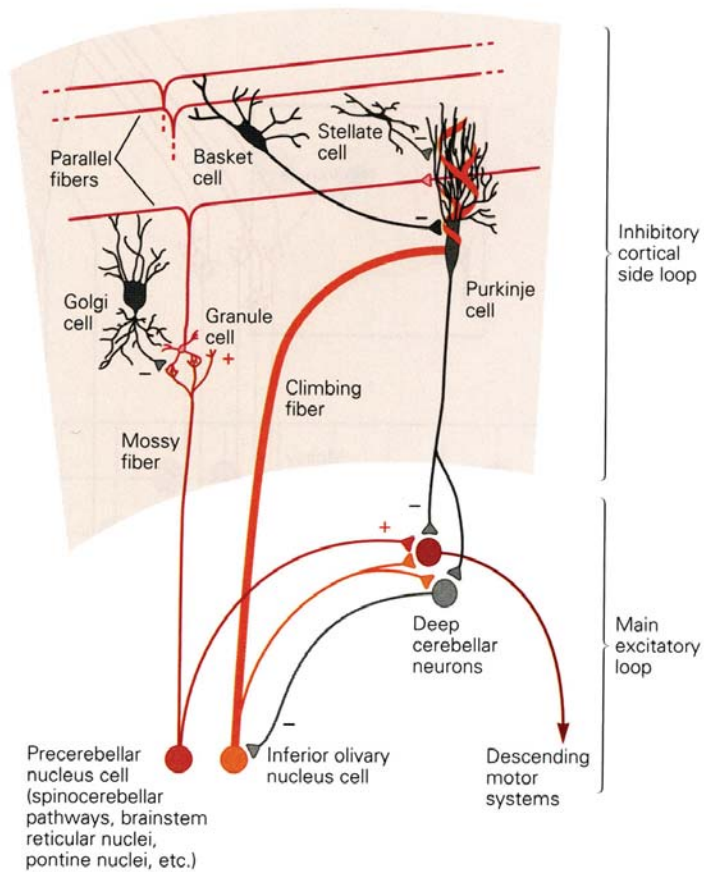
Head oscillations, even when compensated for, increase post-movement variability

Healthy participants



Early after increasing weight healthy subjects show head oscillations, which lead to gaze instability. Late trials show optimized trajectories.

