Neural control of movement

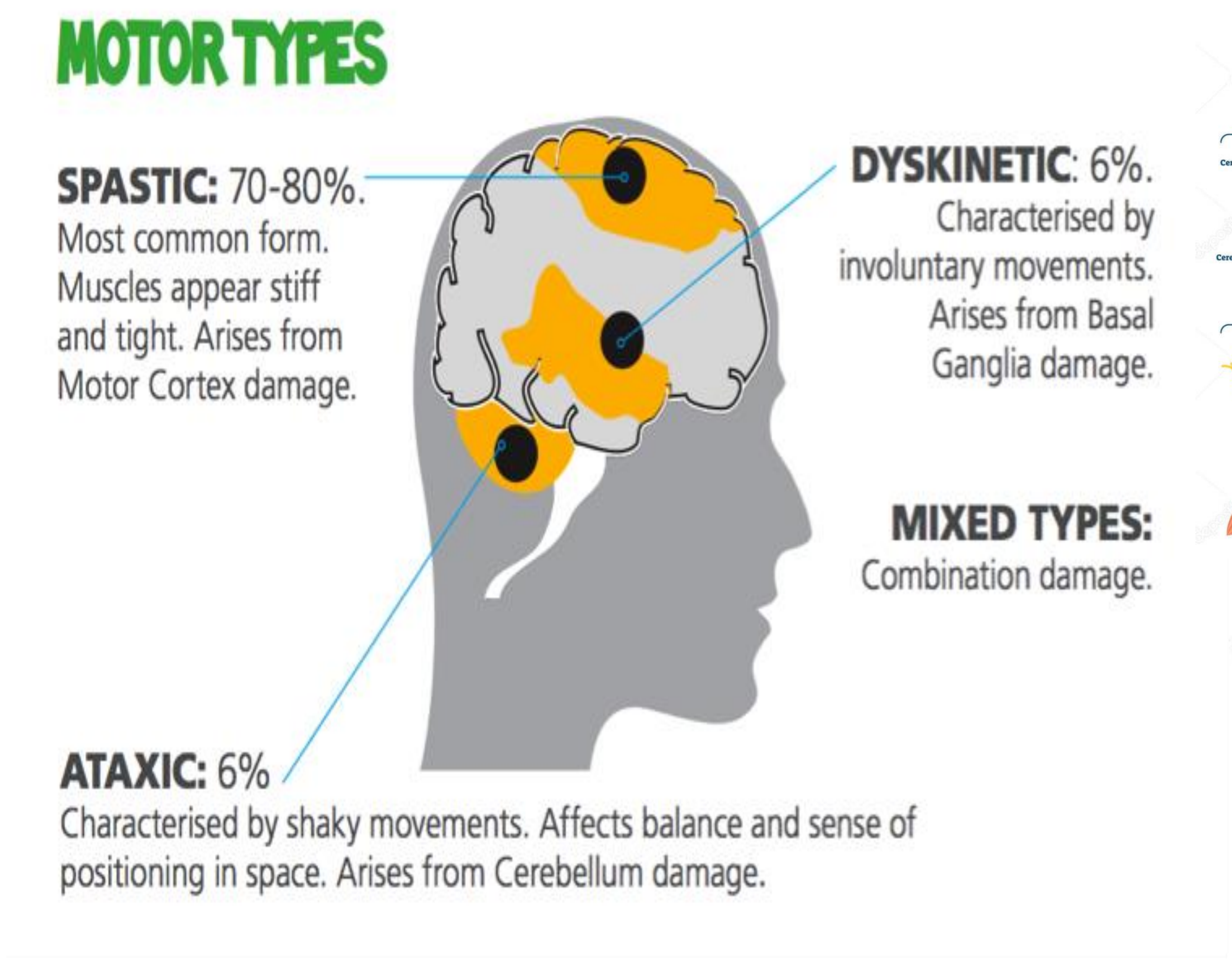
Movement control is difficult

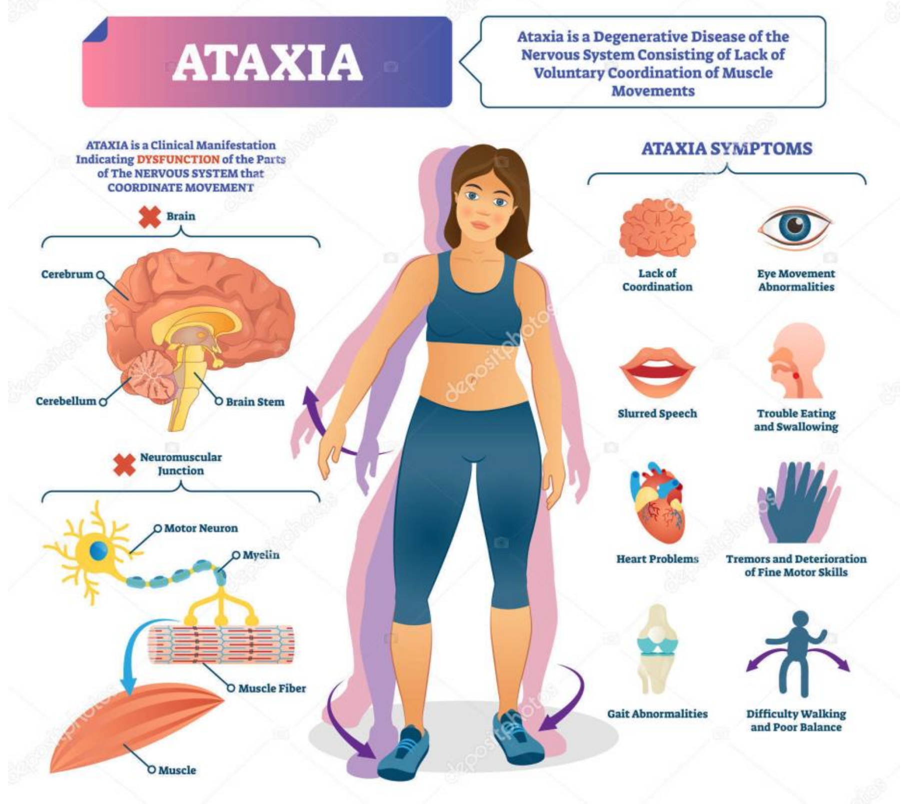
Humans and in general animals exhibit remarkably complex movement behaviors.

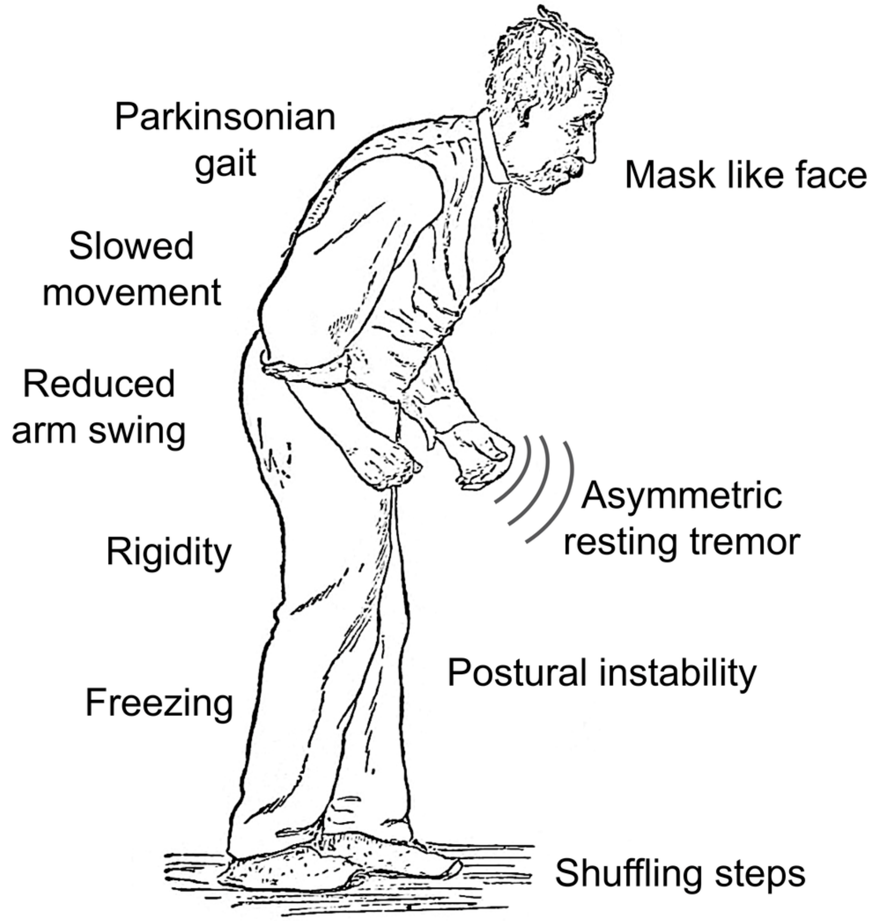
Possible due to several brain regions taking care of specific control issues like **disturbance rejection**, **state-estimation**, **prediction**, **internal models** about the body and the world and several other features unexplored in artificial systems