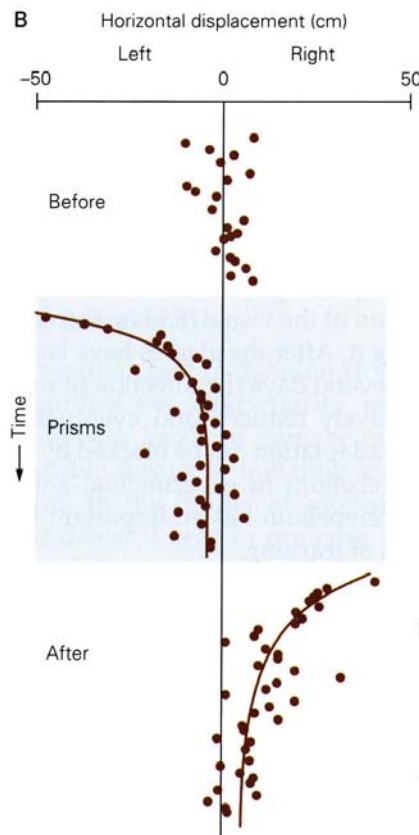
Motor learning involves the cerebellum



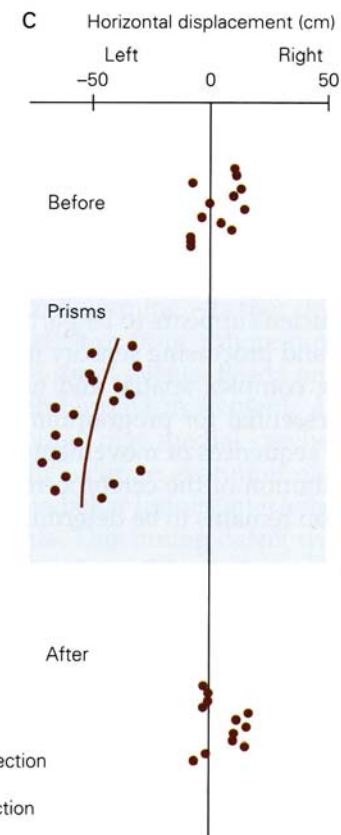
A



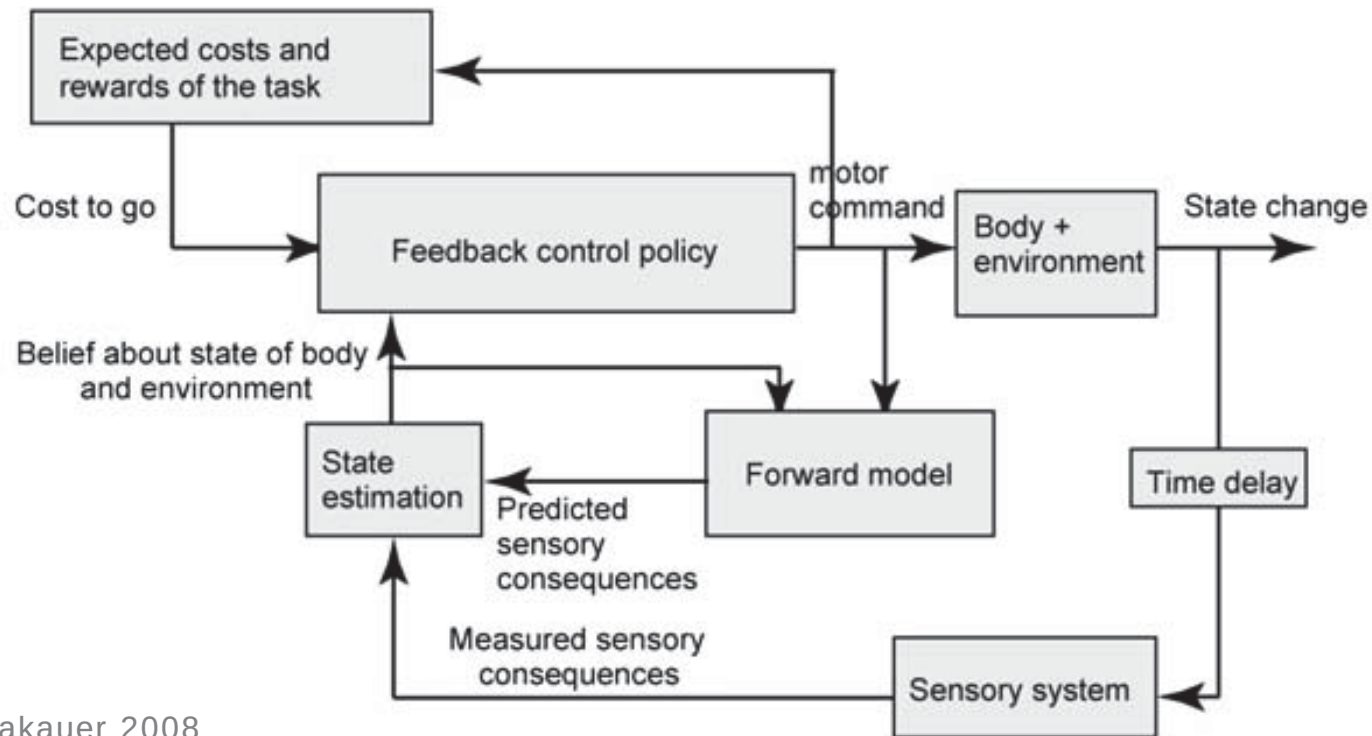
B



C



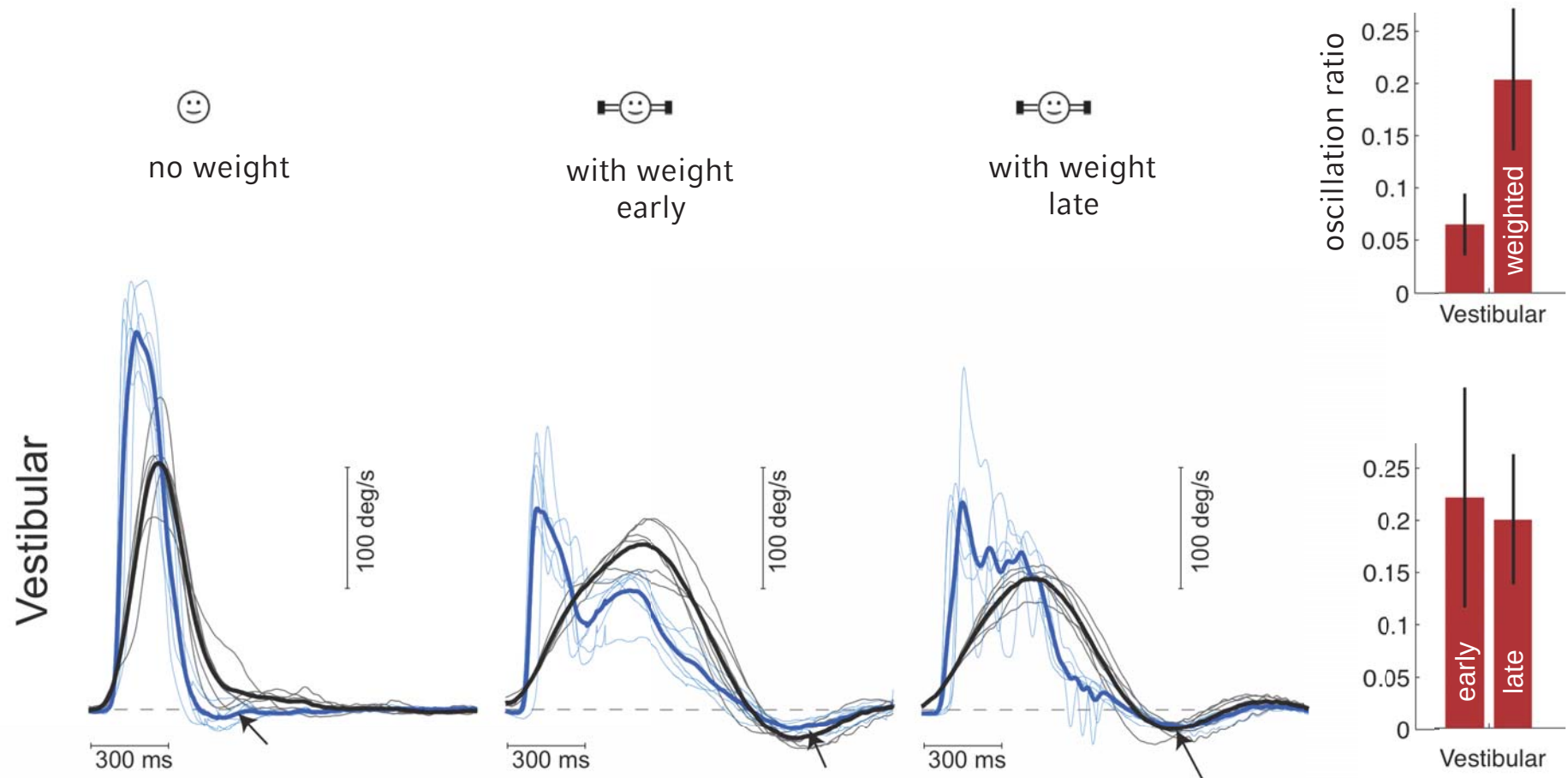
Cerebellum: forward models



Shadmehr & Krakauer 2008

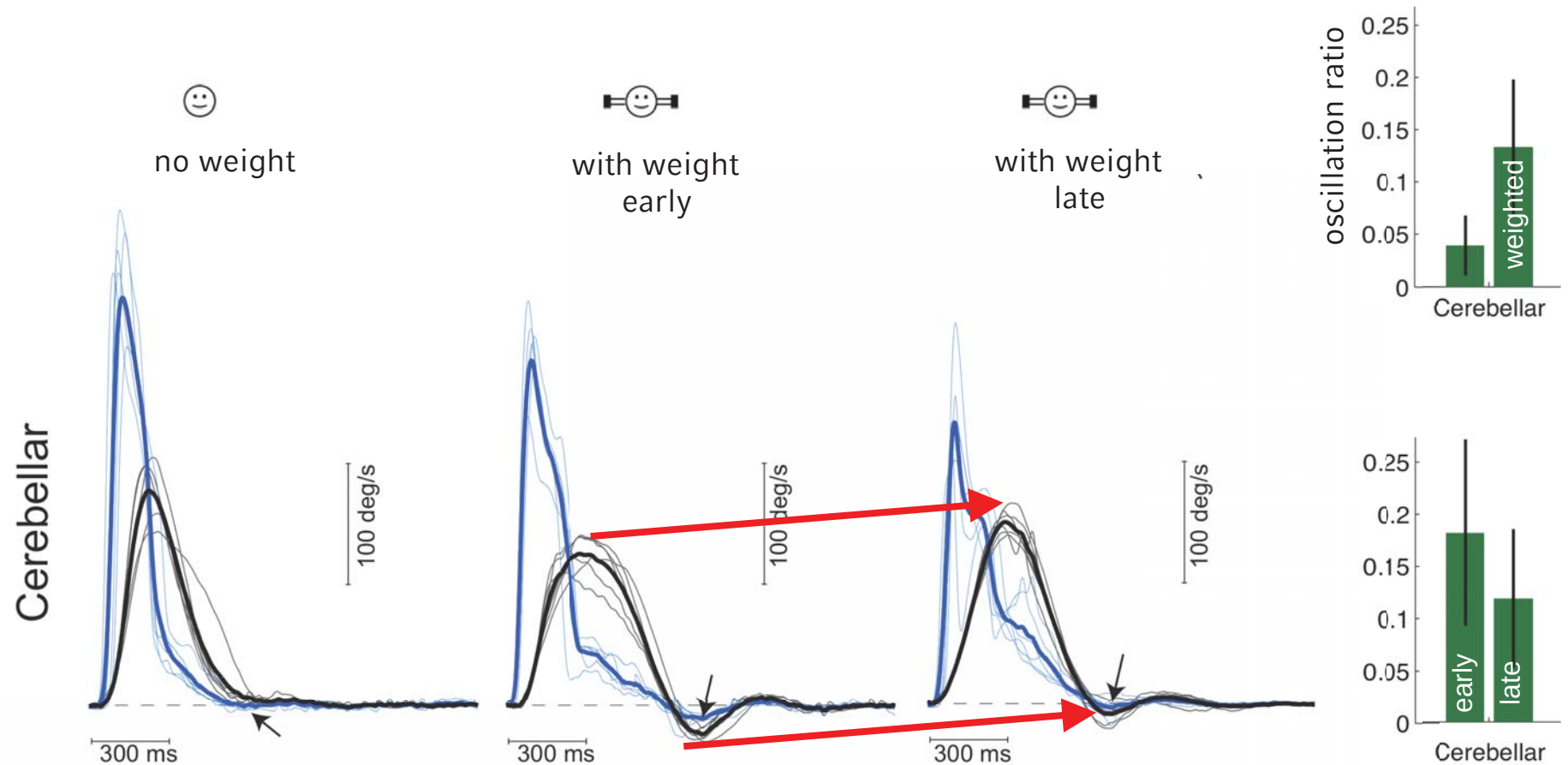
The cerebellum is supposed to implement forward models

Bilateral vestibular deficit



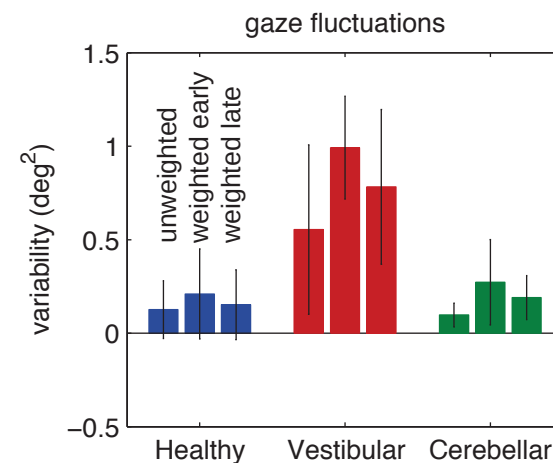
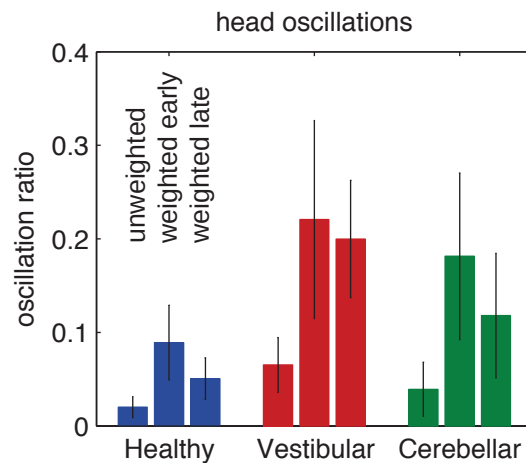
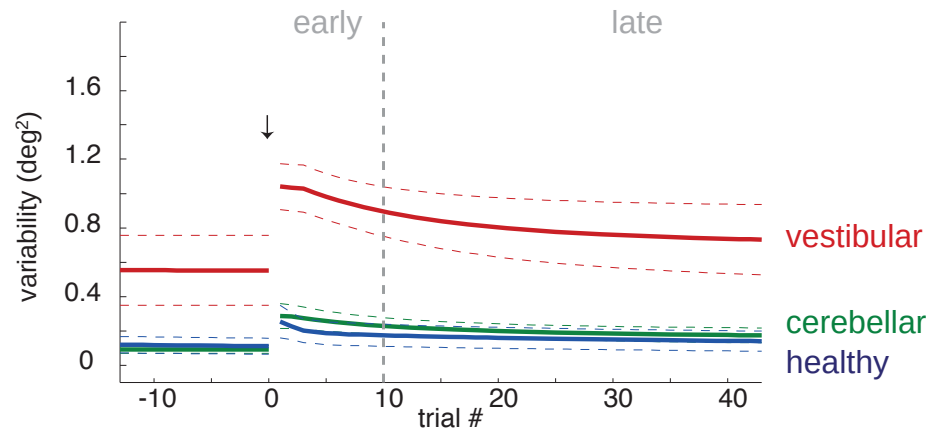
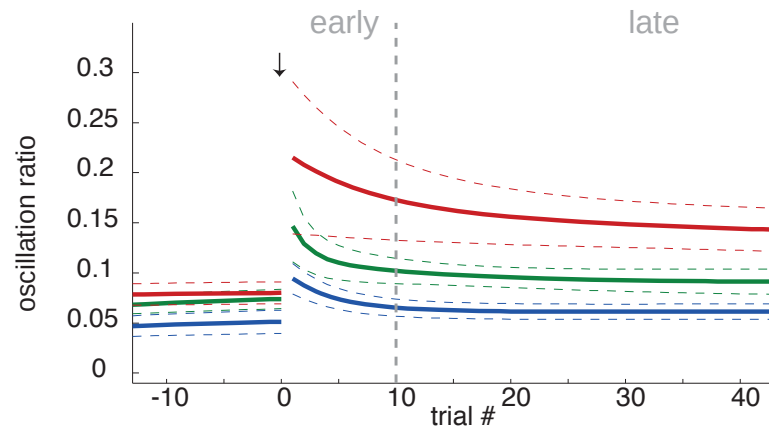
Patients with bilateral vestibular deficit show head oscillations, but no adaptation.

Cerebellar atrophy



Patients with cerebellar atrophy show early head oscillations and adaptive improvement with later trials.

Effect on gaze variability

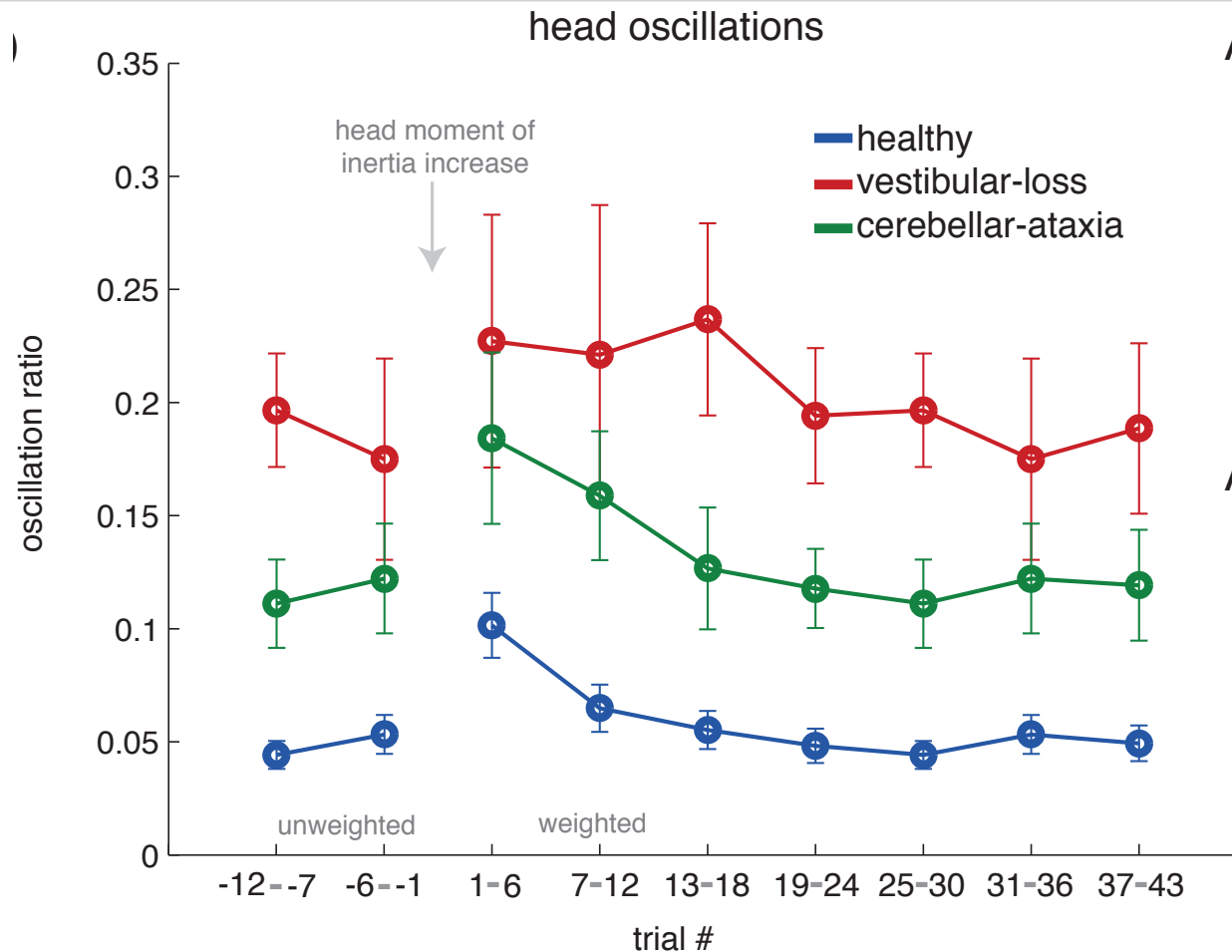


Head oscillations and gaze fluctuations remain high in vestibular patients.

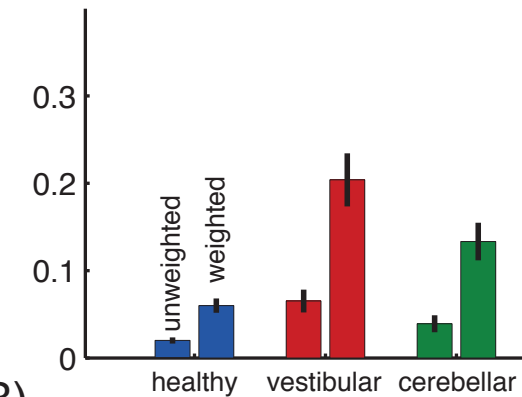
Cerebellar patients exhibit low gaze fluctuations despite oscillations.