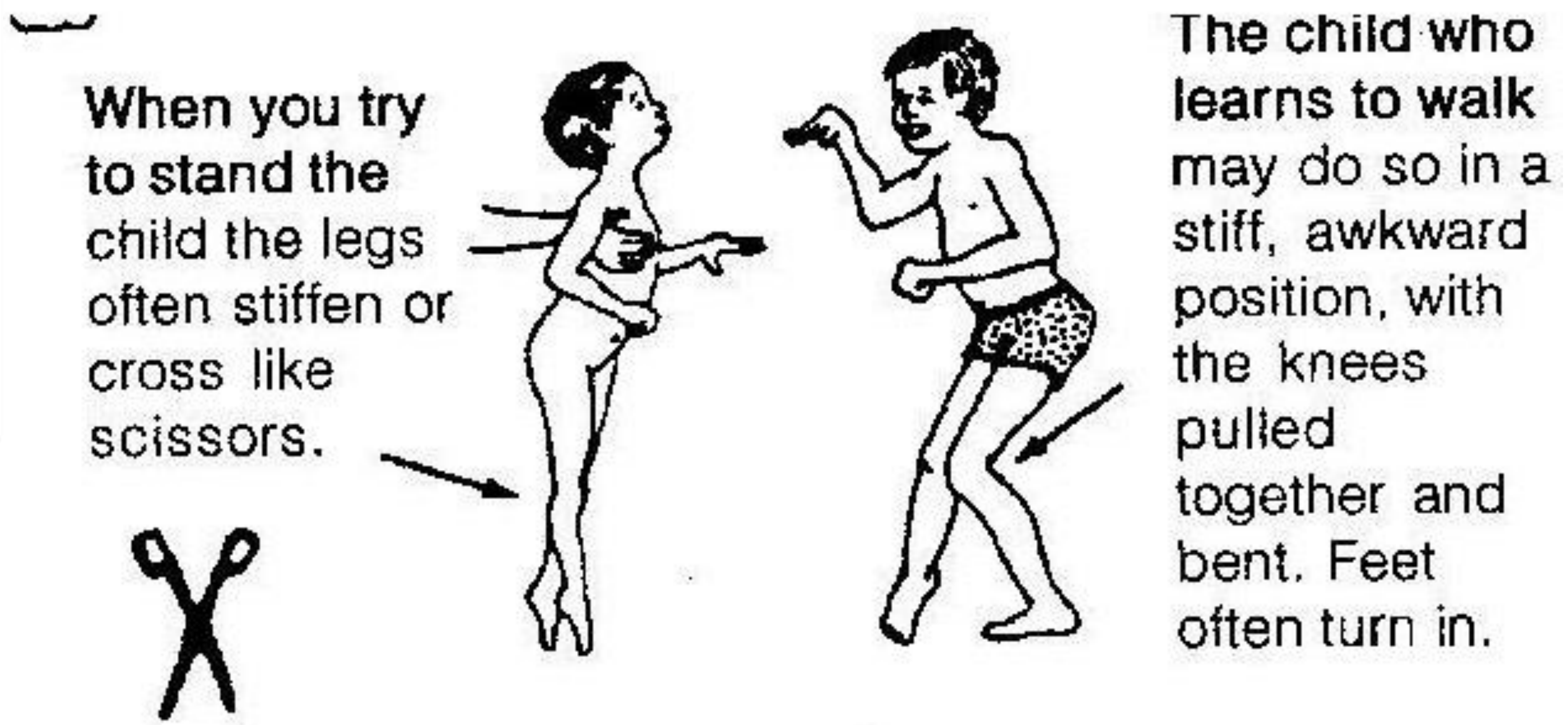
Disorders are equally puzzling

Damages to different regions results in different deficits



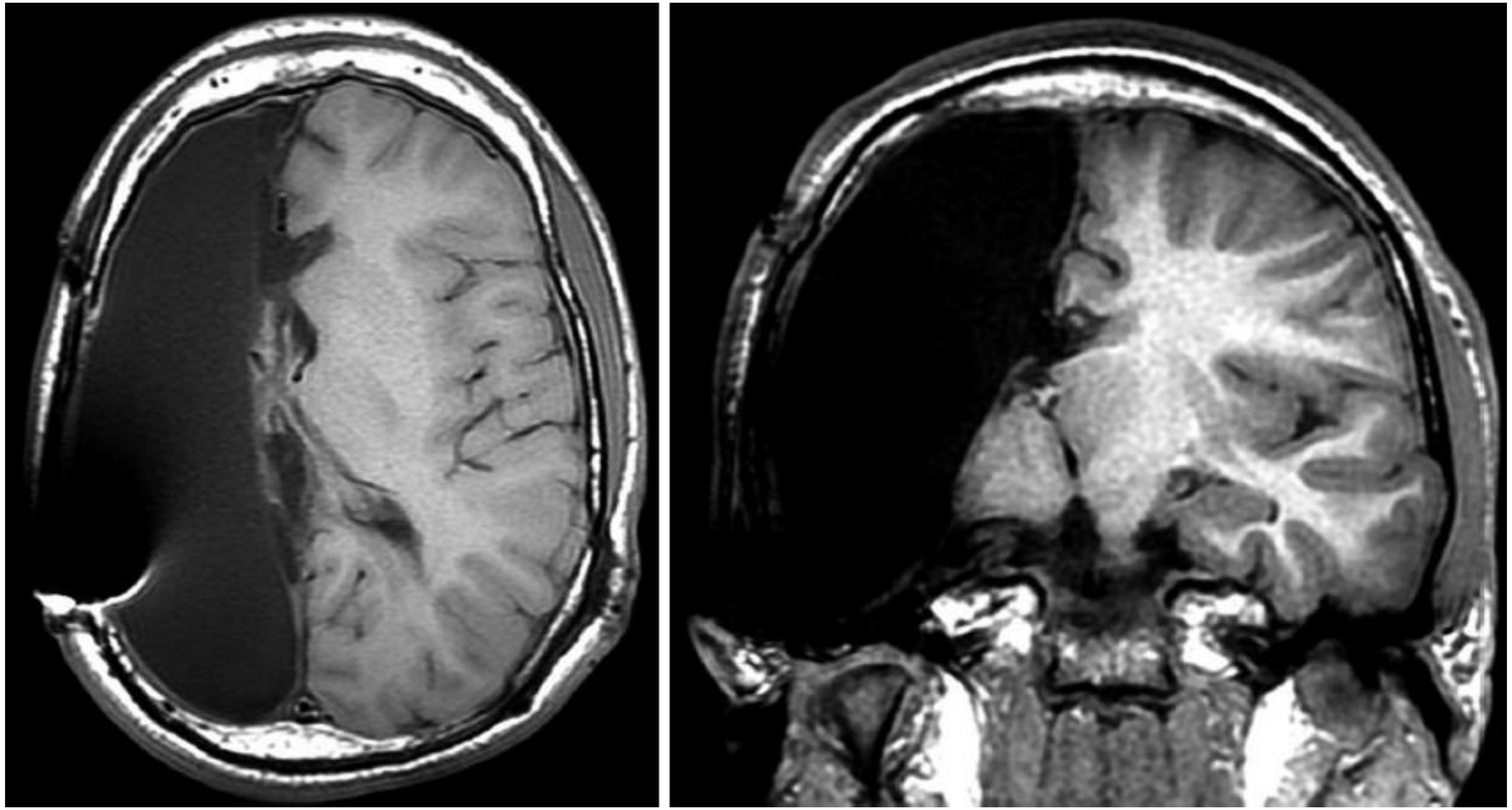






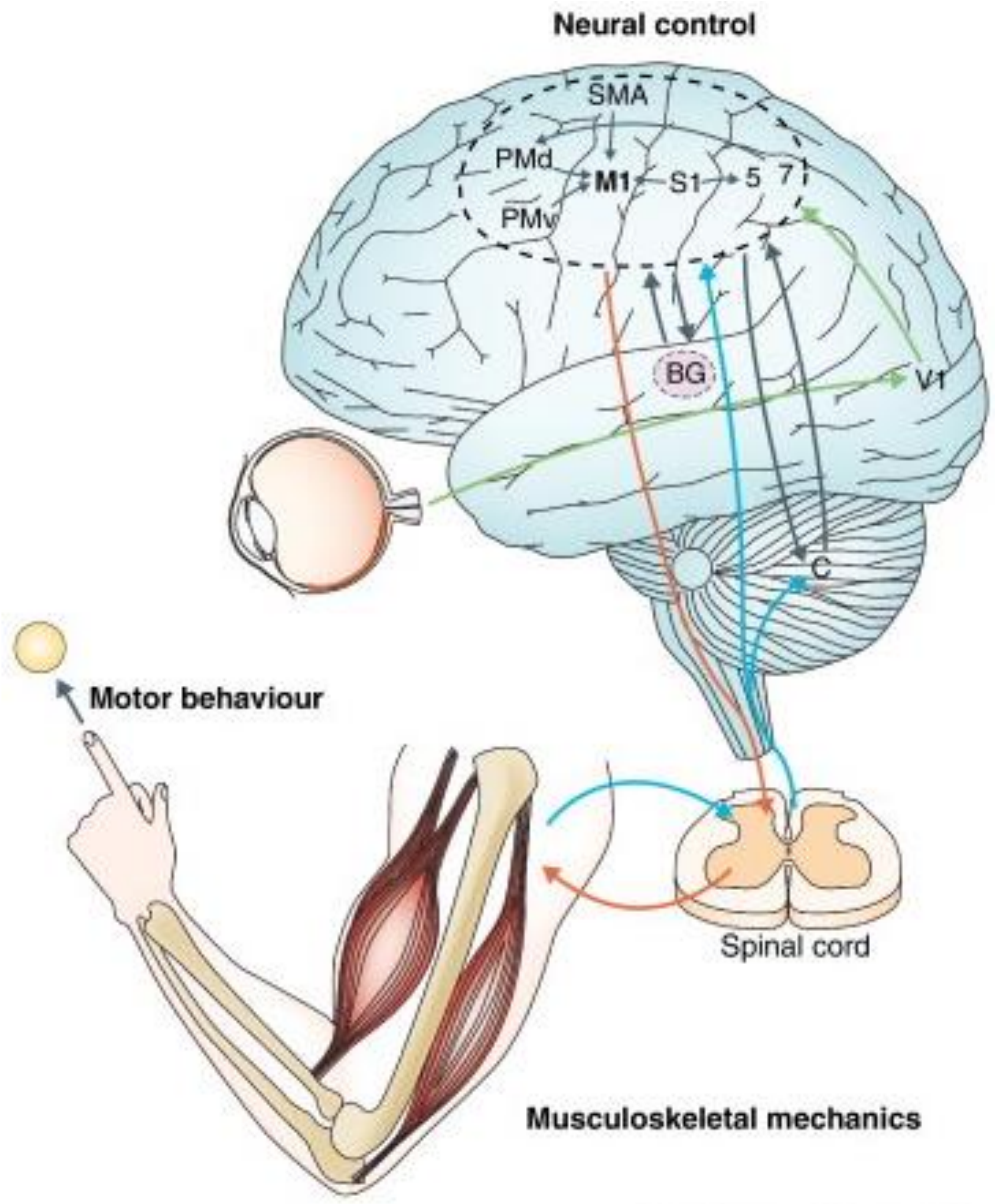
At the same time…..

Recoveries are even more mysterious

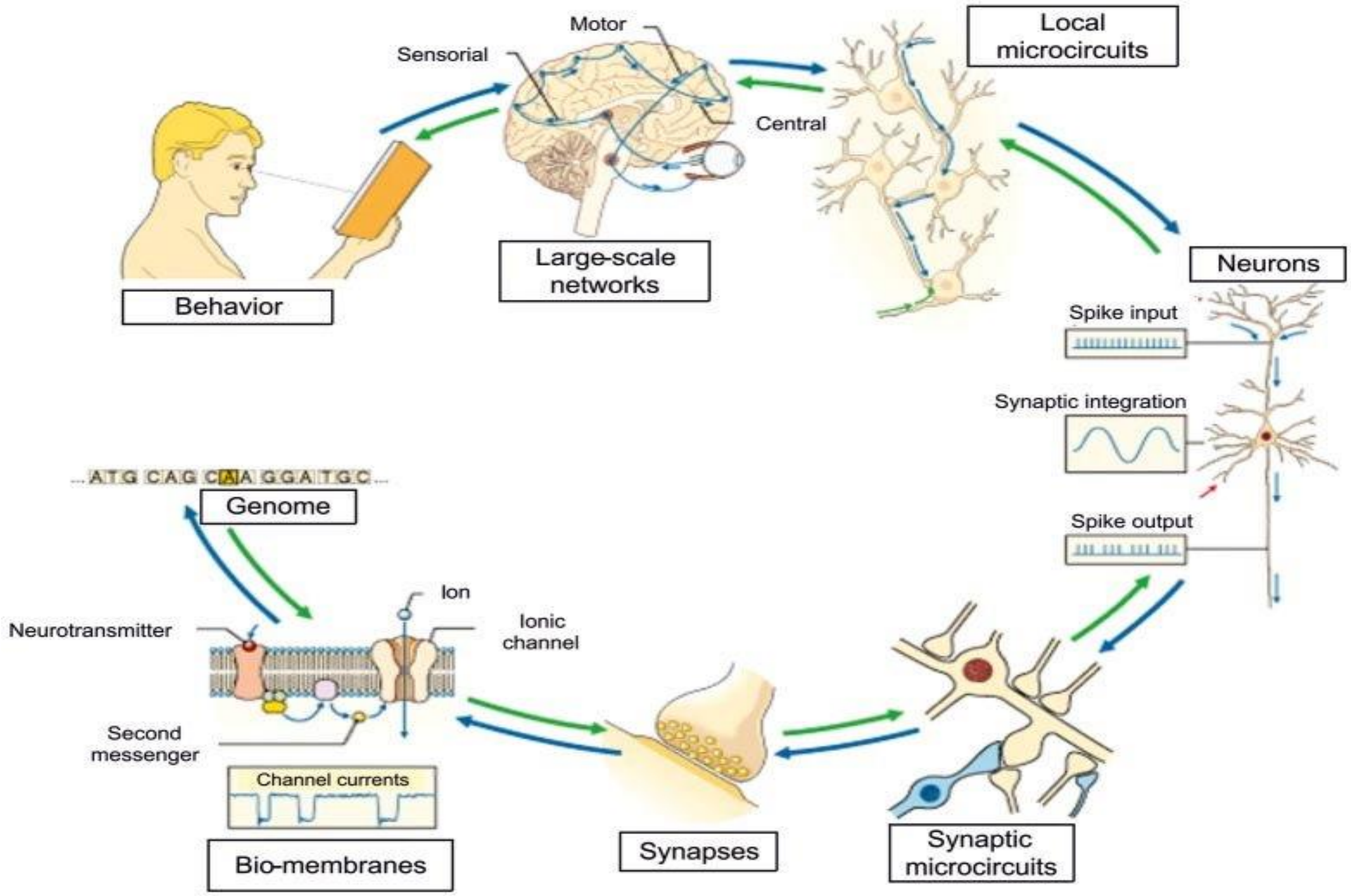


Slicing off half the brain at an appropriate age to deal with epilepsy doesn't really cause major limitations in any behaviour – memory, motor, personality etc.,

From sensation to movement and back

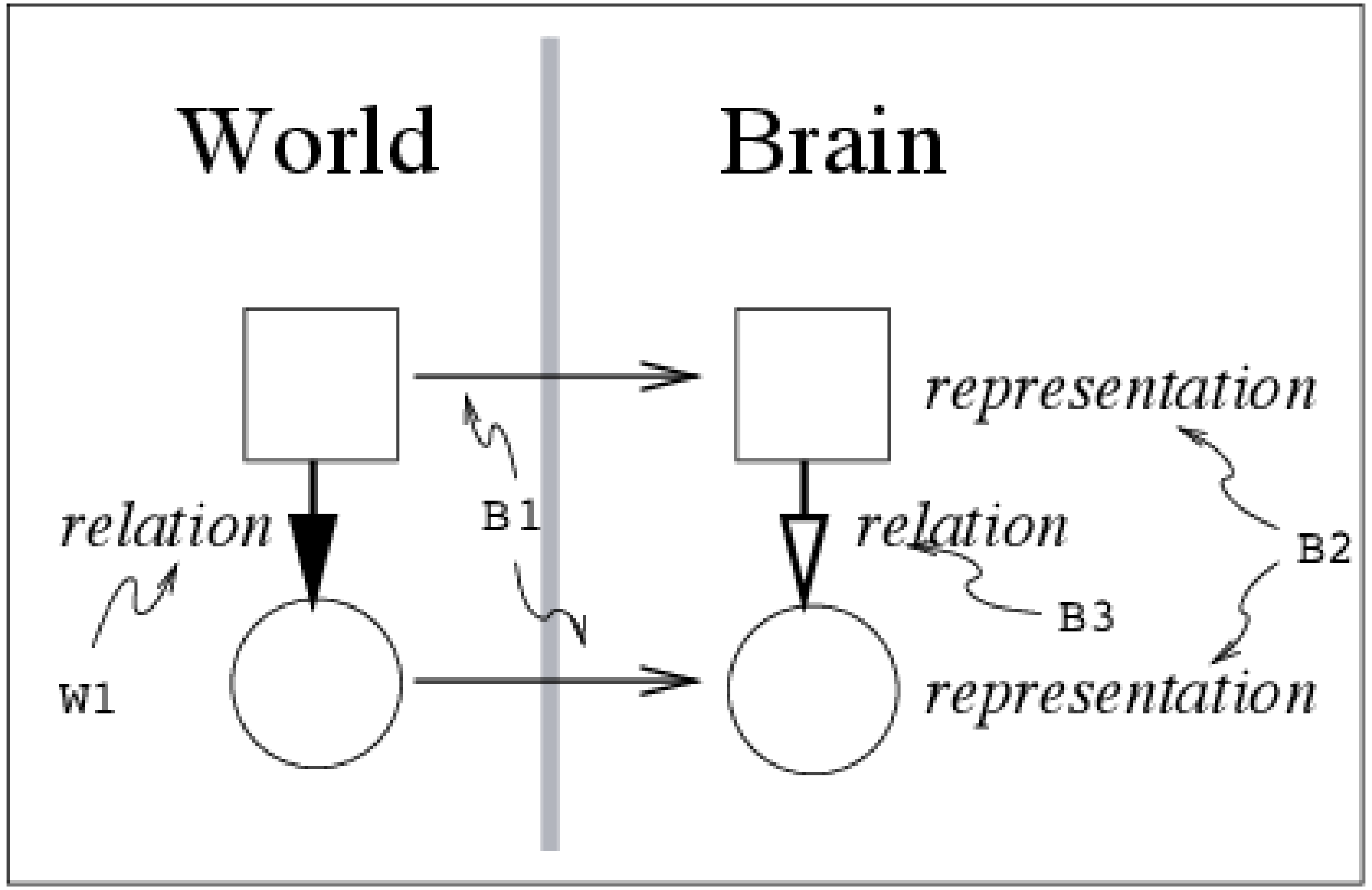


The difficulty is due to the multi-scale brain organization



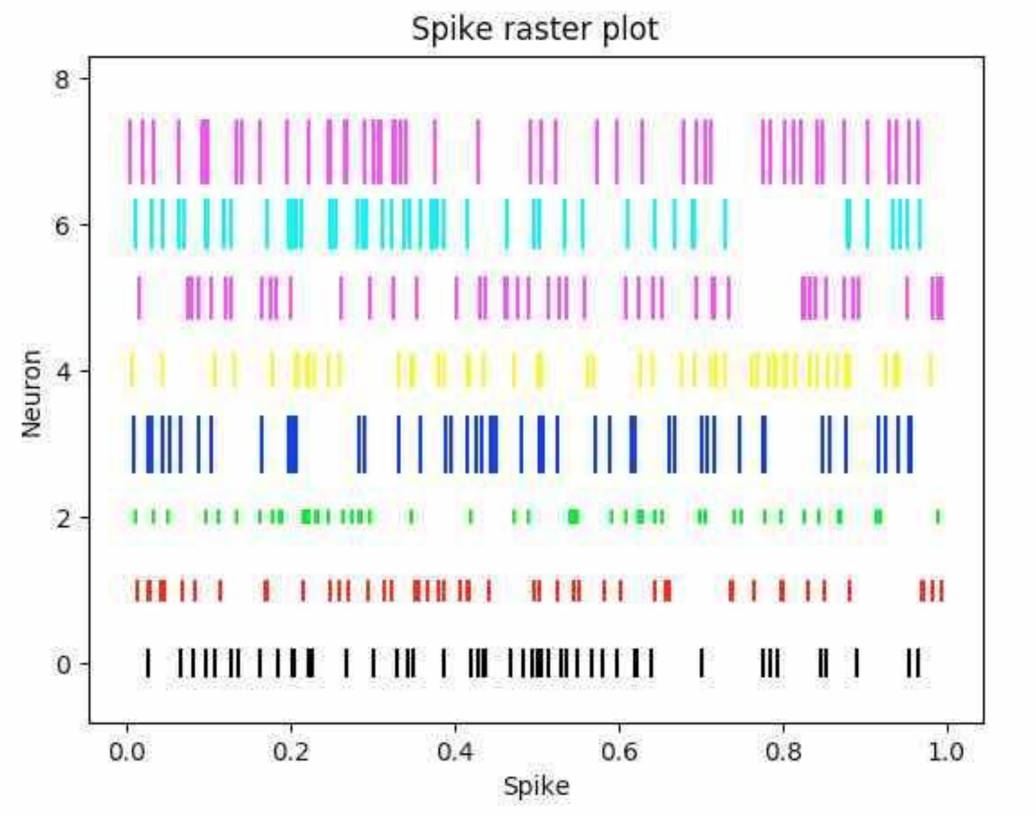
Pursuit to understand Brain as an encoding/decoding machine

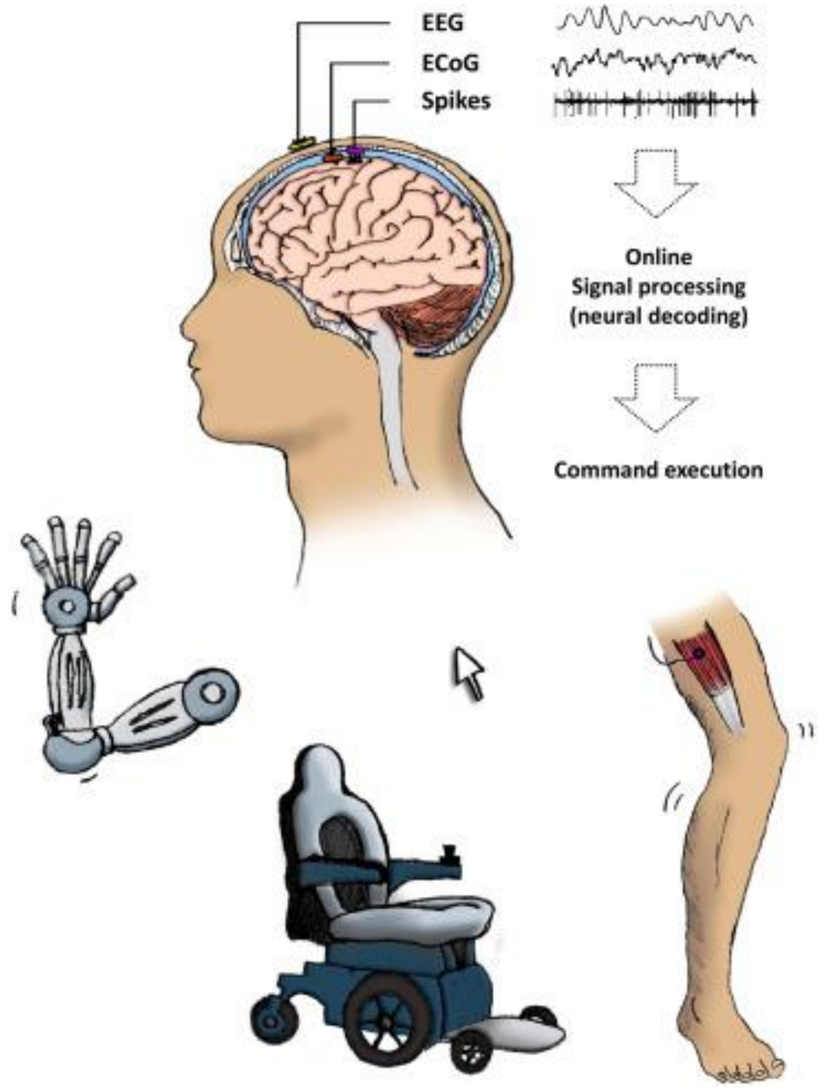
- The nature of the world is stored/encoded in the electrical firing patterns of brain circuits
- Different brain regions read-out/decode the neural activity for generating meaningful action
- <u>Encoding:</u> how does a stimulus cause a pattern of responses? p(r | s)
- <u>Decoding:</u> what do these responses tell us about the stimulus? p(s | r)



Stimulus - ‘s’

Response - ‘r’





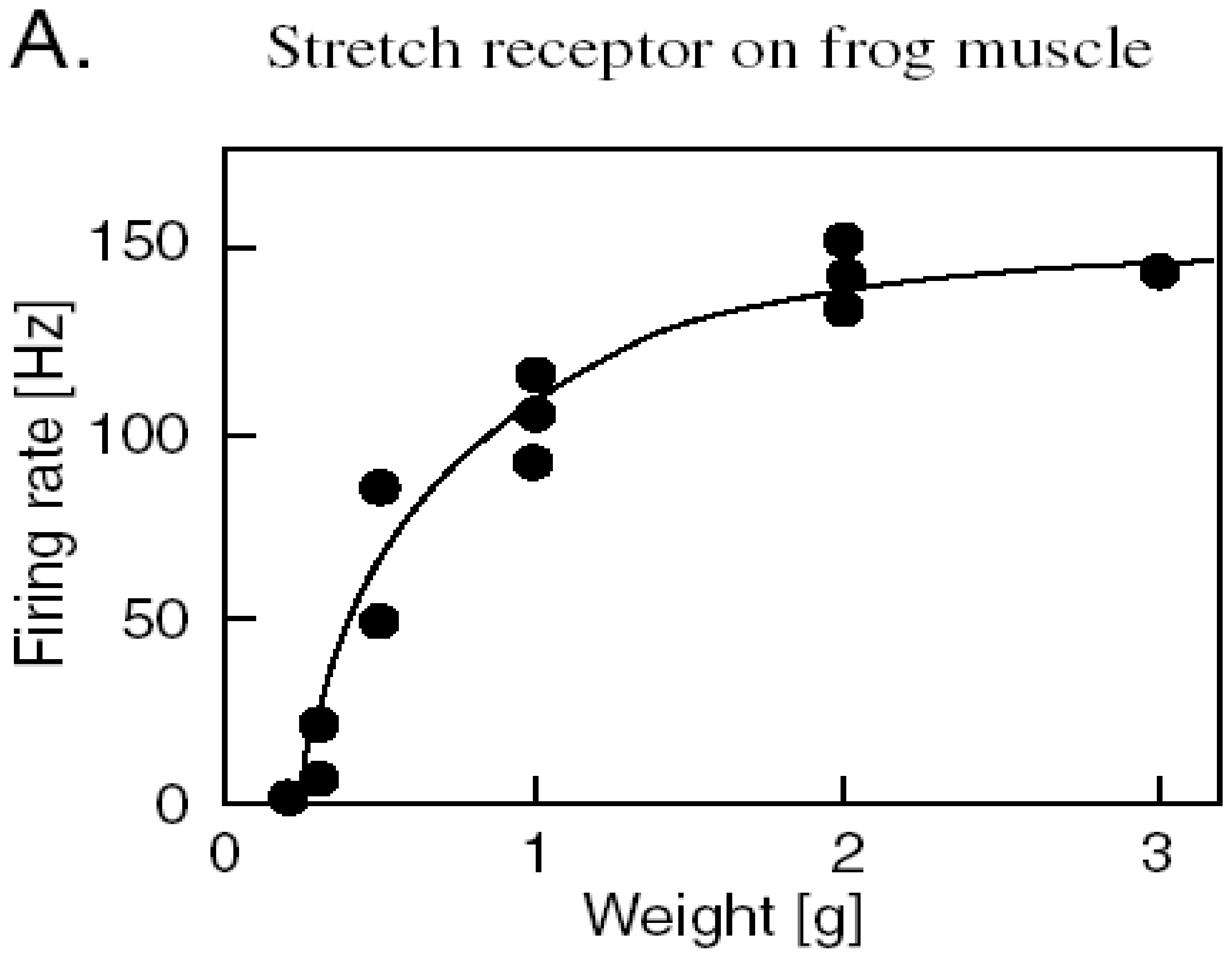
What is stimulus and what is neural response ?