Saglam M, Glasauer S, Lehen N: Vestibular and cerebellar contribution to gaze optimality. Brain 2014

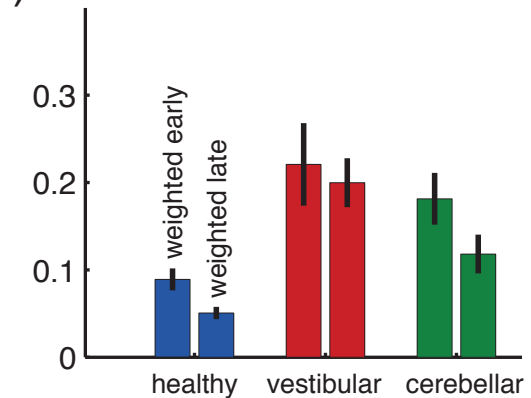
Effect on head control



A2)

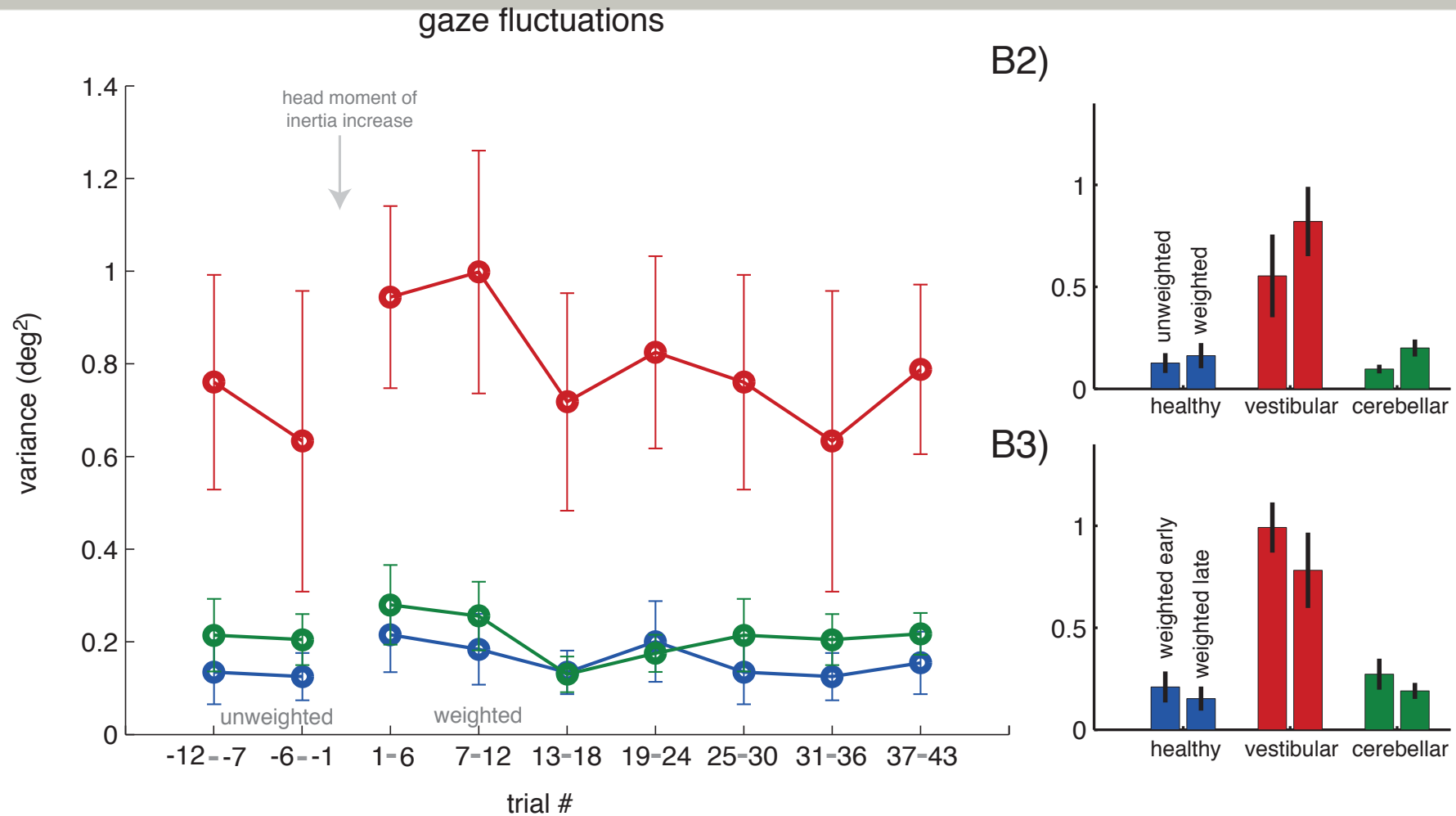


A3)



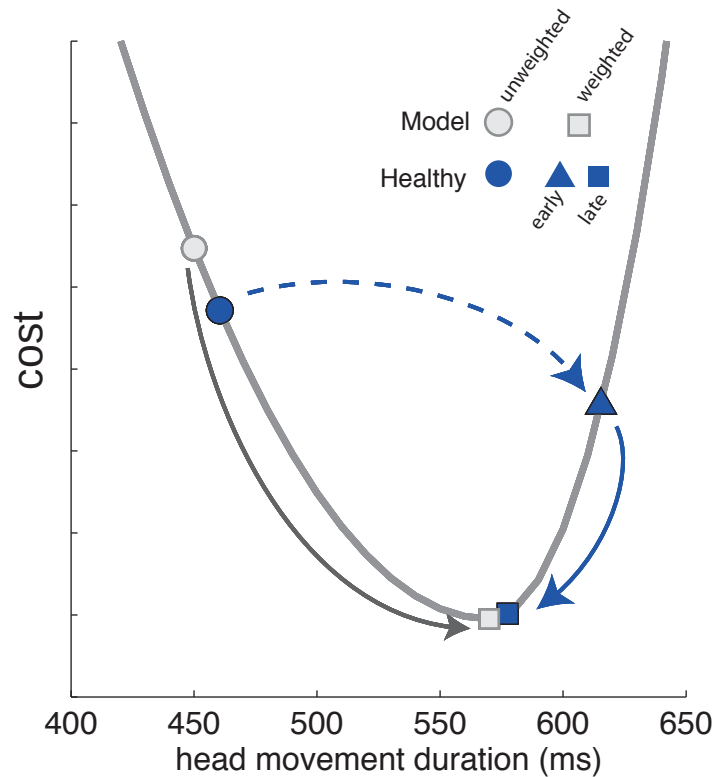
Head oscillations (and gaze fluctuations) remain high in vestibular patients.

Effect on gaze fluctuations

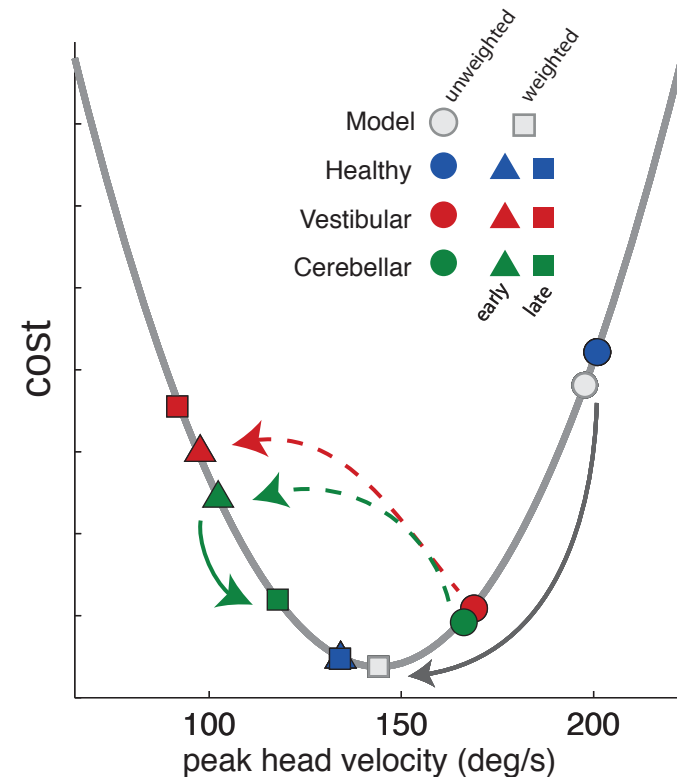


Cerebellar patients can improve gaze fluctuations

Optimizing the movement

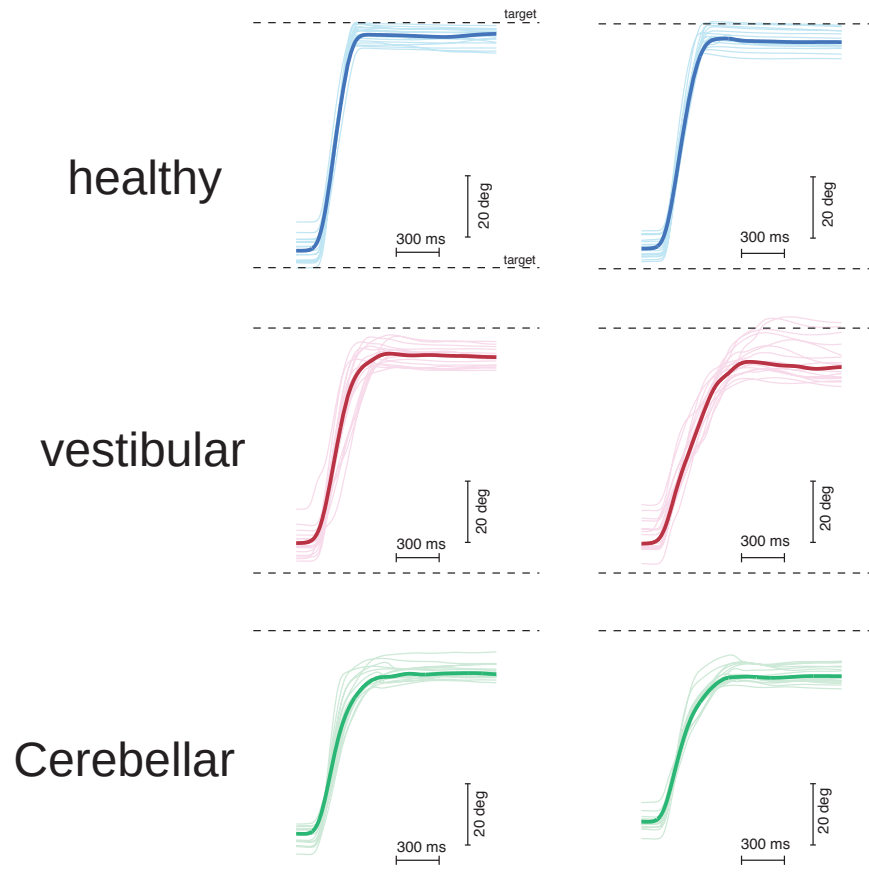


Head movement duration increases
with weight



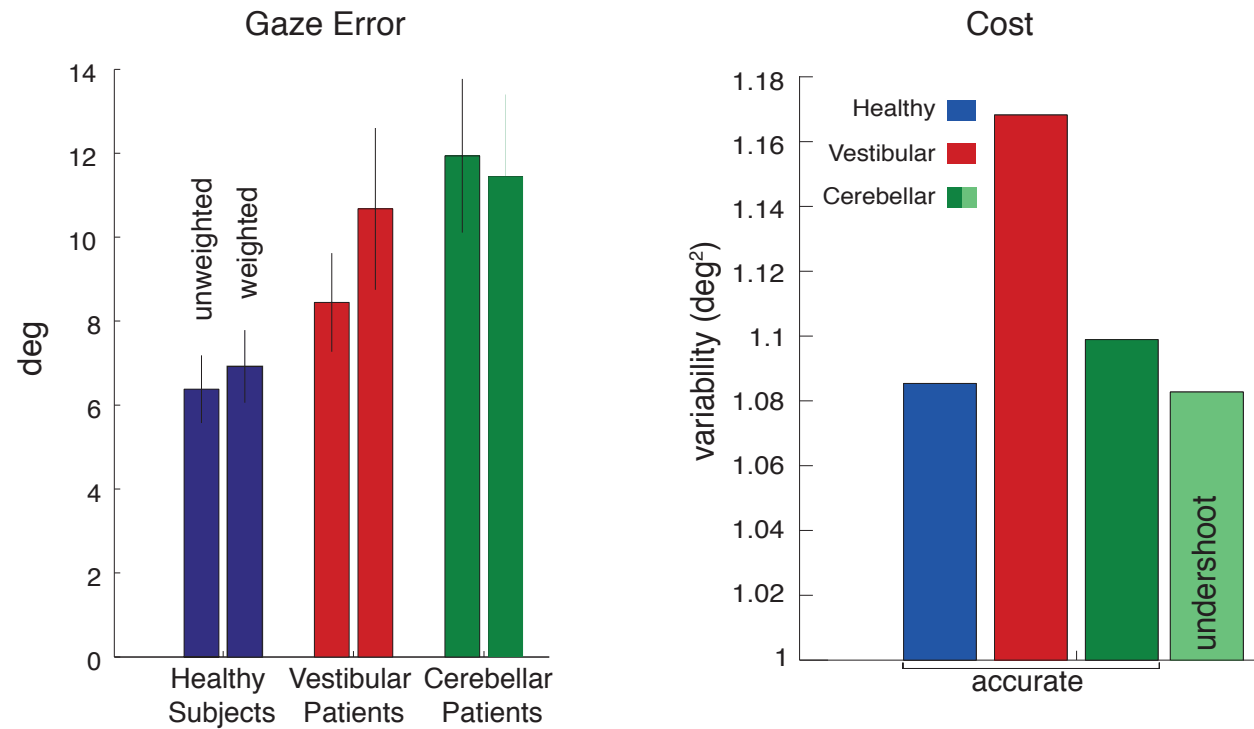
Peak head velocity duration
decreases with weight

Gaze shift accuracy



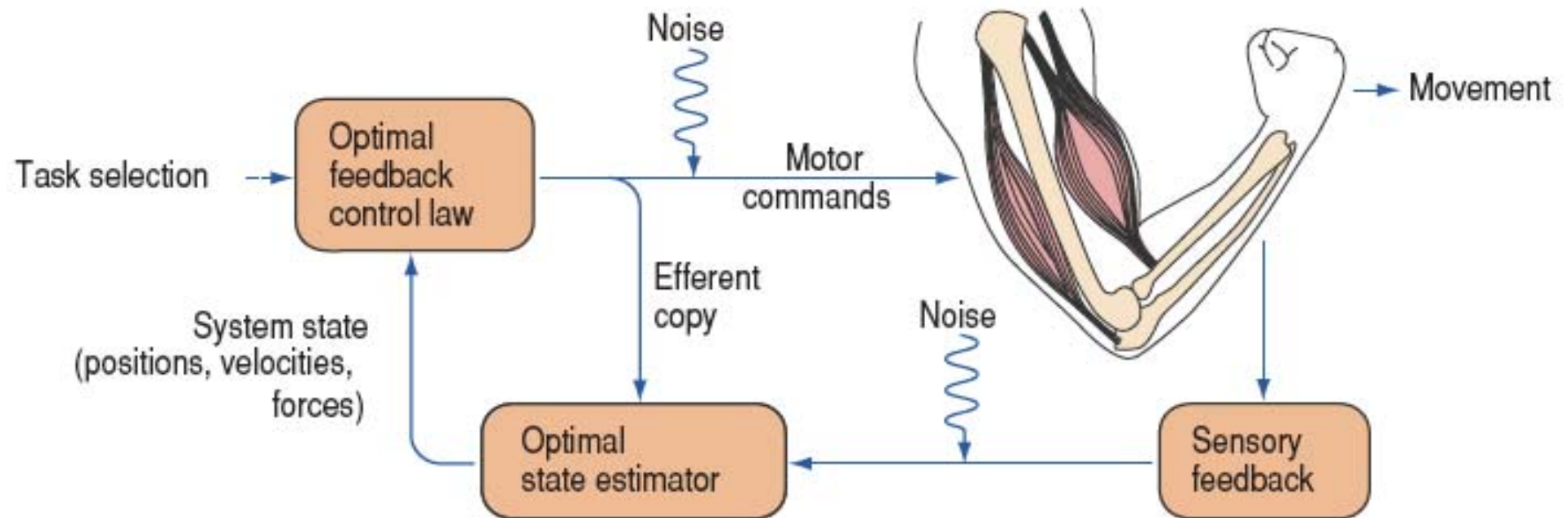
Cerebellar patients show consistent undershoots
which are *not* corrected for

Gaze shift accuracy



Cerebellar patients show consistent undershoots which are not corrected but lead to smaller variability (comparable to healthy)

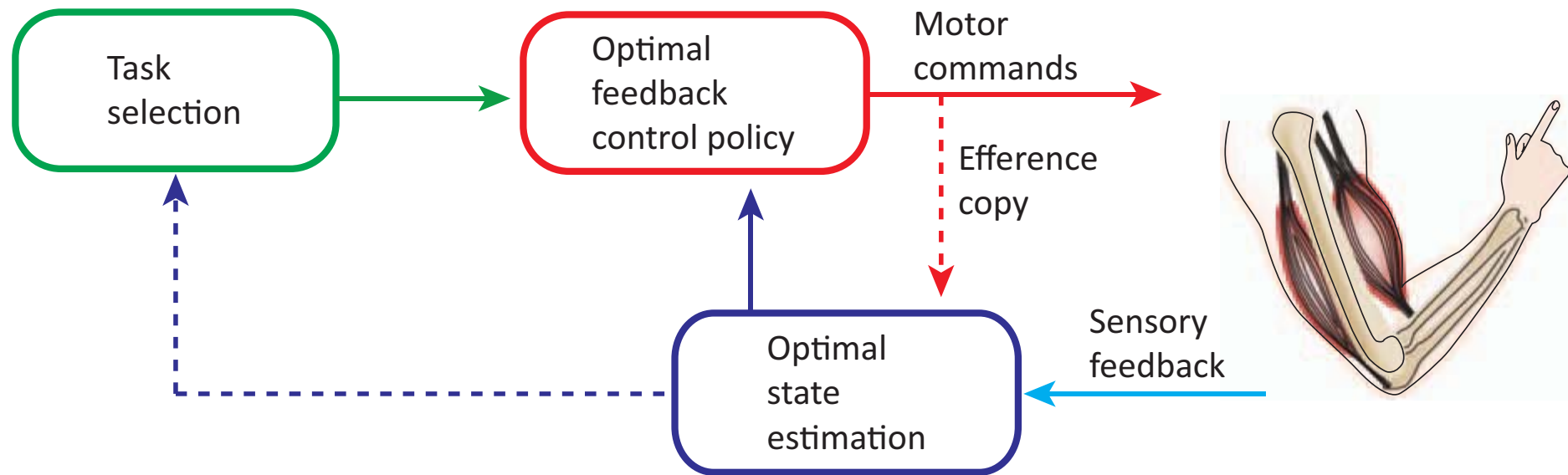
Optimal feedback control



Scott 2008

Optimal feedback control provides a framework for investigating motor control

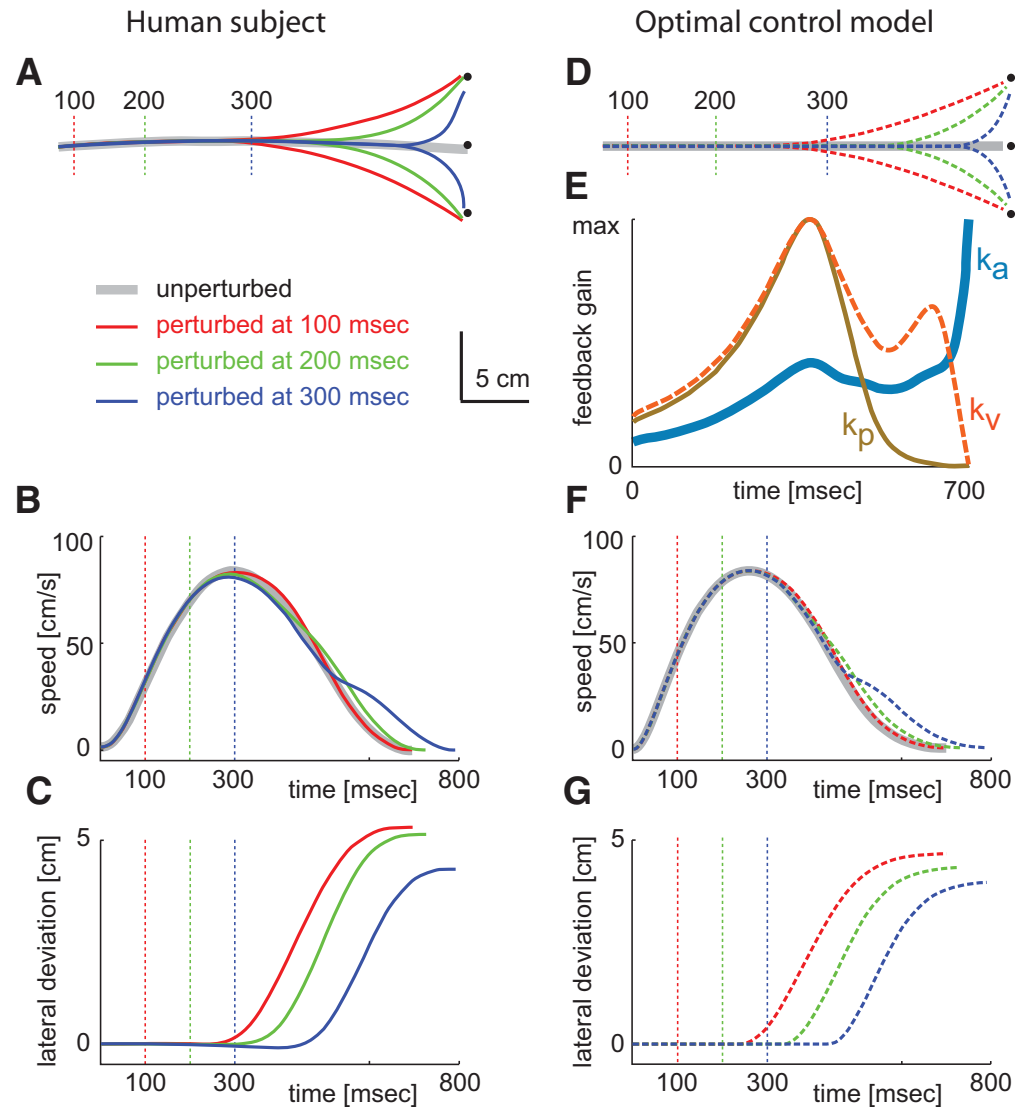
Optimal feedback control



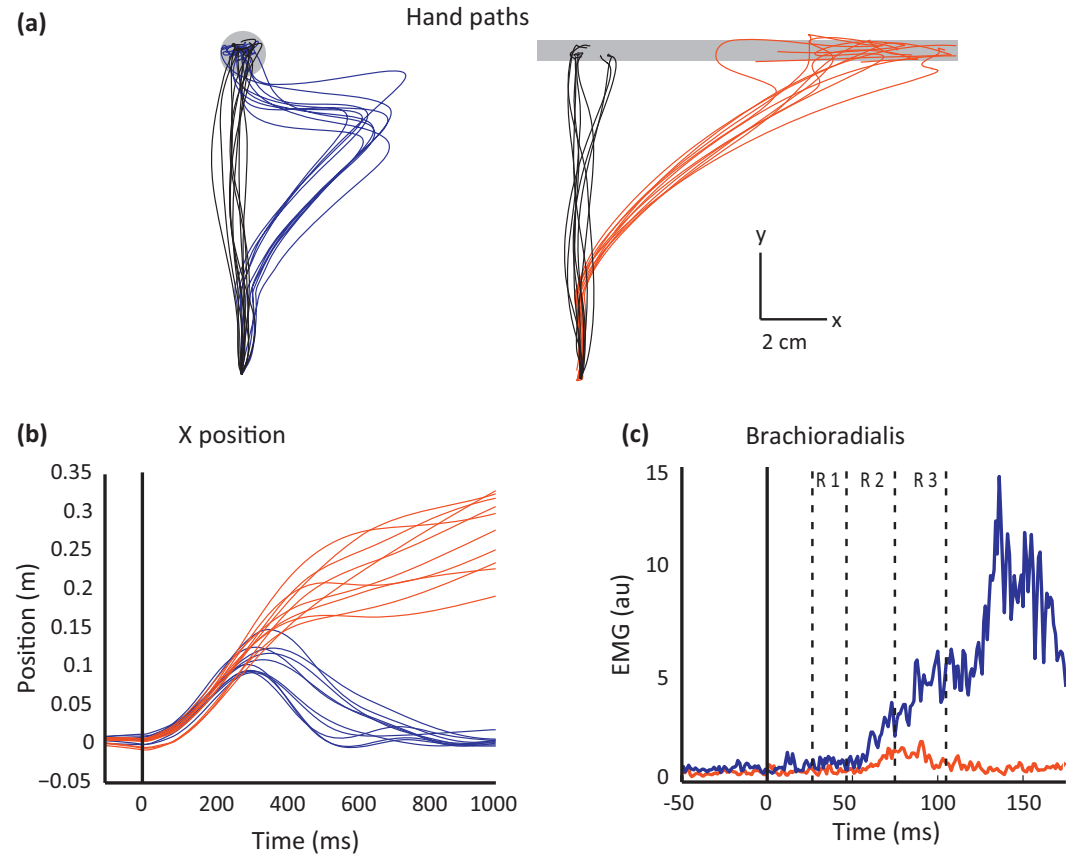
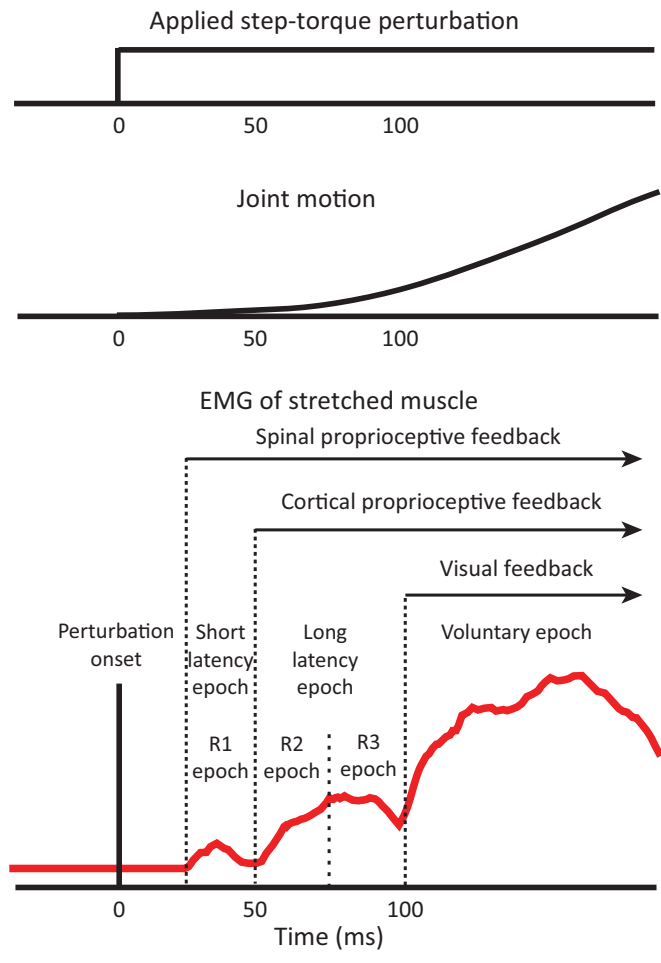
Scott 2012