- ‘s(t)’ can represent quantitative characteristics of the sensory data like the edge properties in the visual image, strength of the smell etc.,

- ‘r(t)’ is a function of the spikes in the neural response vector i.e., r(t) = f(r1,r2,r3…..rn). Two broad types of responses of most neurons:
  - Spike count
  - Spike timing

Firing rate – spike count hypothesis

The intensity or/and identity of stimulus is encoded by the number of spikes emitted by the neuron.
Firing rate = number of spikes per second



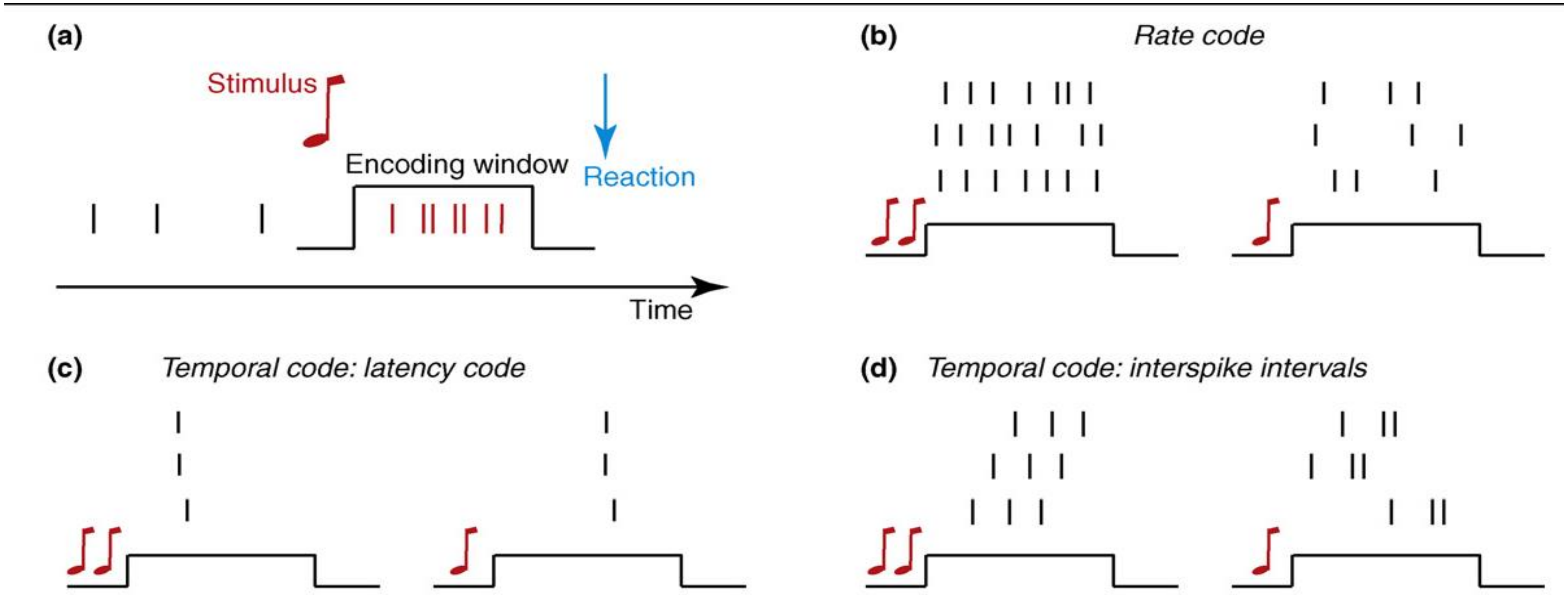
Lord Adrian (1928). Showed that the number of spikes emitted by a frog's stretch receptor on a muscle increased when increasing the weight load applied to the muscle.

Spike counts increased with stimulus intensity

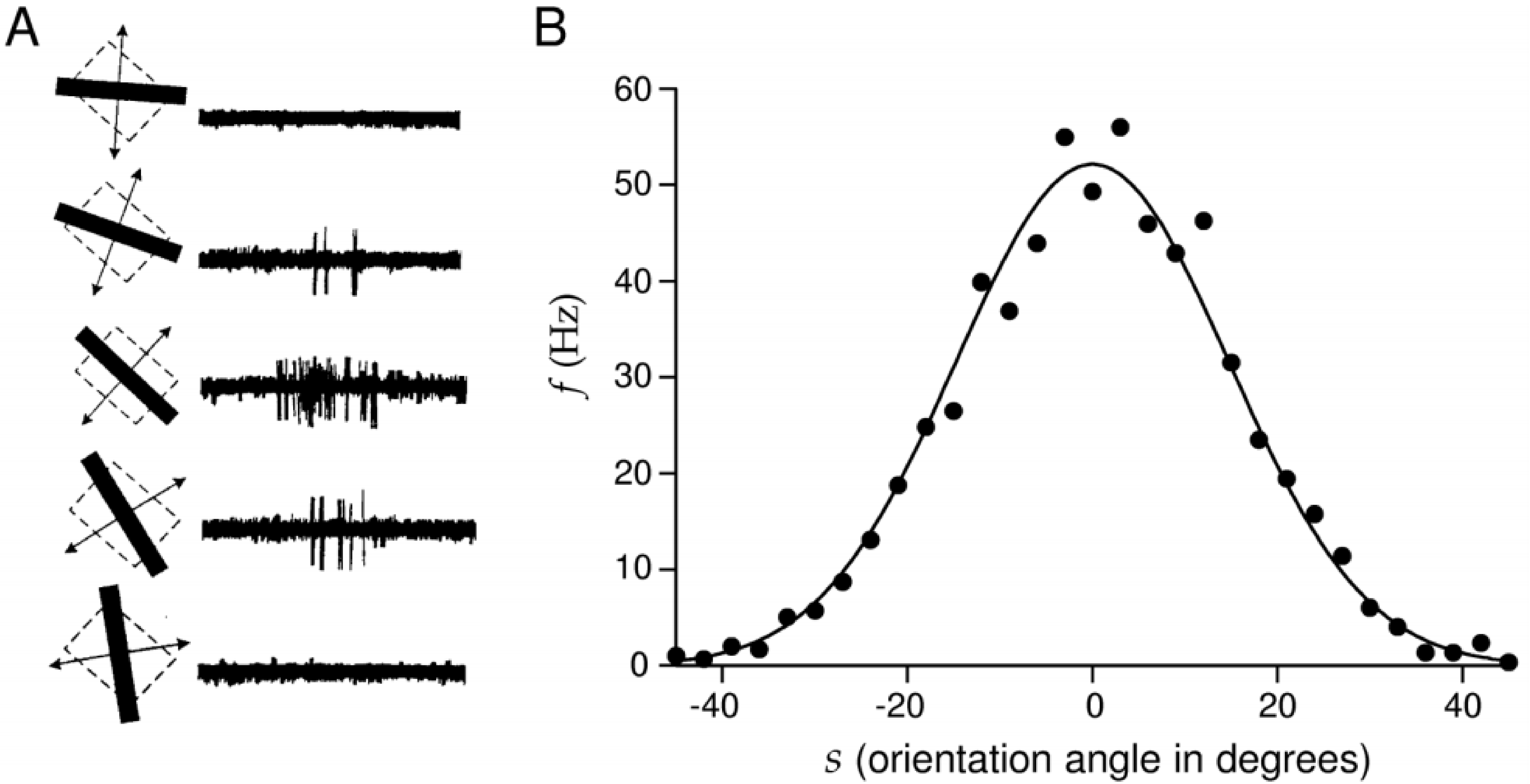
Example for firing rate encoding of identity is the face-selective neurons in inferior temporal cortex (IT) of the monkeys

Temporal coding – Spike time hypothesis

Not only the number of spikes per second, but also the temporal patterns of successive spikes can be used for encoding the stimuli

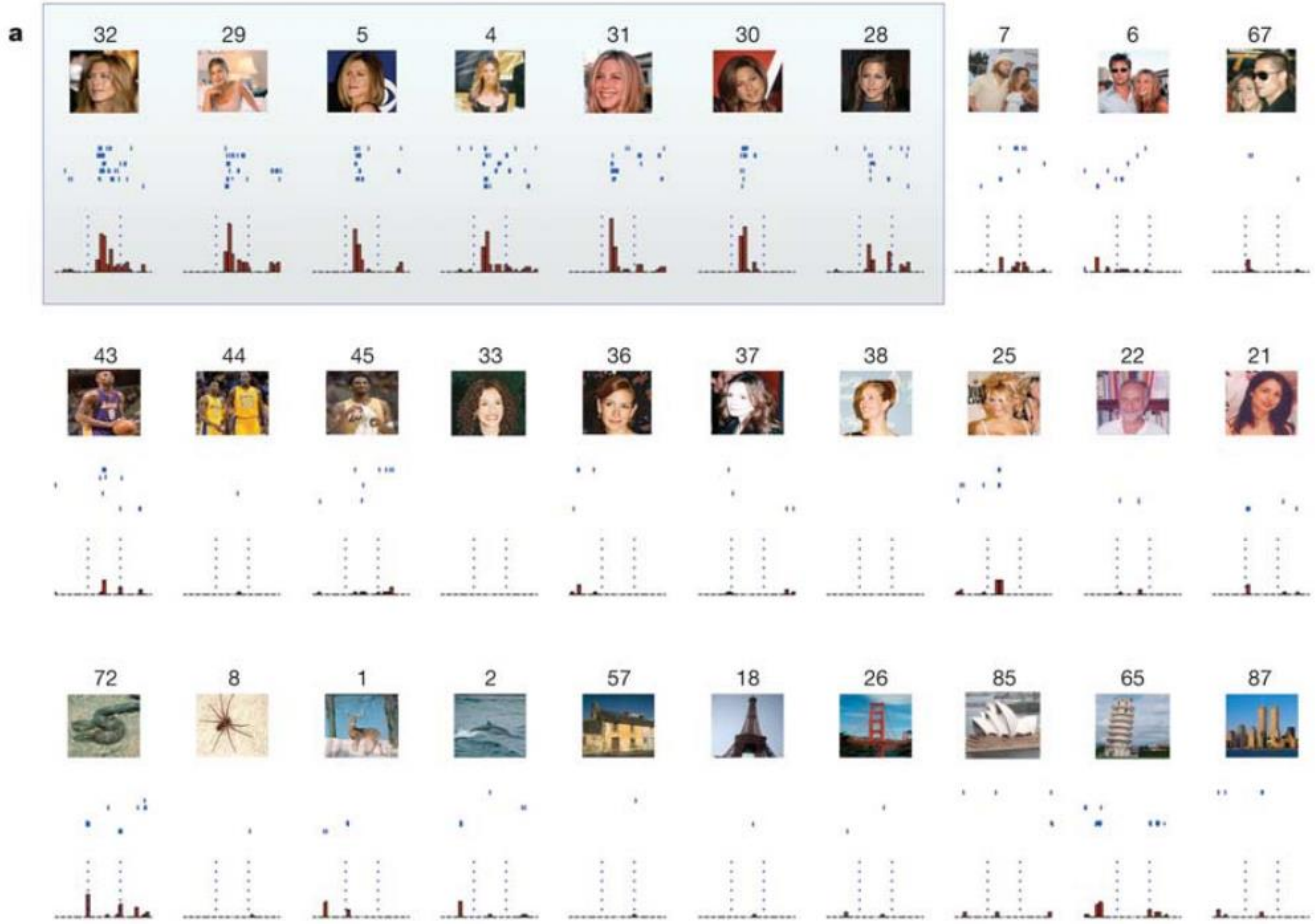


Hierarchical encoding of stimuli - V1 stimulus representation



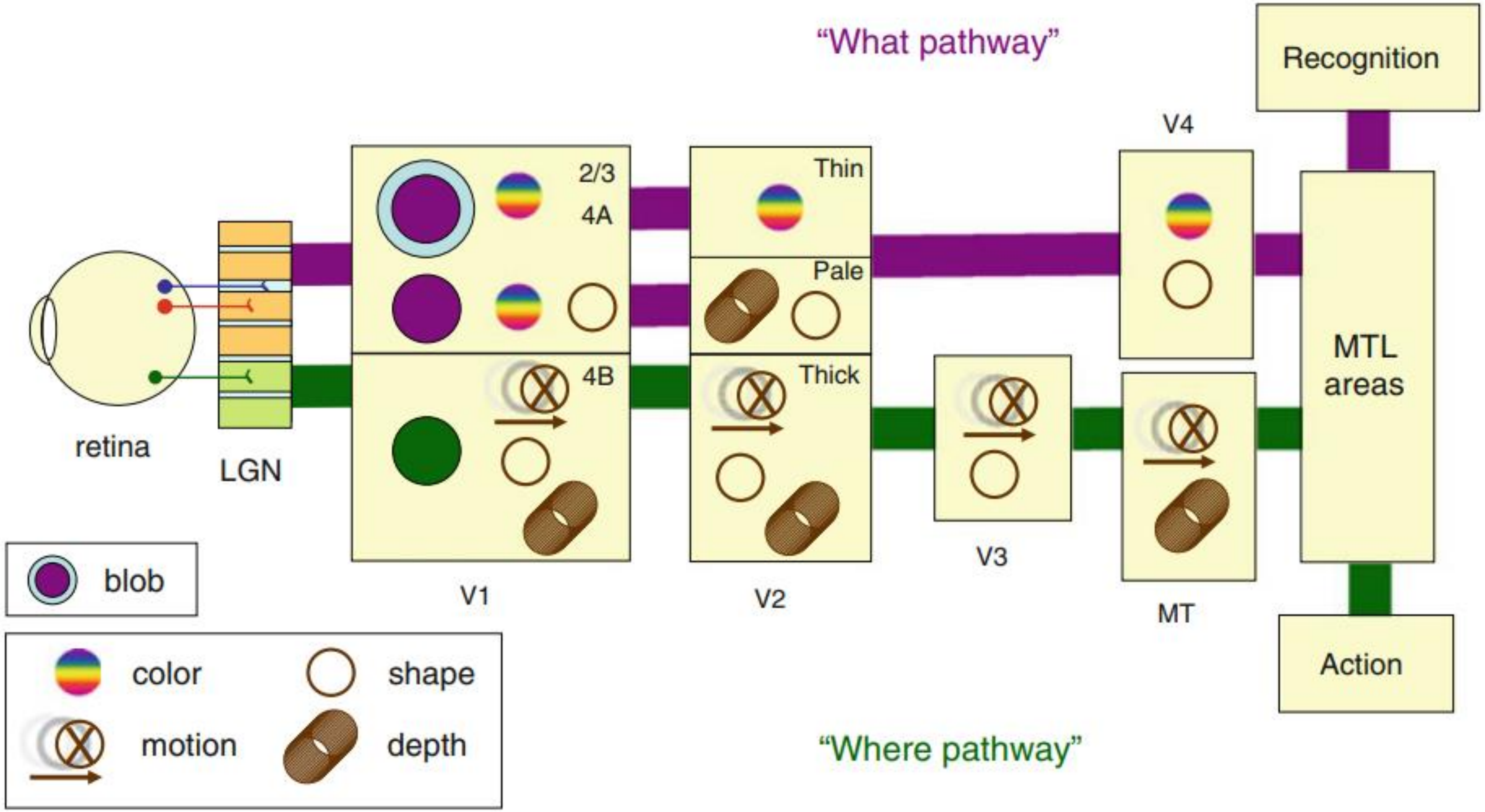
Gaussian tuning curve of a cortical (V1) neuron