Optimal feedback control provides a framework for investigating motor control

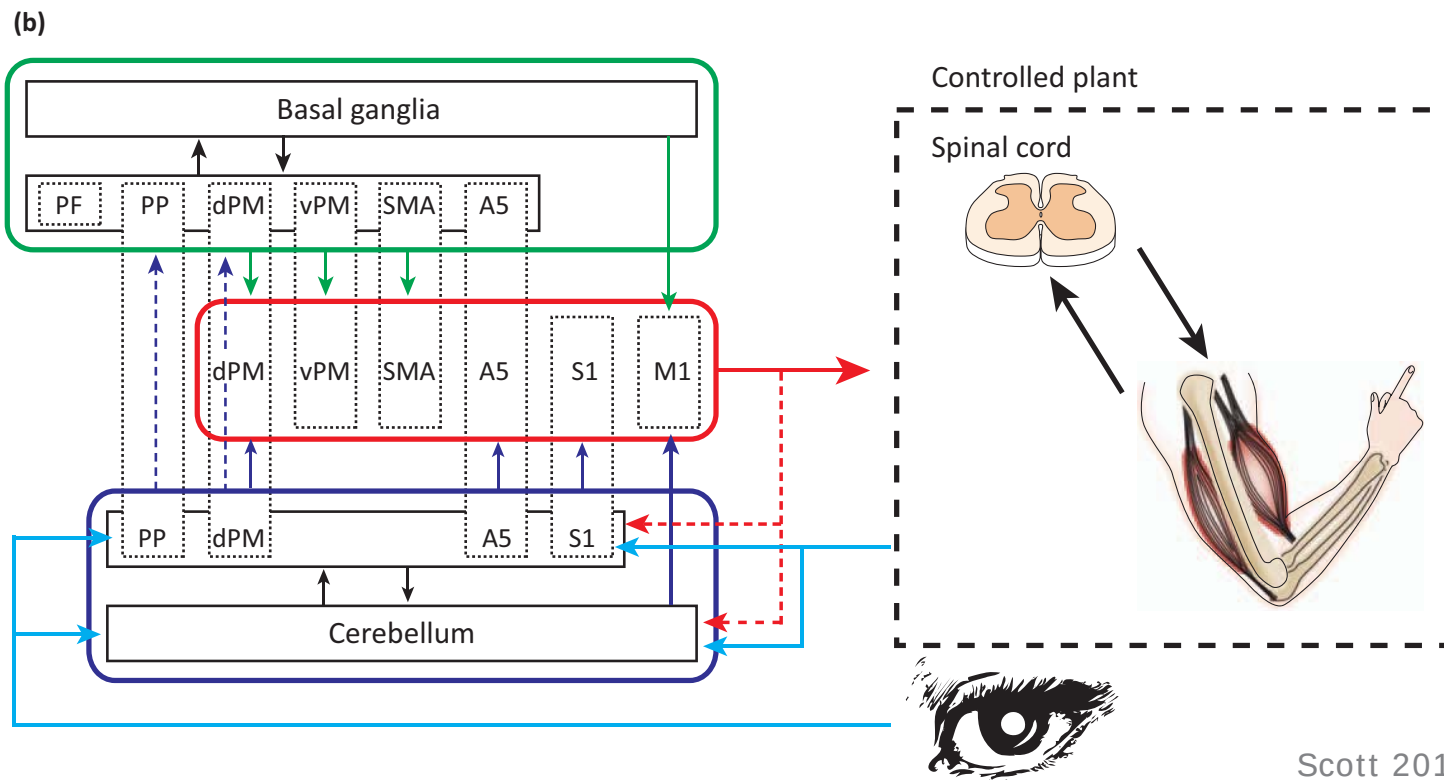
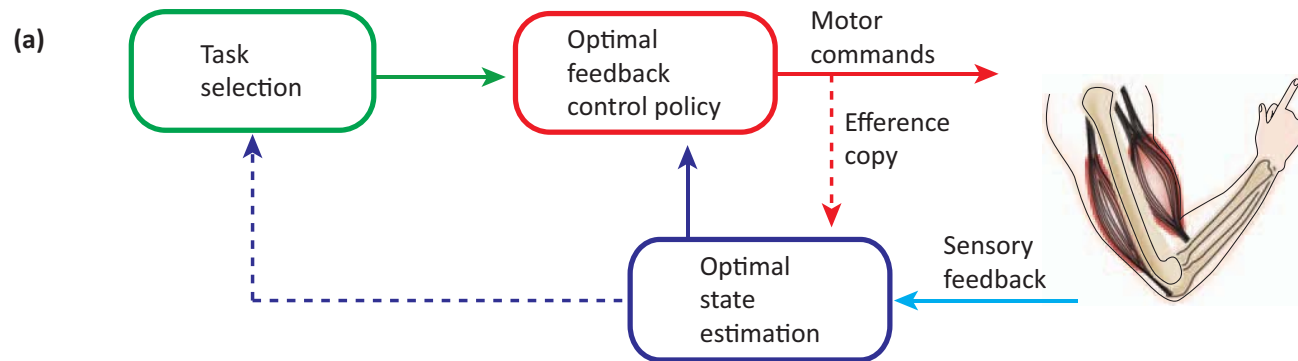
The importance of feedback



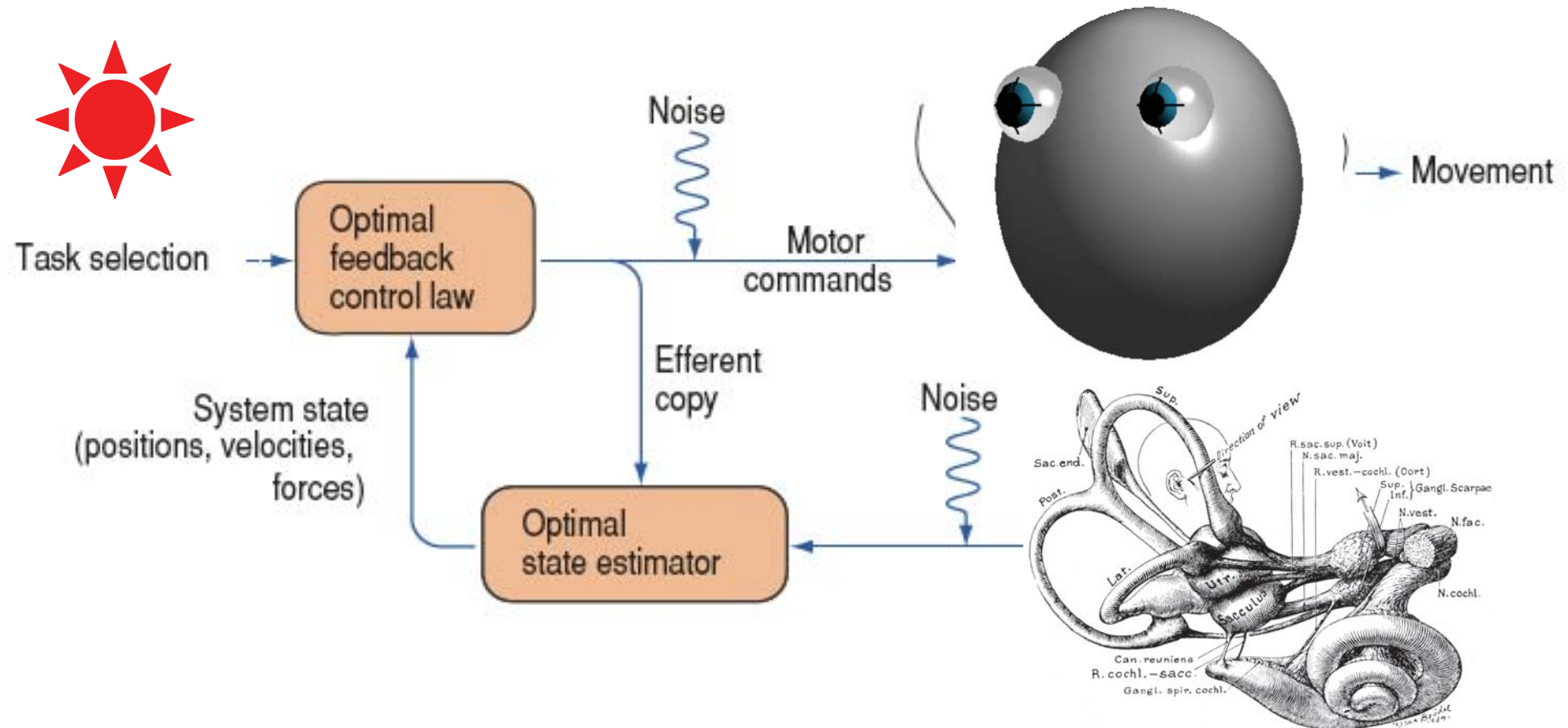
The importance of feedback



Optimal feedback control

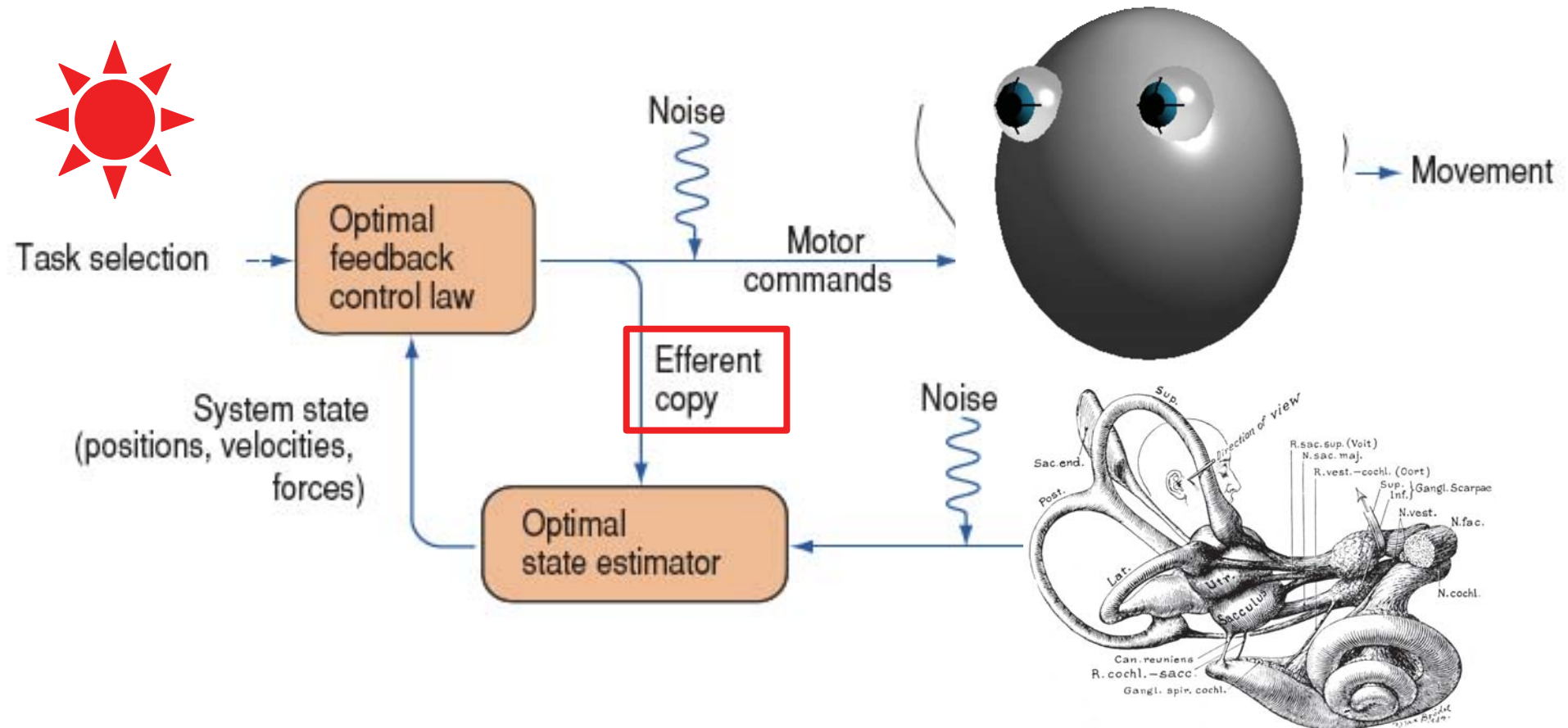


Eye-head control



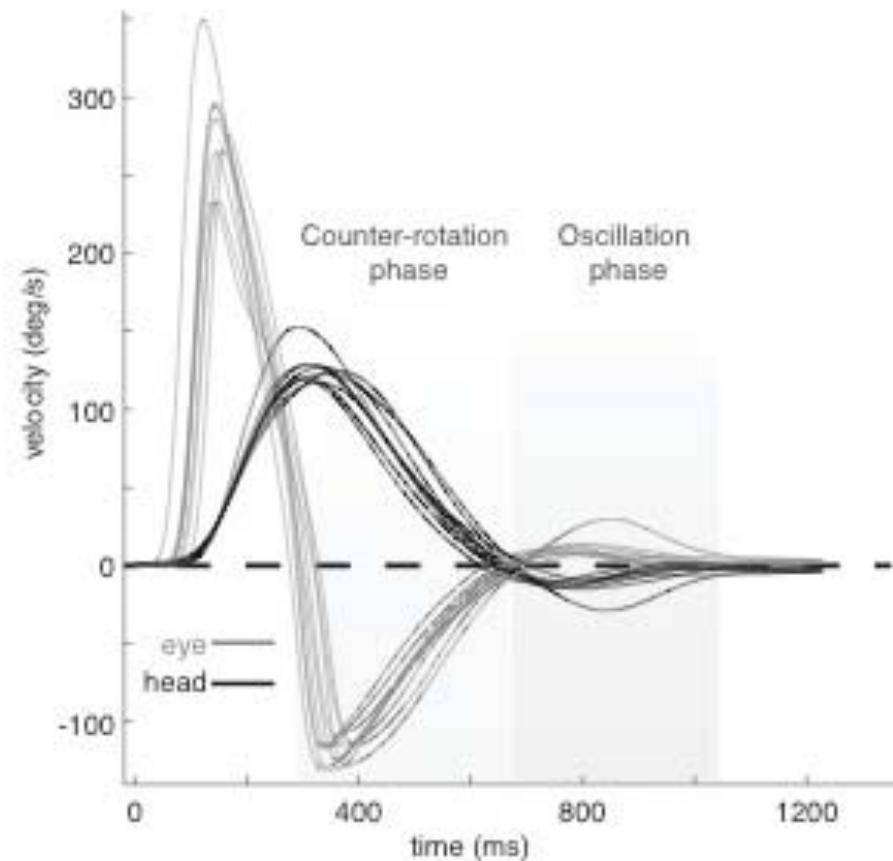
Eye-head control as specific case for motor control