Hierarchical encoding - MTL stimulus representation



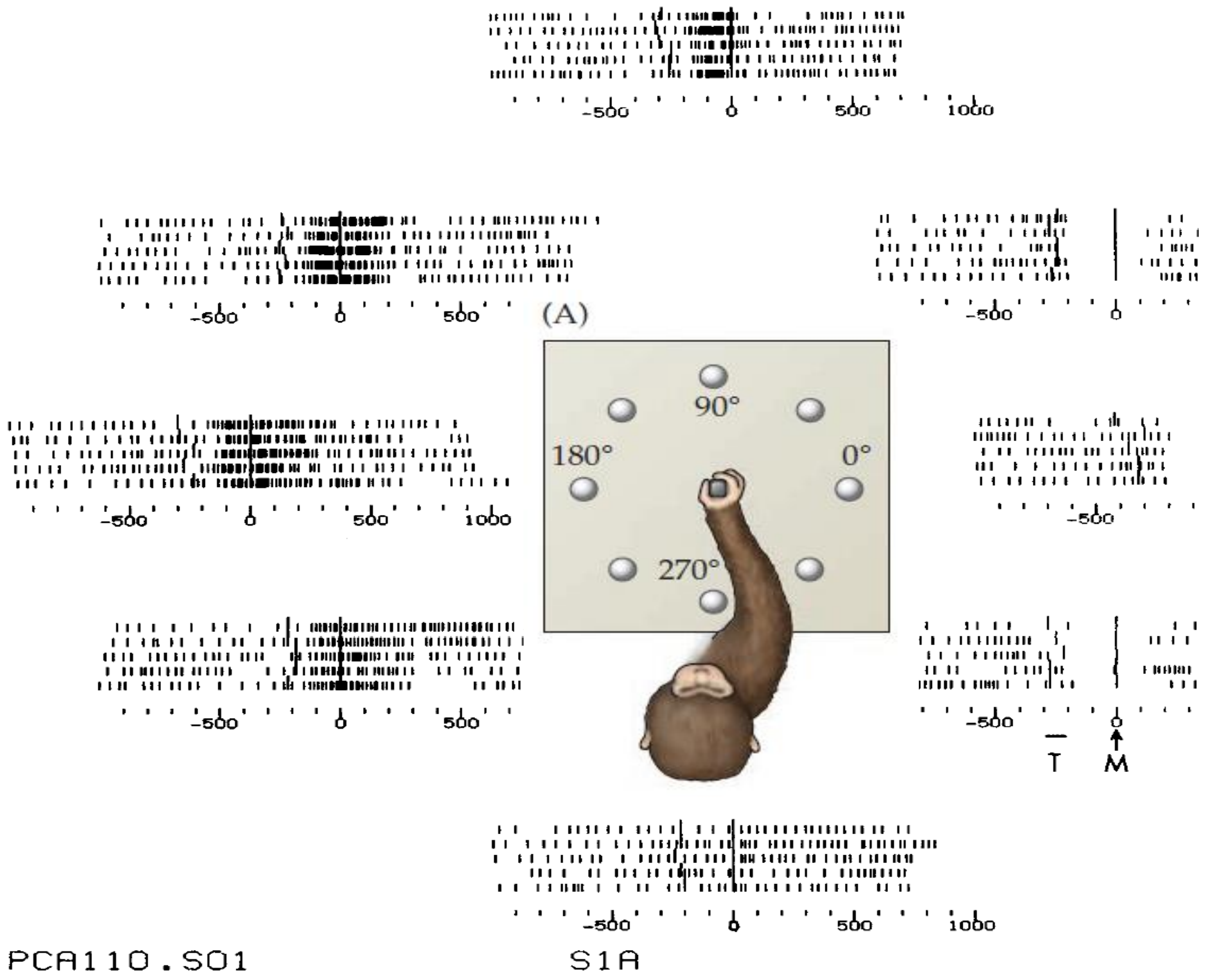
Medial temporal lobe - complex tuning like faces invariant to the image transformation *R. Quian Quiroga et al Nature 2005*

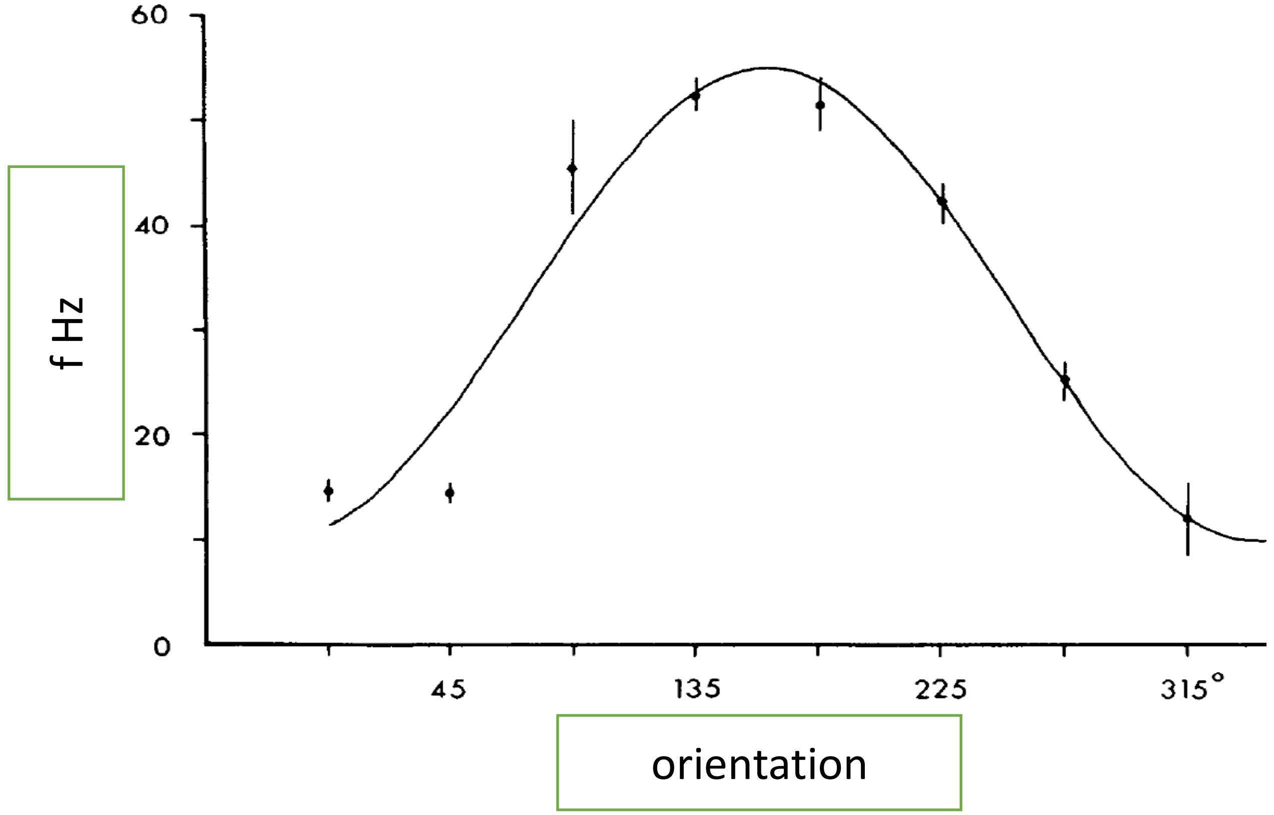
Hierarchical encoding - sensory stimulus representation



Z.Khan et al. CMLS 2011

Hierarchical encoding - Motor cortex (M1) movement representation

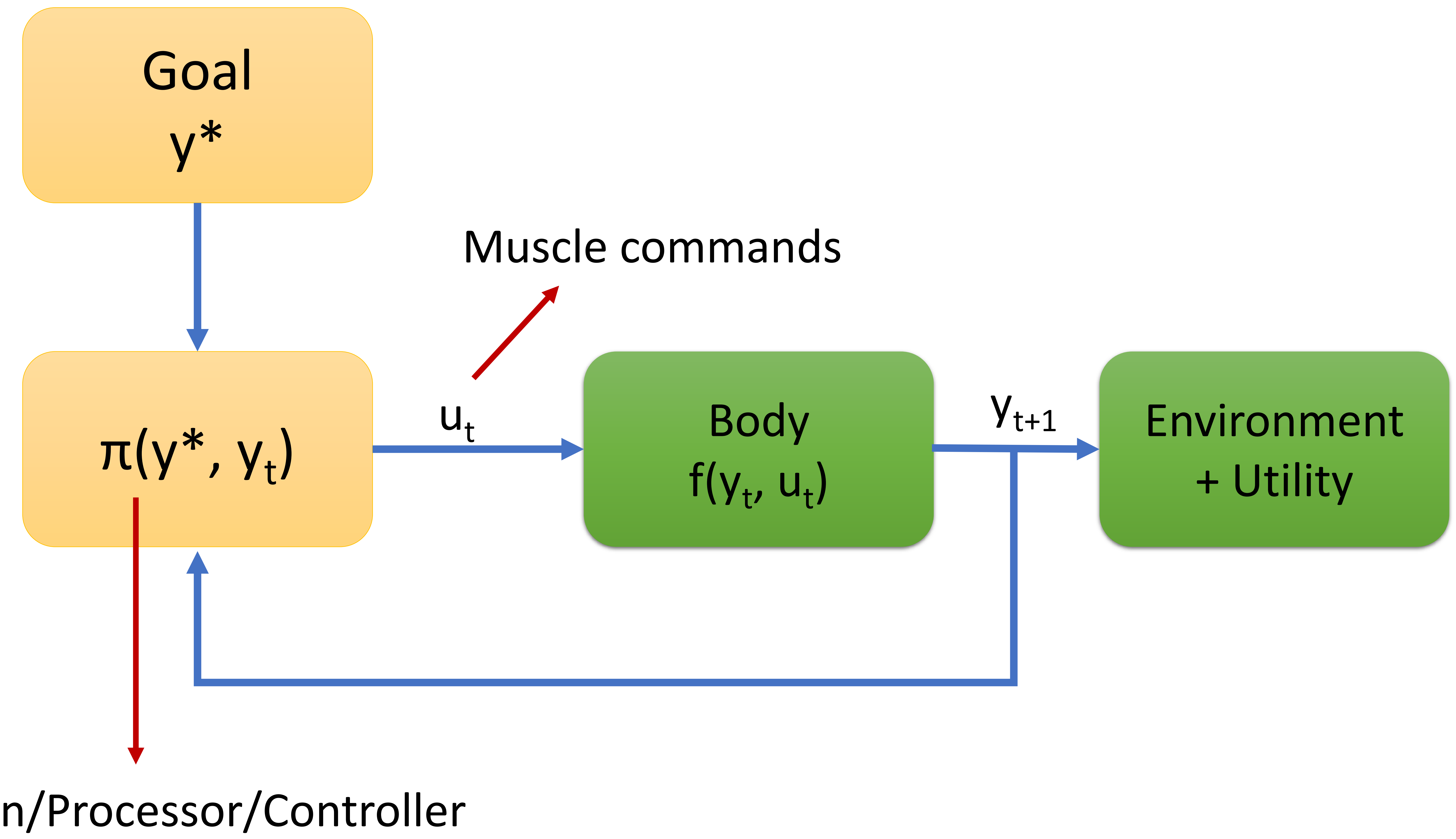




Encoding view is only descriptive

- Multiple codes
- Importance of mechanism
- For example, the descriptive models would not have anything to predict if the body under the experimentation undergoes a physical change unless more data is explicitly collected for this specific case