Efference copy and feedback



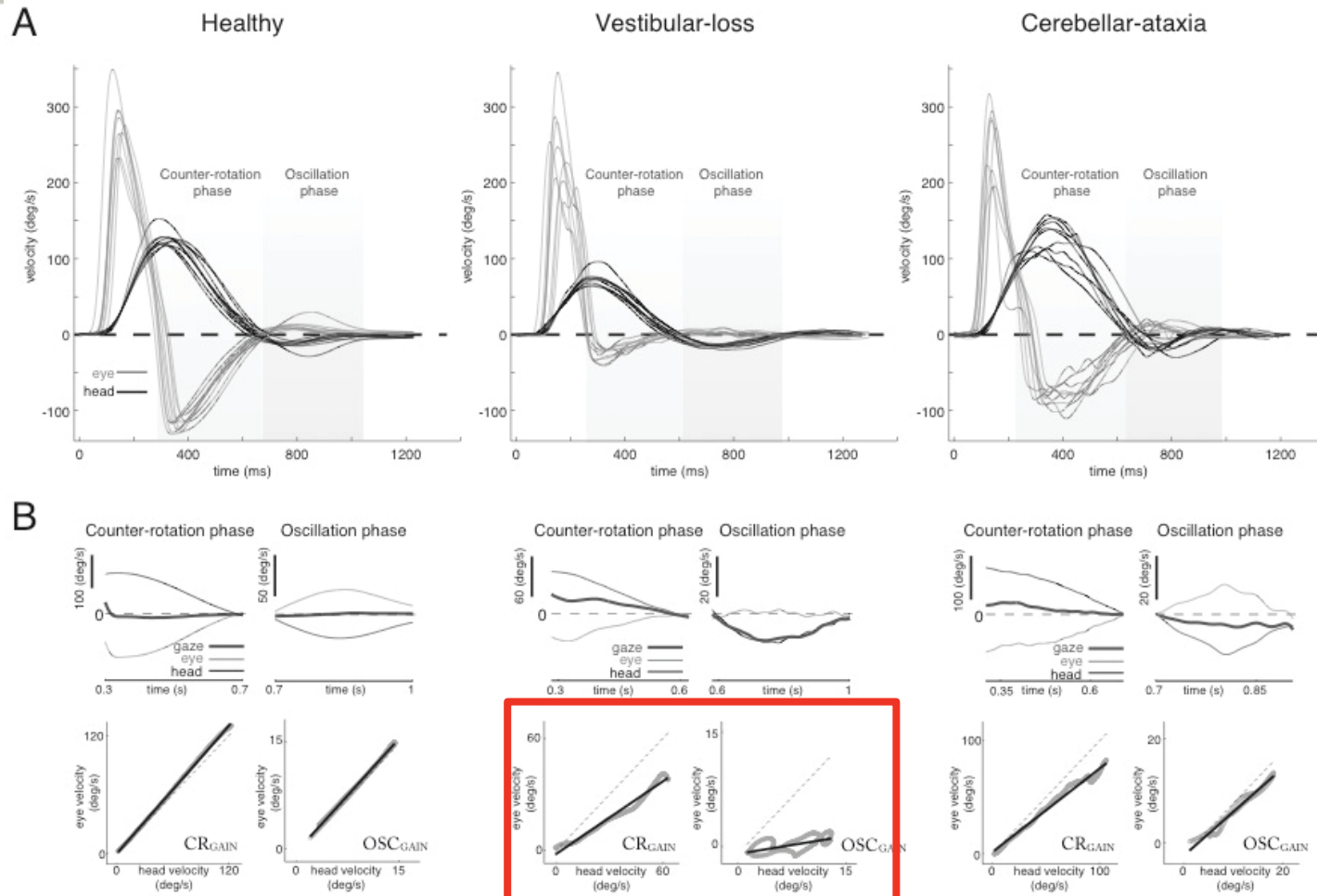
What are the specific roles of efference copy and sensory feedback for online control?

The role of the efference copy



We can use the counterrotation vs. oscillation to investigate the question!

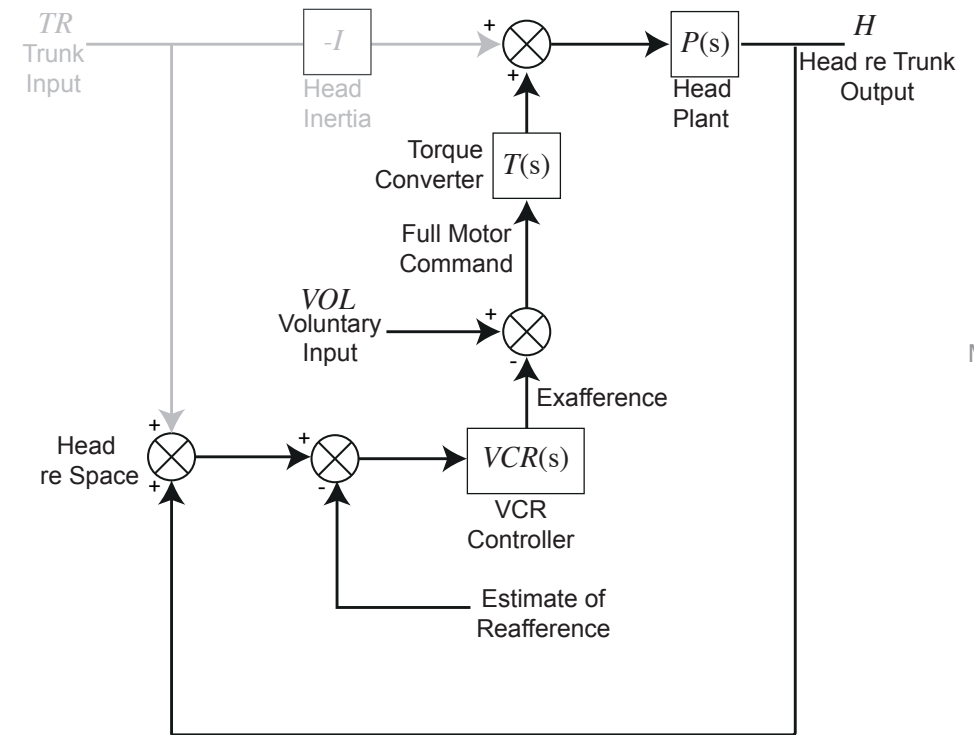
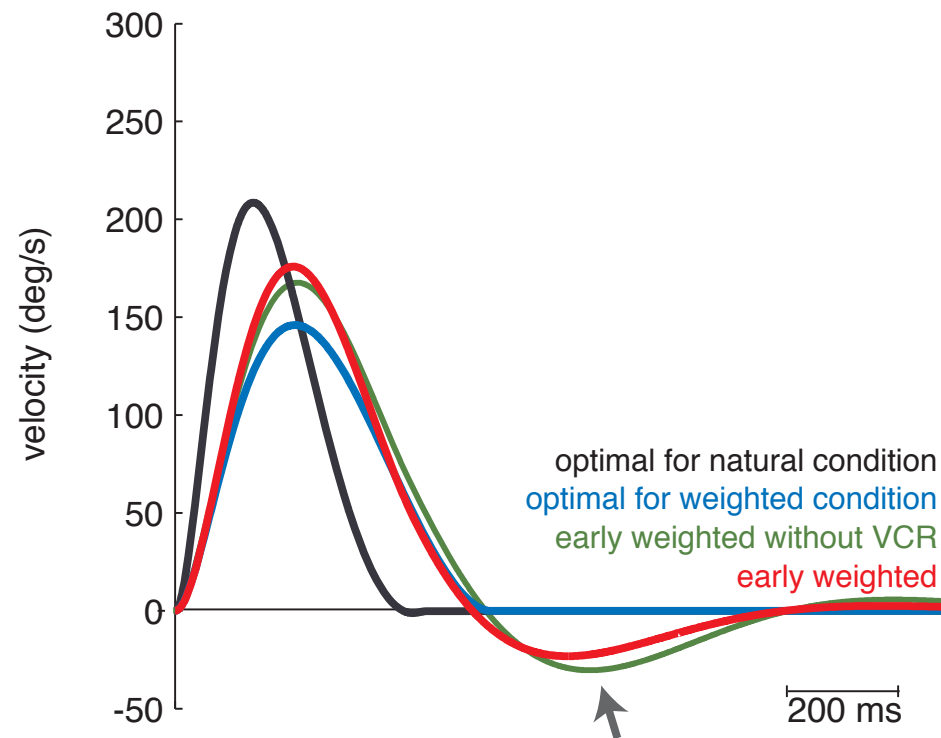
The role of the efference copy



Bilateral vestibular patients show higher VOR gains during counterrotation phase than during oscillation phase

What about the sensory feedback?

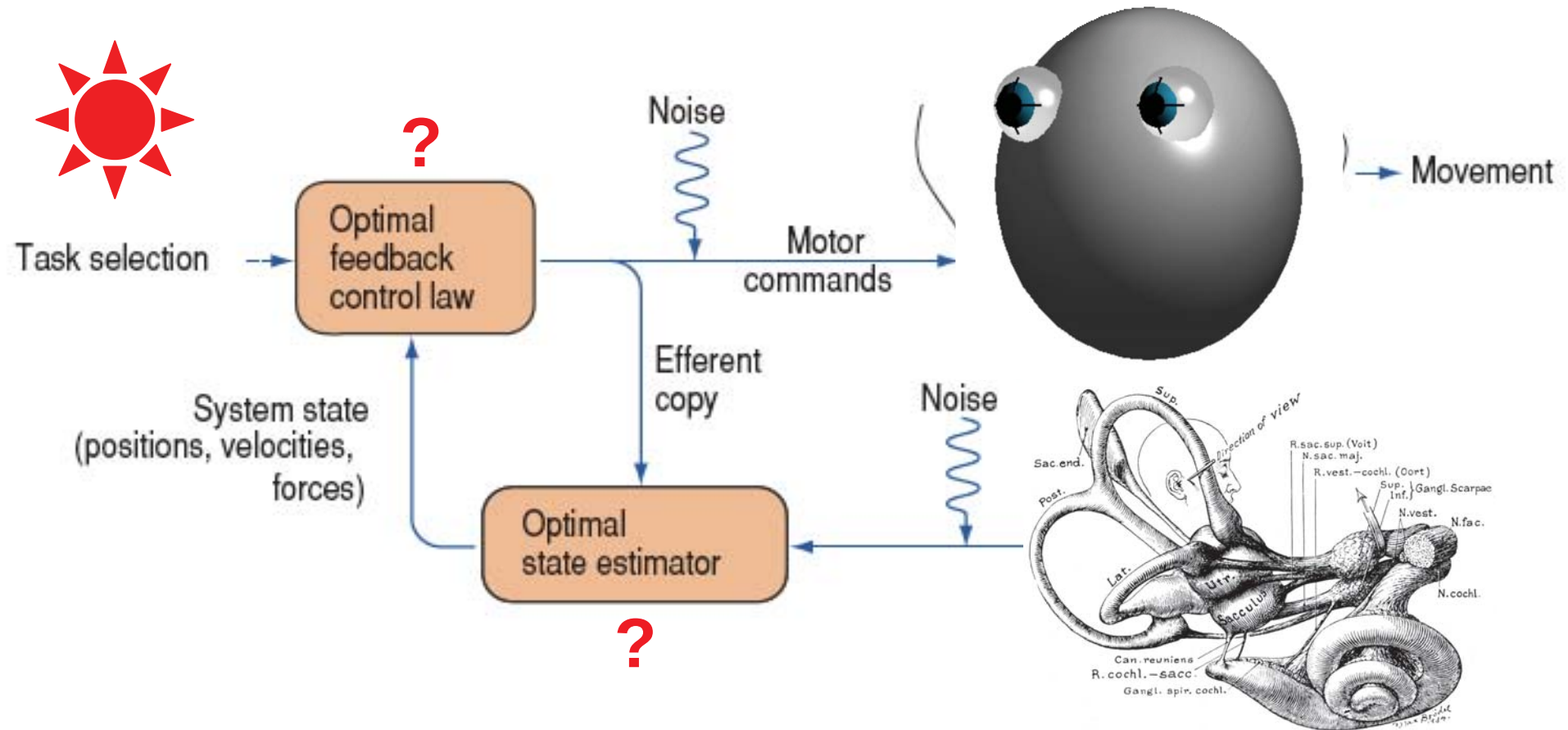
model



after Peng et al. 1996

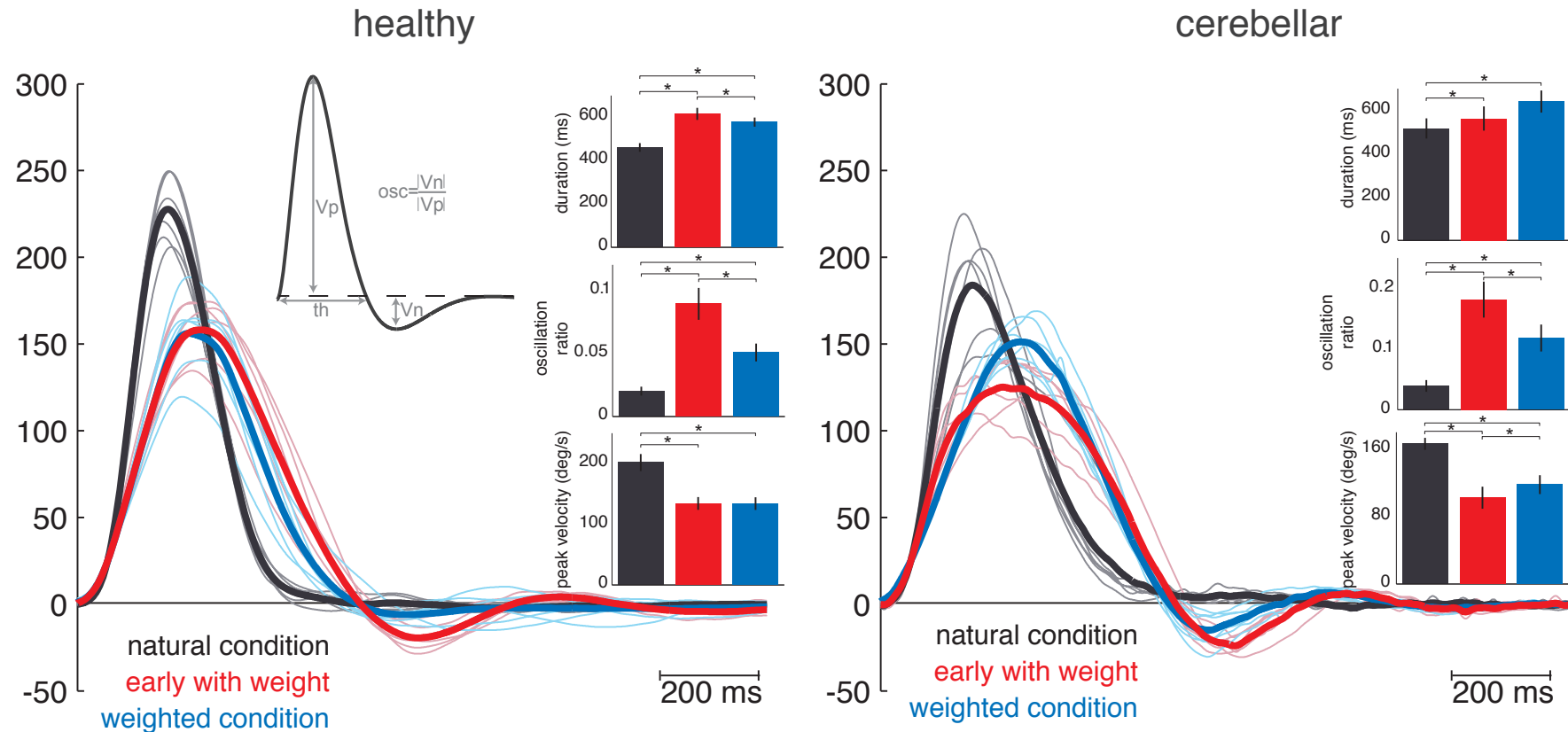
Vestibulo-collic reflex alone cannot eliminate oscillations

What goes wrong in cerebellar patients?



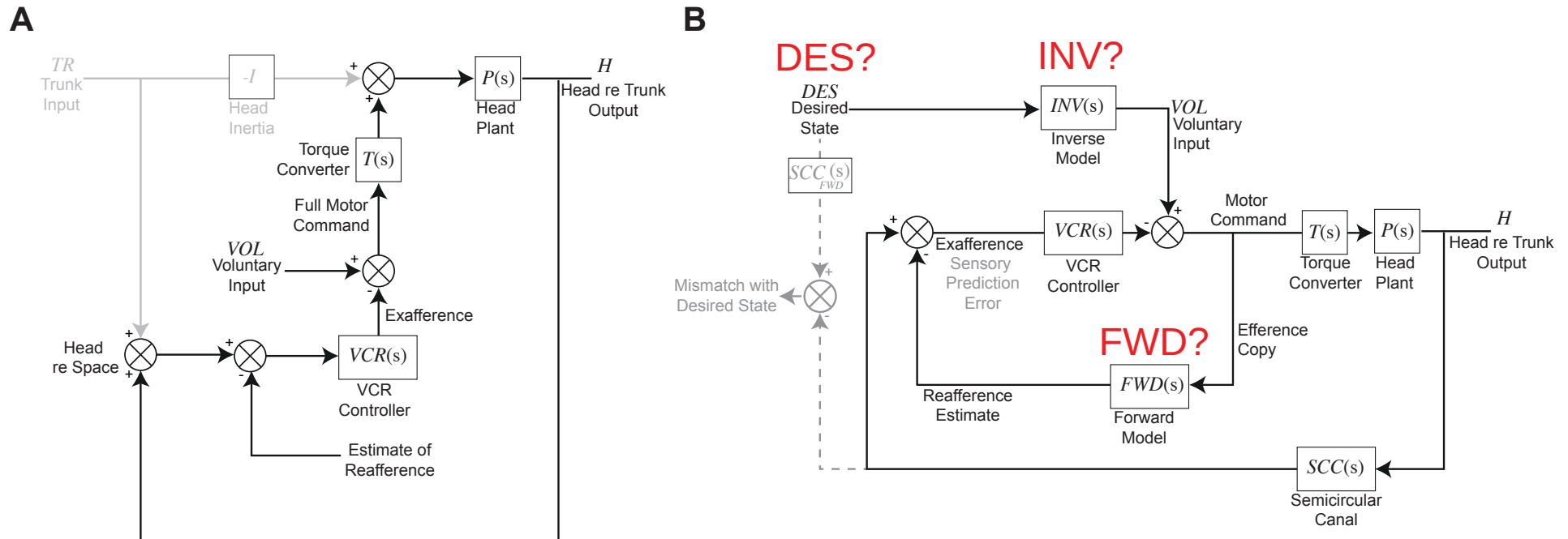
Where is the specific deficit of cerebellar patients located functionally?

What goes wrong in cerebellar patients?



Cerebellar patients show clear adaptation to the weighted condition, but don't show complete optimization

The vestibulo-collic reflex

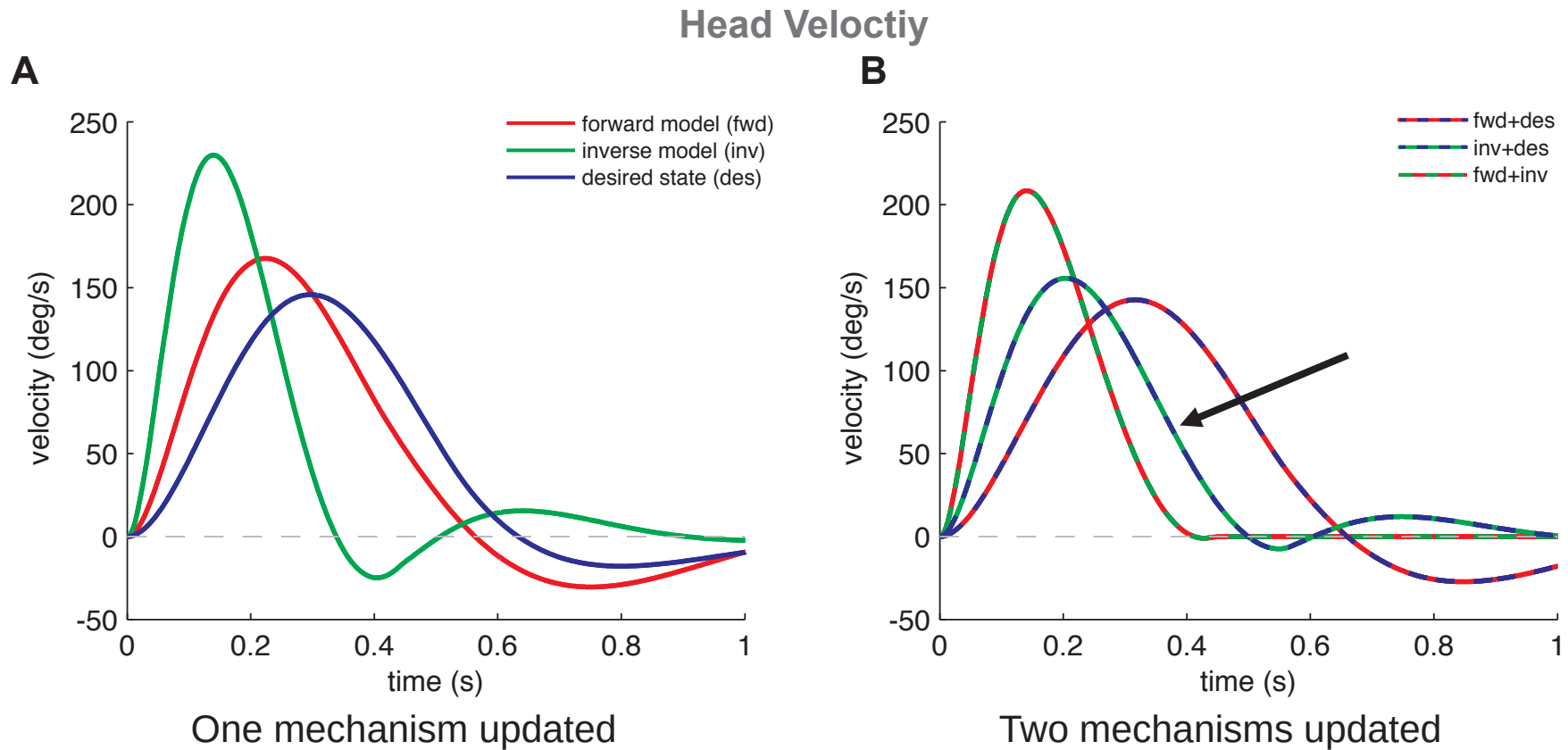


Modified after Peng et al. 1996

The vestibulo-collic reflex contributes to head movements as online feedback control.

There are three possible locations for failure (DES, INV, FWD).

Simulated head movements



Updating inverse model and desired state, but not forward model, leads to best match with results of cerebellar patients

Summary

Combined eye-head movements minimize the consequences of motor noise (i.e., gaze variability)

Short-term flexibility/adaptation of sensorimotor control to compensate for changing properties of the world/body

Adaptation requires vestibular (or visual) sensory feedback

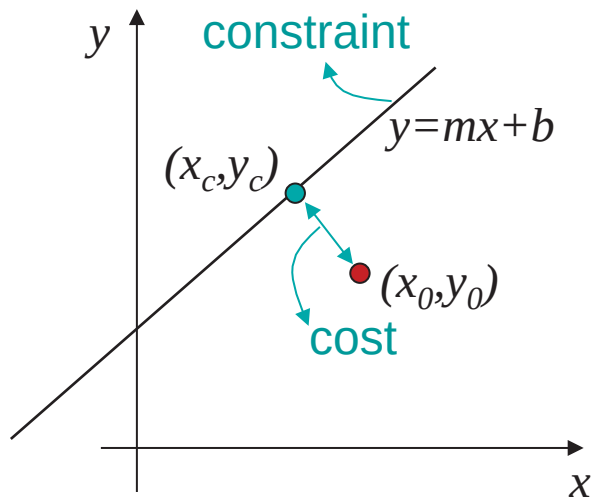
Cerebellar atrophy does not prevent adaptation
optimizing the post-movement variability for motor control

Cerebellar patients show hypometric gaze shifts

Results in cerebellar patients can be explained by a failure to update the internal forward model that implements online control

Funded by the BMBF (German Center for Vertigo and Balance Disorders)

How to find an optimal solution?