Goal-driven understanding



Optimal control formulation to find policy parameters

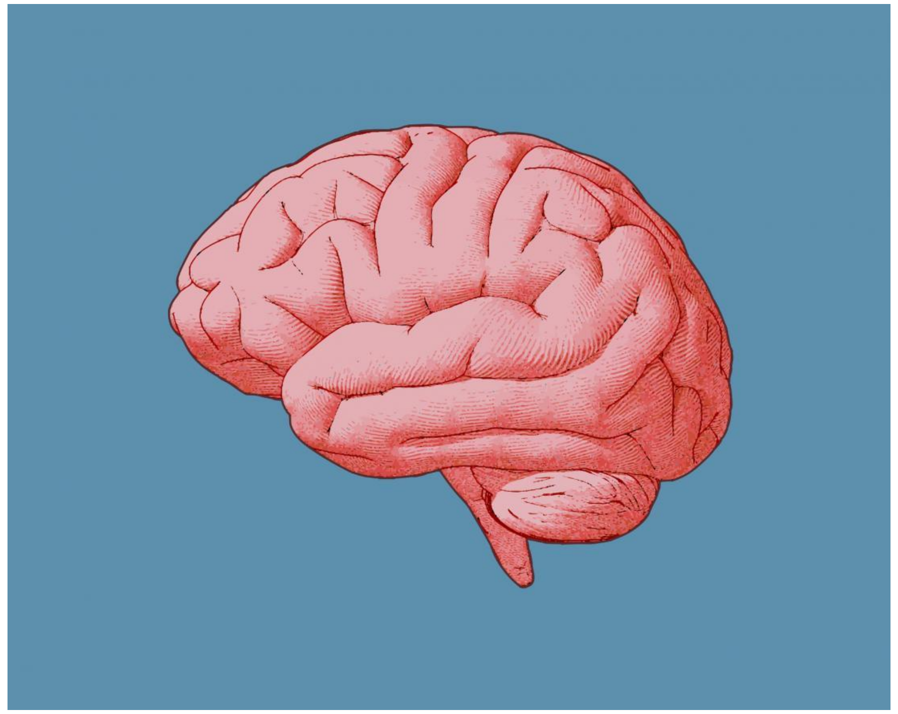
$$\boldsymbol{J} = y_f[N]^T Q_f y_f[N] + \sum_{t=0}^{N} (y[t]^T Q y[t] + u[t]^T R u[t])$$

$$such\ that\ \ \dot{y}[t] = \ f(y[t], u[t])$$

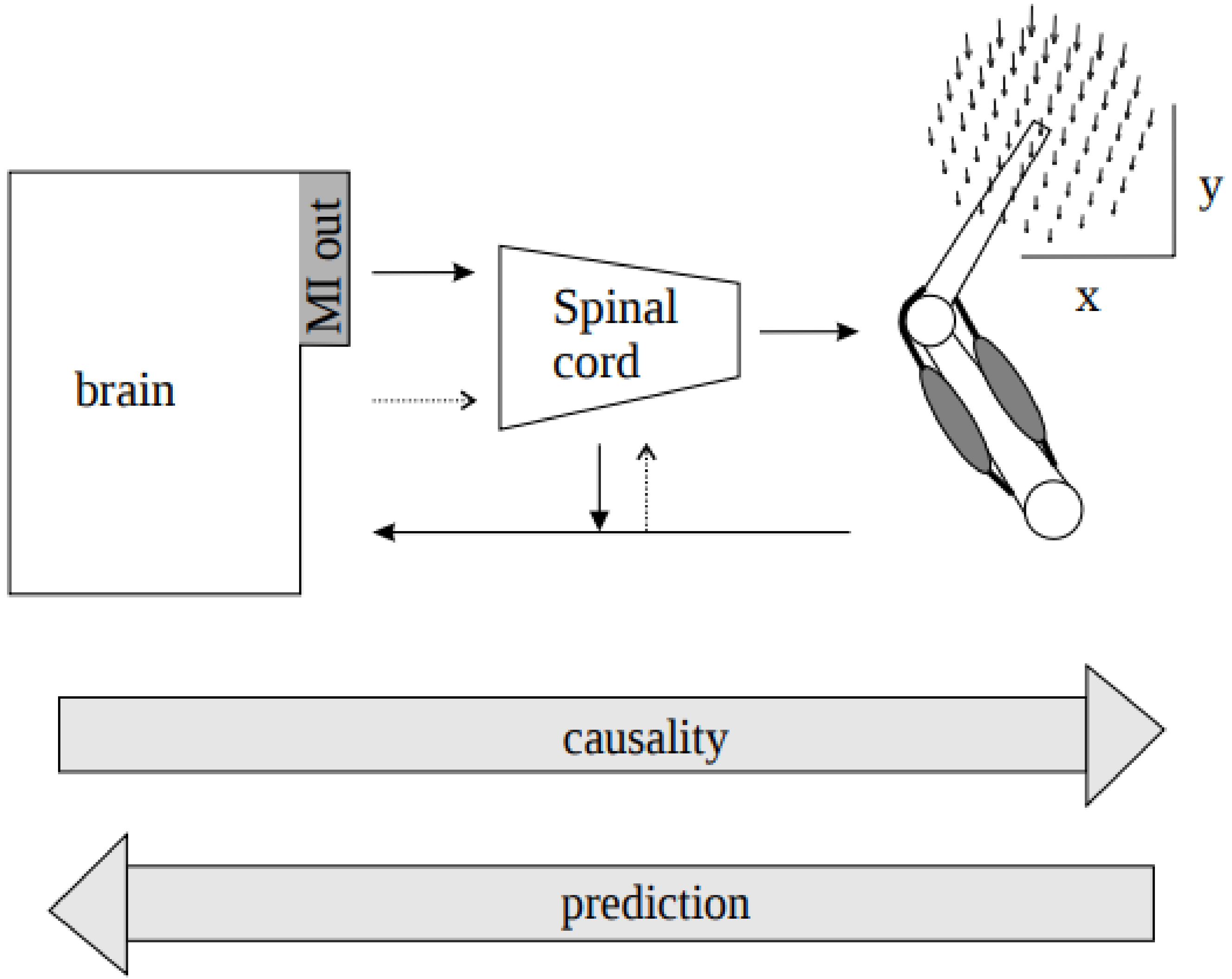
$$u[t = 0{:}\, N] = \pi(y*, y) = arg \min_{\pi} \boldsymbol{J}$$

Neural System Identification

$\pi(y^*, y)$



Goal-driven understanding



$$Uc(t-\Delta) = F^{-1}\mathbf{f}(t) + m\ddot{\mathbf{x}}(t) + b\dot{\mathbf{x}}(t) + k\mathbf{x}(t)$$

M = 1kg, b=10N.s/m, k=50N/m

E. Todorov , Nature neuroscience 2000

- The 'brain' receives sensory feedback, combines it with motor plans, and <u>**somehow 'decides'**</u> what to do next.
- The focus of the model is the causal flow from the MI output through spinal processing, muscle force production and multijoint mechanics to endpoint force.
- First we hypothesize how M1 might be causing movement
- And then any correlations could be explained as emergent properties of the causal flow

Body dynamics determines the neural encoding

Problem with a simple feedback based model

1. <u>Sensorimotor delays</u>

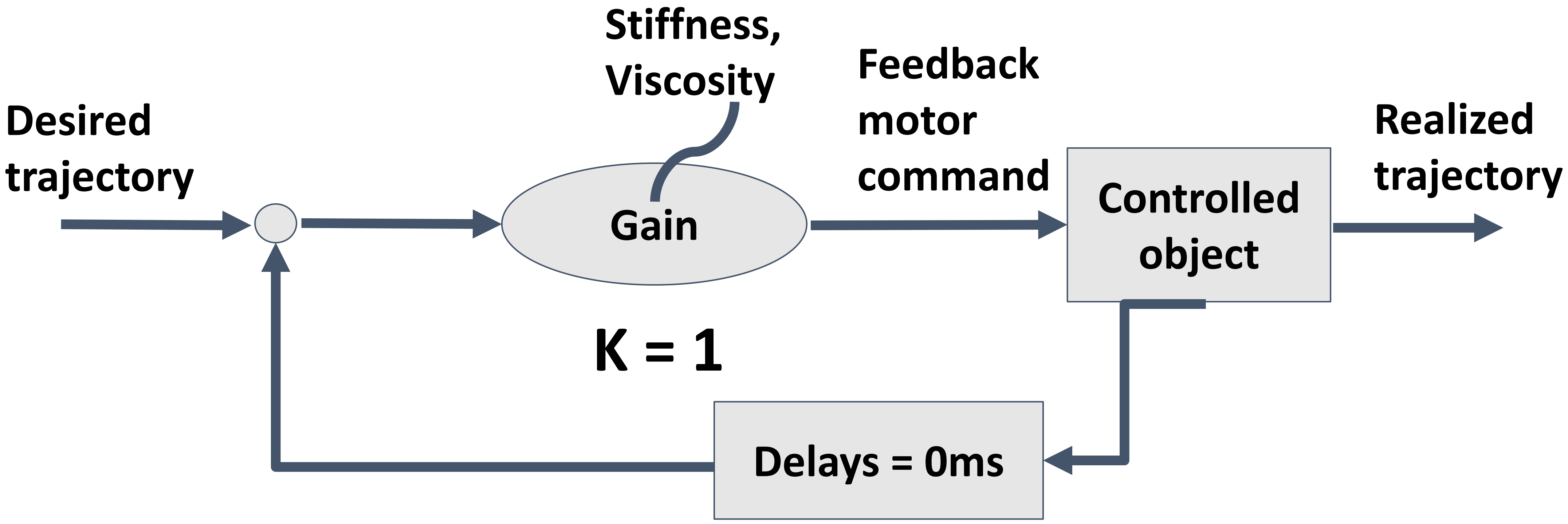
2. Stochastic process

3. Redundancies

Let us consider the problem posed by sensorimotor delays in animal movement control in detail, and for now ignore the other issues

A simple example of the effect of feedback delays

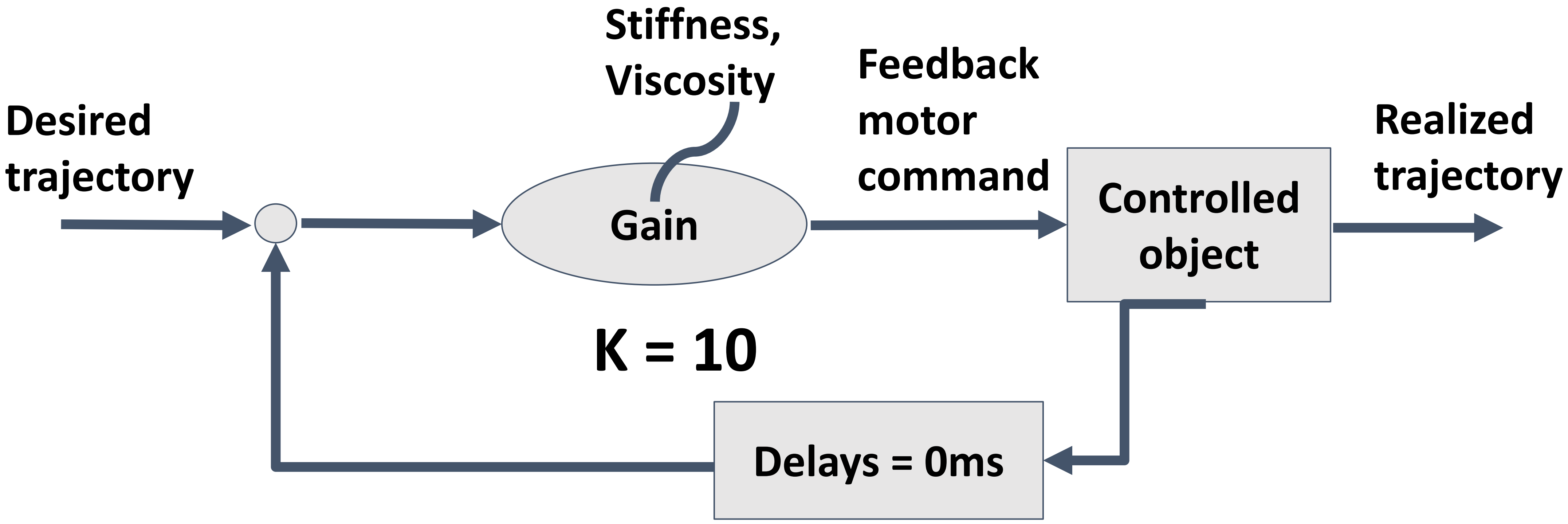
Consider a simple feedback control loop
with proportional feedback gain



Low gain + No delay

A simple example of the effect of feedback delays

Consider a simple feedback control loop
with proportional feedback gain



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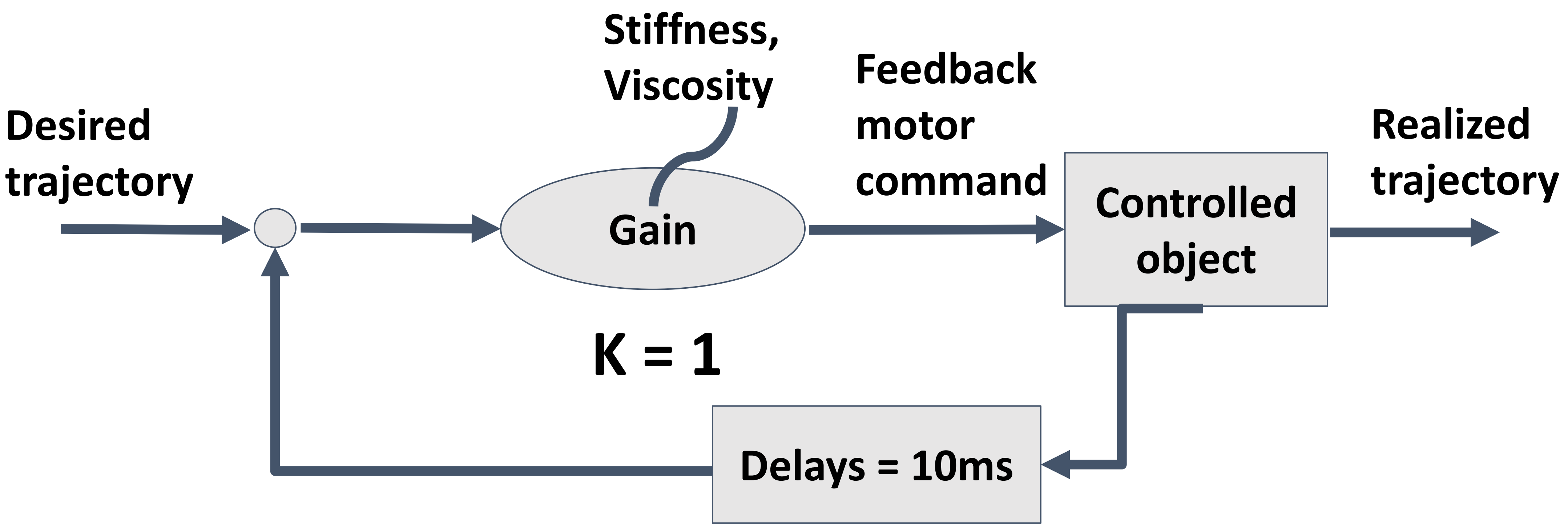

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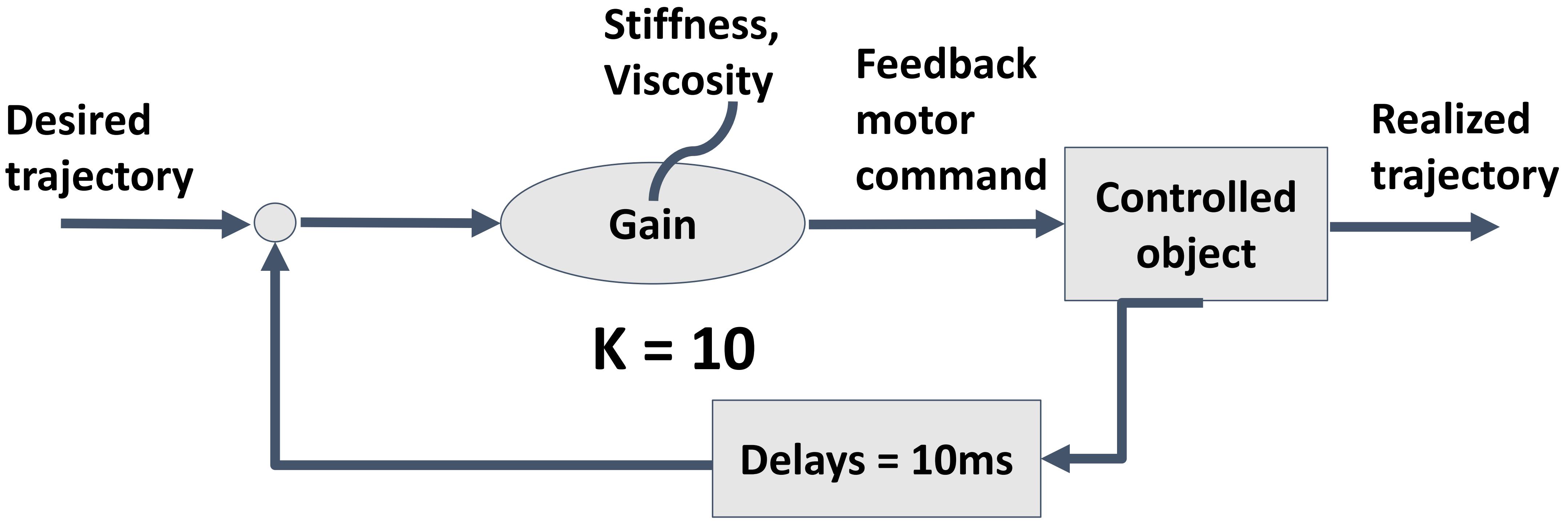


High gain + delay

How does the brain deal with delayed sensory feedback?

Two possibilities

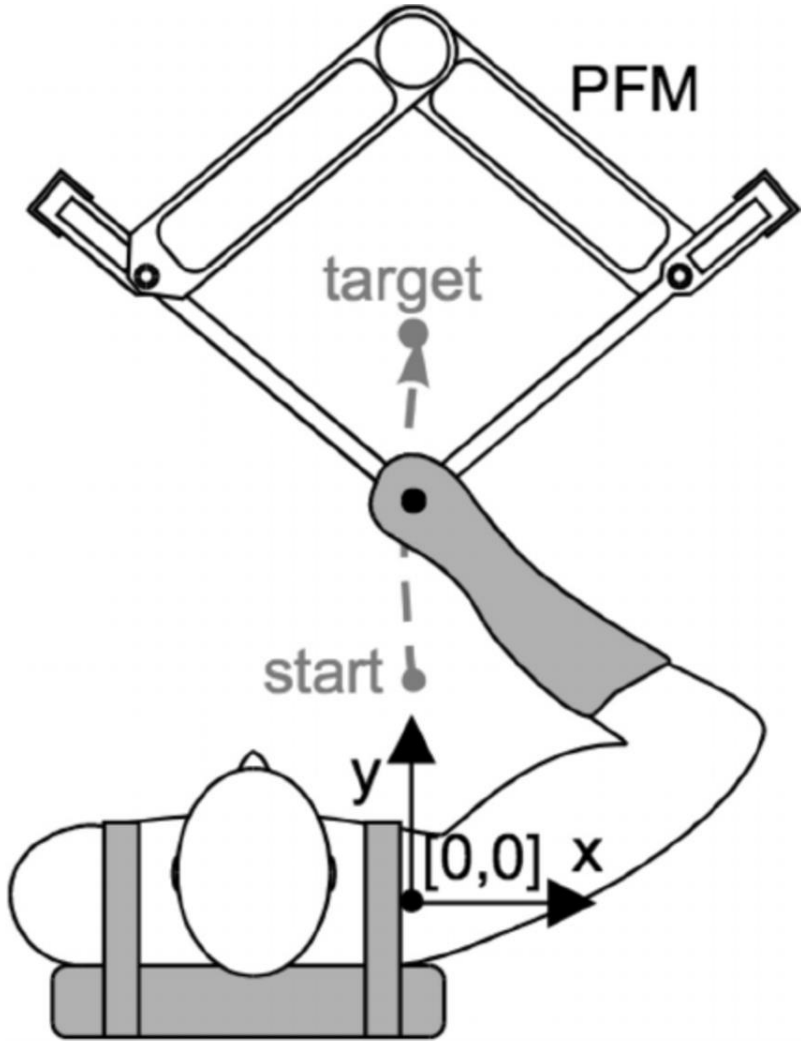
1. Equilibrium point control - Simple brain command & complex spring-like muscle control

2. Internal model based control - Predictive brain command & simple muscle control

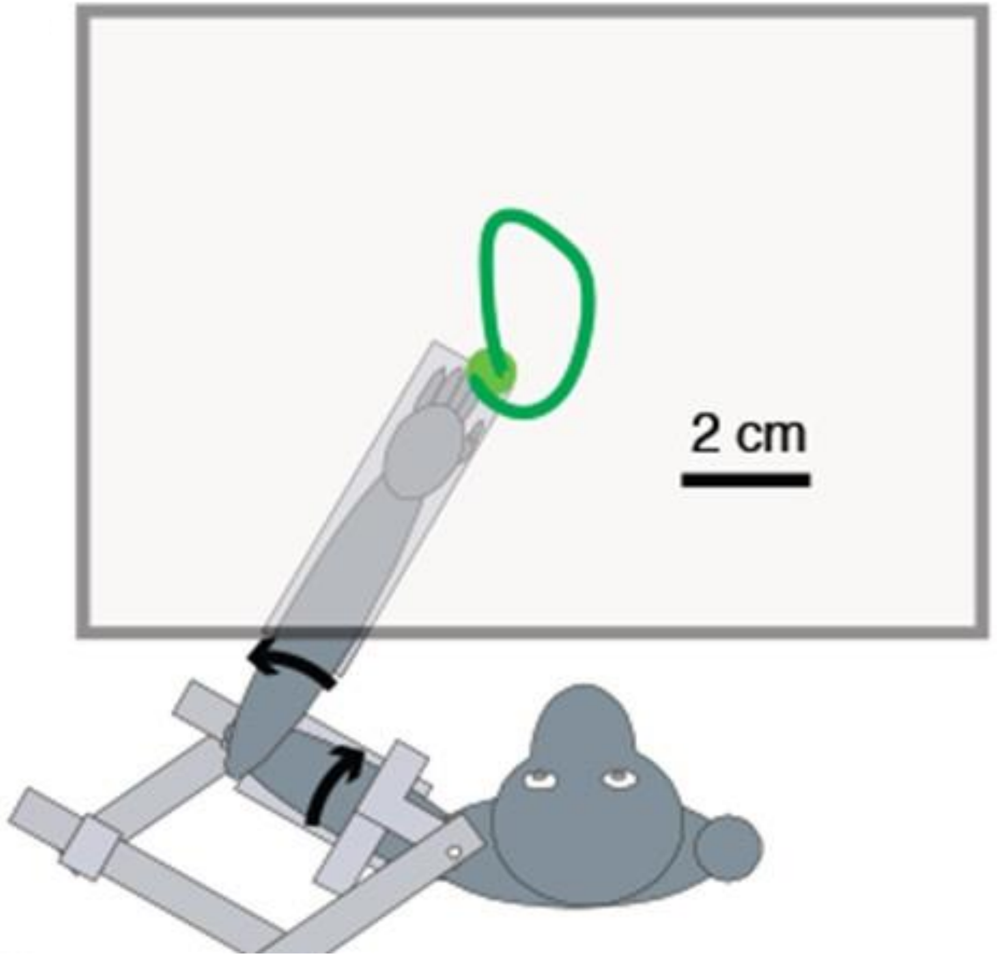
As simulated earlier, the effect of delays in feedback is more pertinent when we have to compensate for the error in movement

So we consider situations where we have to successfully deal with errors caused by mechanical/visual disturbances