Problem:

Find the point (x_c, y_c) along the line $y=mx+b$ that is closest to the point (x_0, y_0) .

Find the control signal u that moves the eye to the target with minimum post-movement variability

What we should decide:

point (x_c, y_c)

control signal u

Constraint :

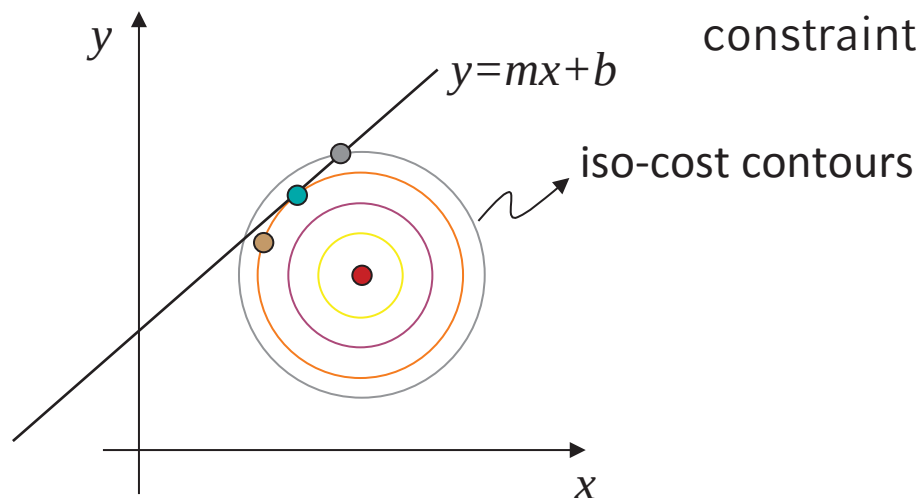
point should be on the line $y=mx+b$

control signal u must bring the eye to the target

Cost/Criterion:

distance to (x_0, y_0)

post-movement variability



constraint minimization with Lagrange multipliers

cost function $J = (x - x_0)^2 + (y - y_0)^2$

constraint $y = mx + b$

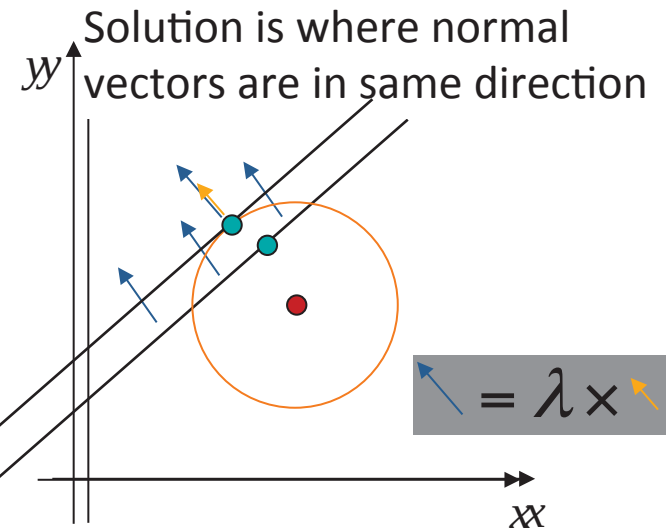
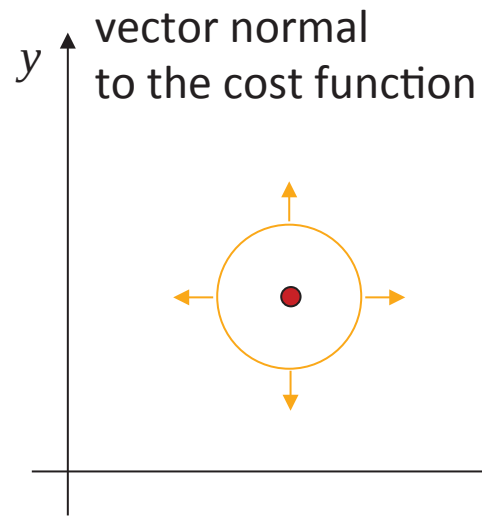
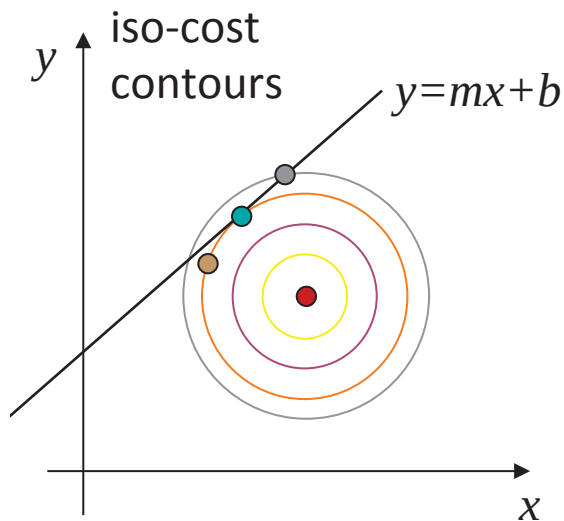
How to find an optimal solution?

cost function

$$J(x, y) = (x - x_0)^2 + (y - y_0)^2$$

constraint

$$g(x, y) = -y + mx + b$$



$$\begin{bmatrix} \frac{dJ}{dx} \\ \frac{dJ}{dy} \end{bmatrix} = \begin{bmatrix} 2x - 2x_0 \\ 2y - 2y_0 \end{bmatrix}$$

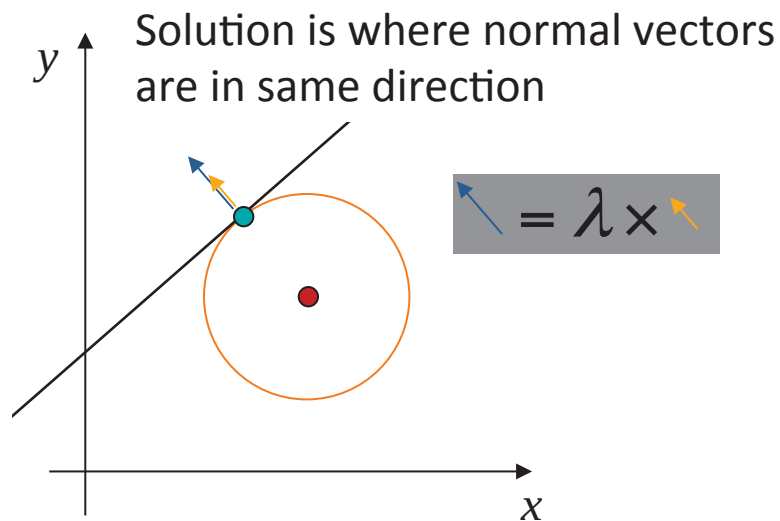
$$\begin{bmatrix} \frac{dJ}{dx} \\ \frac{dJ}{dy} \end{bmatrix} = \lambda \begin{bmatrix} \frac{dg}{dx} \\ \frac{dg}{dy} \end{bmatrix}$$

How to find an optimal solution?

augmented cost function

$$J_a(x, y) = J(x, y) + \lambda g(x, y)$$

$$J_a(x, y) = (x - x_0)^2 + (y - y_0)^2 + \lambda(-y + mx + b)$$



$$\begin{bmatrix} \frac{dJ}{dx} \\ \frac{dJ}{dy} \end{bmatrix} = \lambda \begin{bmatrix} \frac{dg}{dx} \\ \frac{dg}{dy} \end{bmatrix}$$

cost is minimized when

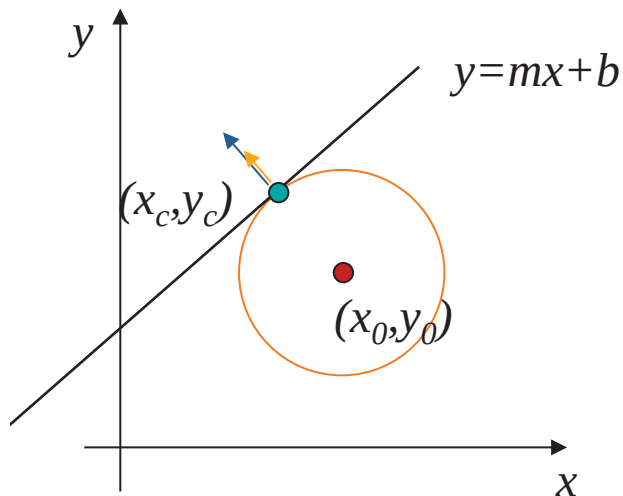
$$\frac{dJ_a(\underline{x})}{d\underline{x}} = \frac{dJ(\underline{x})}{d\underline{x}} + \lambda \frac{dg(\underline{x})}{d\underline{x}} = 0$$

$$g(\underline{x}) = 0$$

How to find an optimal solution?

example

find the point (x_c, y_c) along the line $y=mx+b$ that is closest to the point (x_0, y_0) .



$$\frac{dJ_a(\underline{x})}{d\underline{x}} = \frac{dJ(\underline{x})}{d\underline{x}} + \lambda \frac{dg(\underline{x})}{d\underline{x}} = 0$$

$$g(\underline{x}) = 0$$

$$\begin{bmatrix} 2x_c - 2x_0 \\ 2y_c - 2y_0 \end{bmatrix} + \lambda \begin{bmatrix} m \\ -1 \end{bmatrix} = 0$$

$$y_c = mx_c + b$$

Another simple example

$$\dot{x} = (u - x) / \tau + \varepsilon \cdot u$$

$$x_{t=0} = x_0$$

$$x_{t=1} = x_1$$

$$\text{var}(x_{t=1}) = \min$$

1D trajectory with first-order lowpass dynamics and signal-dependent noise ($\varepsilon = N(0, \sigma^2)$)

Start and endpoint are given

We want to find the command u minimizing the variance of x at the endpoint

First step: discretize the continuous system

Possible via analytical solution (use matrix exponentials for more than 1D)

Or via Euler one-step integration

Discretize

$$\dot{x} = (u - x) / \tau + \varepsilon \cdot u$$

$$\Delta x_t = (u_t - x_t) / \tau + \varepsilon_t \cdot u_t$$

$$x_{t+1} = x_t + \Delta x_t \cdot \Delta t$$

$$x_{t+1} = x_t (1 - \Delta t / \tau) + u_t \Delta t / \tau + \varepsilon_t \cdot u_t \cdot \Delta t$$

Now comes the trick:

Express the whole trajectory using this iterative equation

Calculate the mean response

$$x_{t+1} = x_t(1 - 1/\tau) + u_t / \tau$$

$$x_1 = x_0(1 - 1/\tau) + u_0 / \tau$$

$$x_2 = x_1(1 - 1/\tau) + u_1 / \tau$$

$$= x_0(1 - 1/\tau)^2 + u_0(1 - 1/\tau) / \tau + u_1 / \tau$$

$$x_3 = x_0(1 - 1/\tau)^3 + u_0(1 - 1/\tau)^2 / \tau + u_1(1 - 1/\tau) / \tau + u_2 / \tau$$

...

The trajectory can be expressed by a linear combination of x and u

$$\underline{x} = A \cdot \underline{u} + \underline{b} \cdot x_0$$

The variance

$$\text{var}(x_1) = \text{var}(x_0(1 - 1/\tau) + u_0/\tau + \varepsilon_0 u_0)$$

$$= \text{var}(\varepsilon_0 u_0) = \sigma^2 u_0^2$$

$$\text{var}(x_2) = \text{var}(x_1(1 - 1/\tau) + \varepsilon_1 u_1)$$

$$= \text{var}(\varepsilon_0 u_0(1 - 1/\tau) + \varepsilon_1 u_1) = \sigma^2 (u_0^2(1 - 1/\tau)^2 + u_1^2)$$

...

Thus, the variance can be expressed as a function of $\underline{u}$:

$$\text{var}(\underline{x}) = \text{var}(V \cdot \underline{u})$$

Formulation for Matlab

The Matlab function `quadprog` solves problems with a quadratic cost function and constraints.

The cost function has to be of the form $\underline{u}^T \cdot H \cdot \underline{u}$

Our cost function:

$$\text{var}(x_{end}) = \text{var}(V(end,:) \cdot \underline{u}) = \underline{u}^T \cdot \text{diag}(V(end,:)^2) \cdot \underline{u}$$

The constraint:

$$x_1 = A(end,:) \cdot \underline{u} + b_{end} \cdot x_0$$

$$A(end,:) \cdot \underline{u} = b_{end} \cdot x_0 - x_1$$