Feedback Perturbation experiments

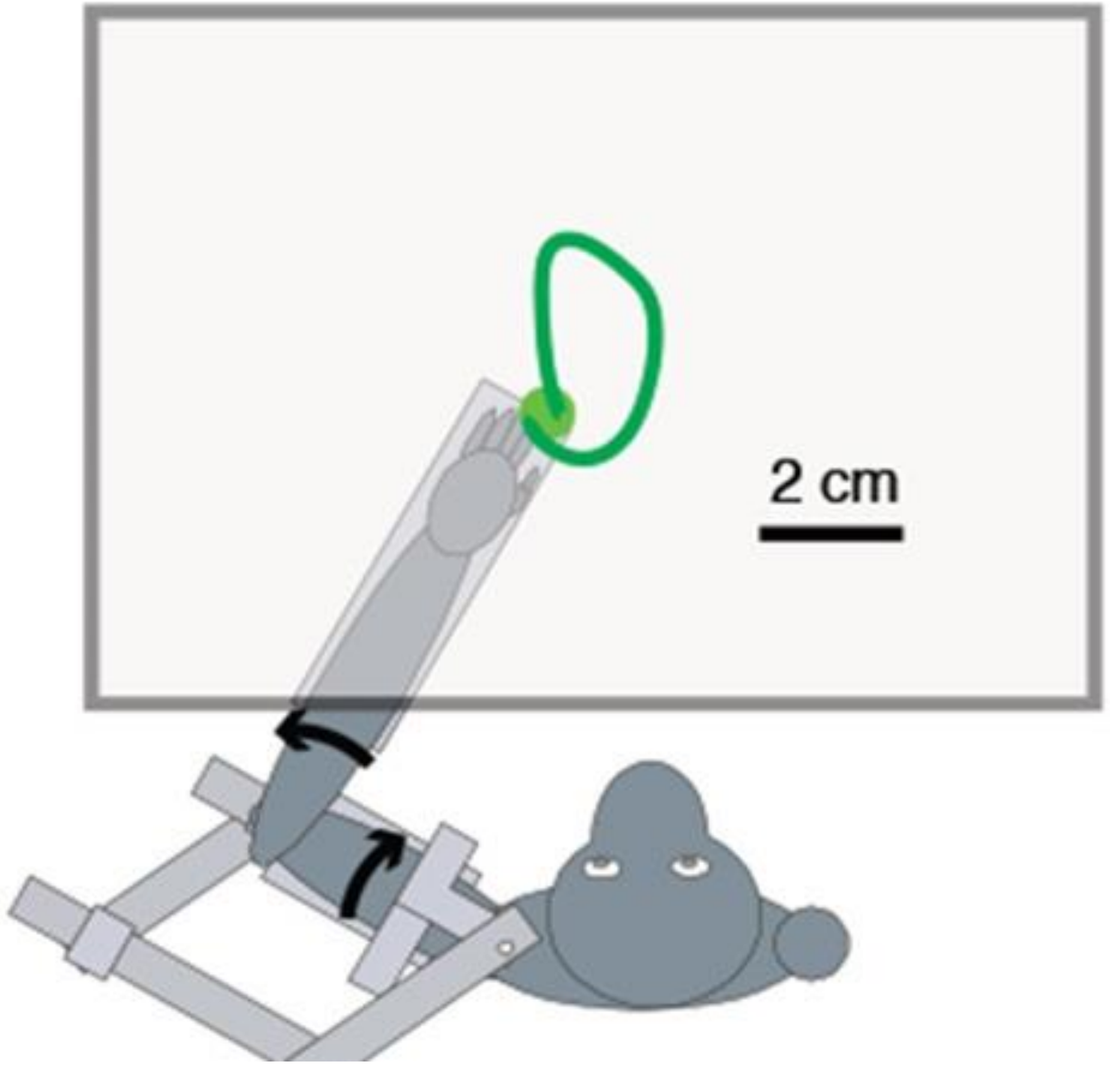


Reaching under perturbations



Posture control against mechanical loads

EMG responses to perturbation



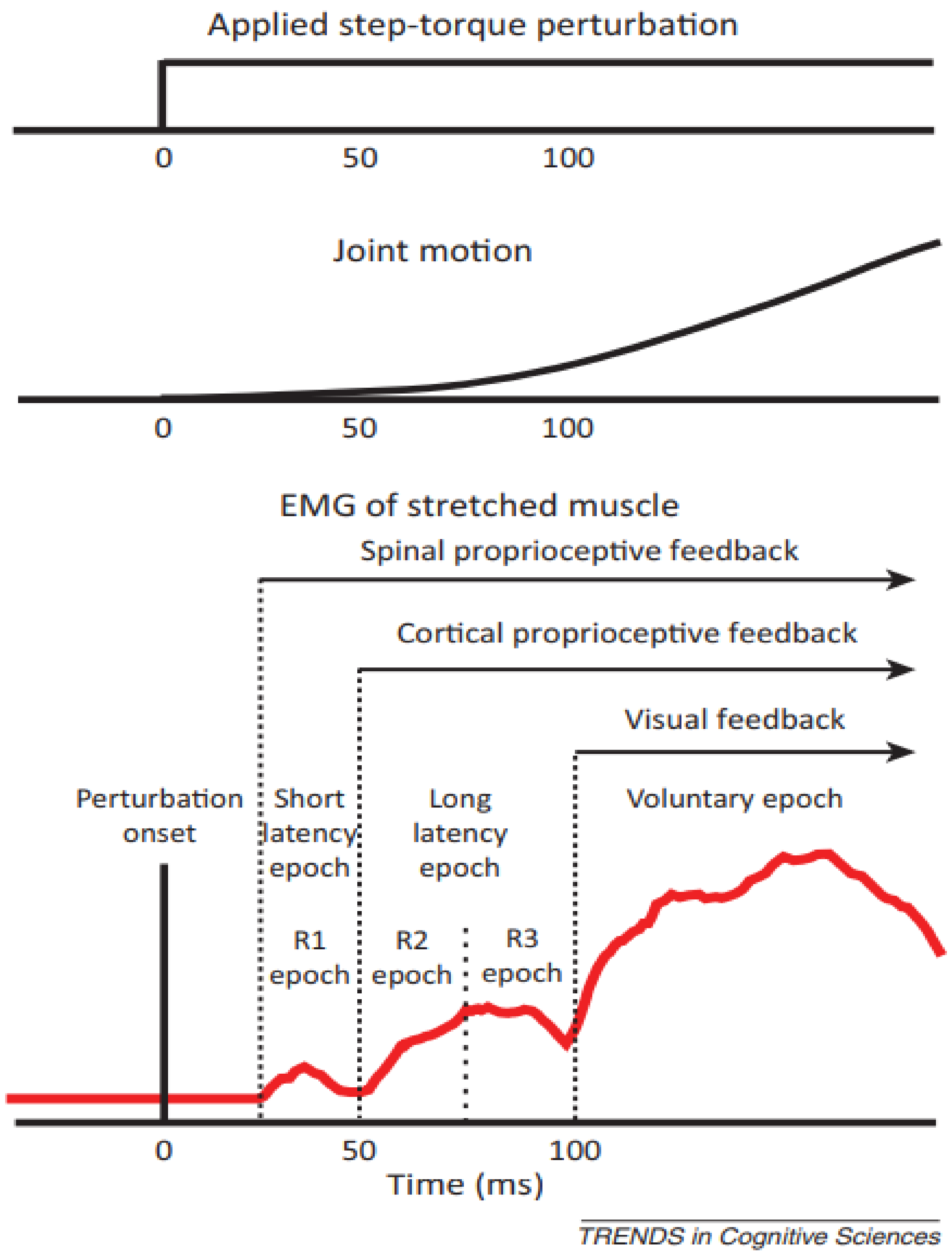
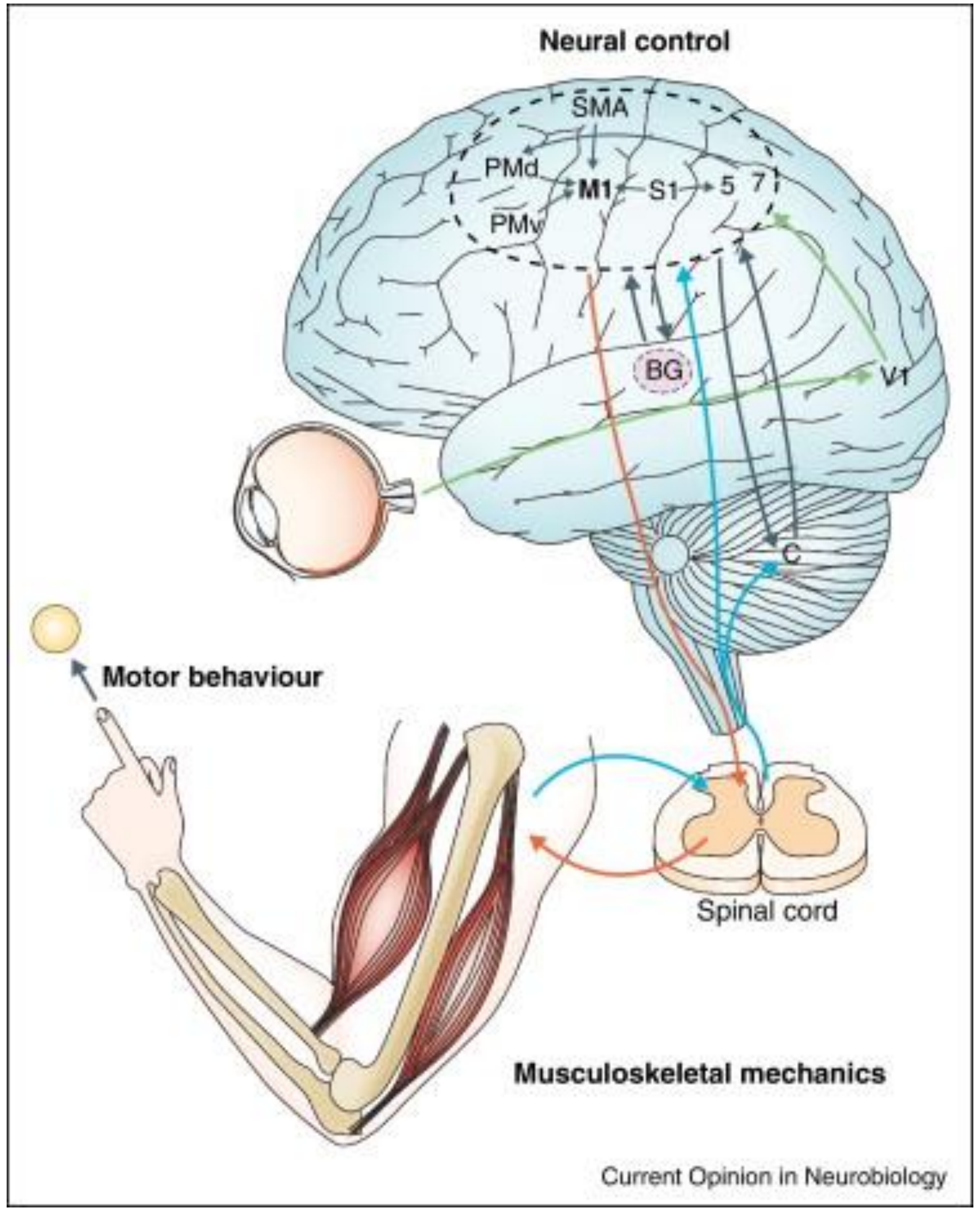
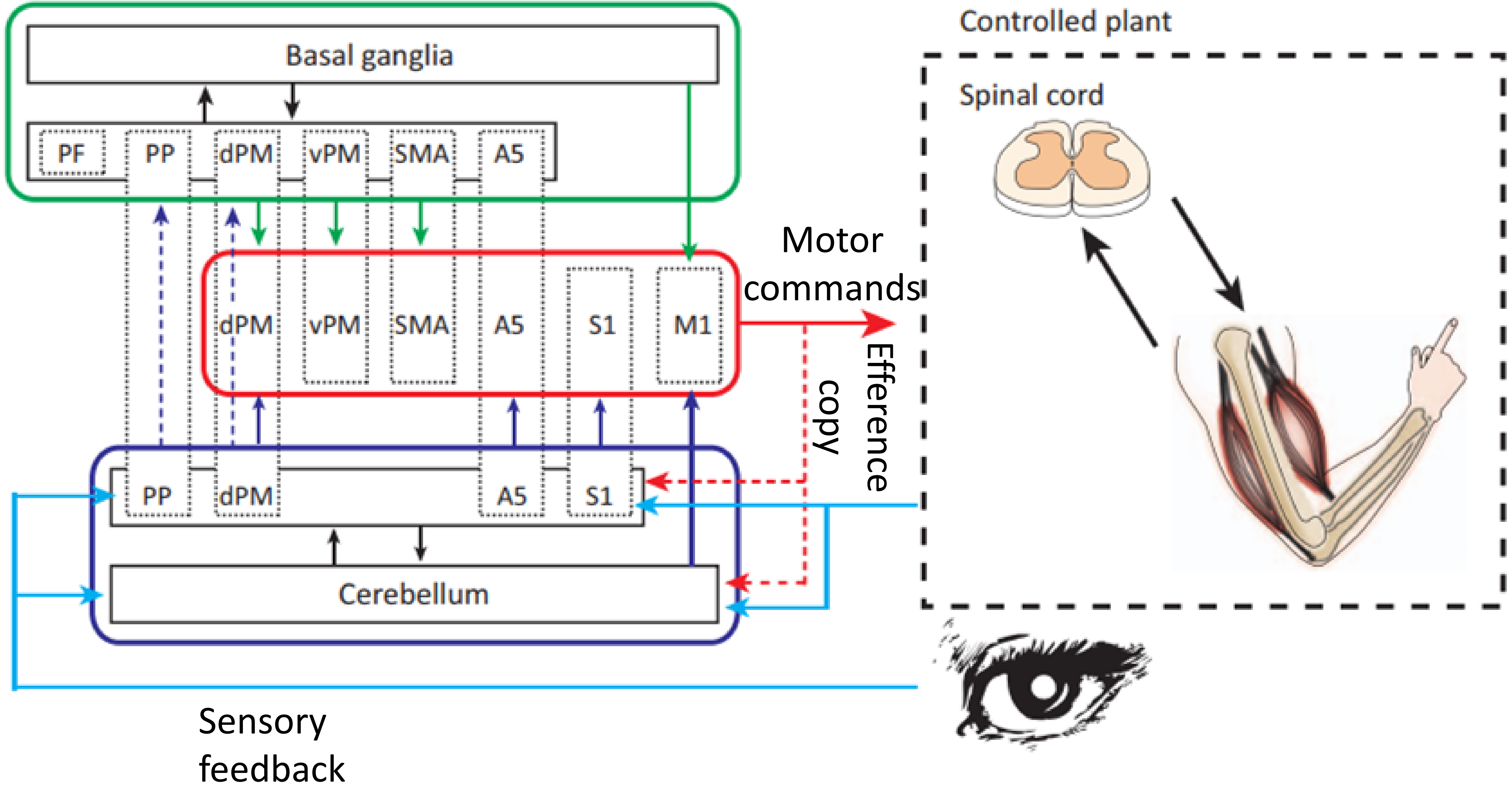


Figure I. Mechanical perturbation applied to a joint causes joint motion and a multiphasic electromyographic response in stretched muscles.

The majority of the EMG response is observed during the long-latency epoch. Hence ascertaining that spinal processing plays limited role during the stretch control

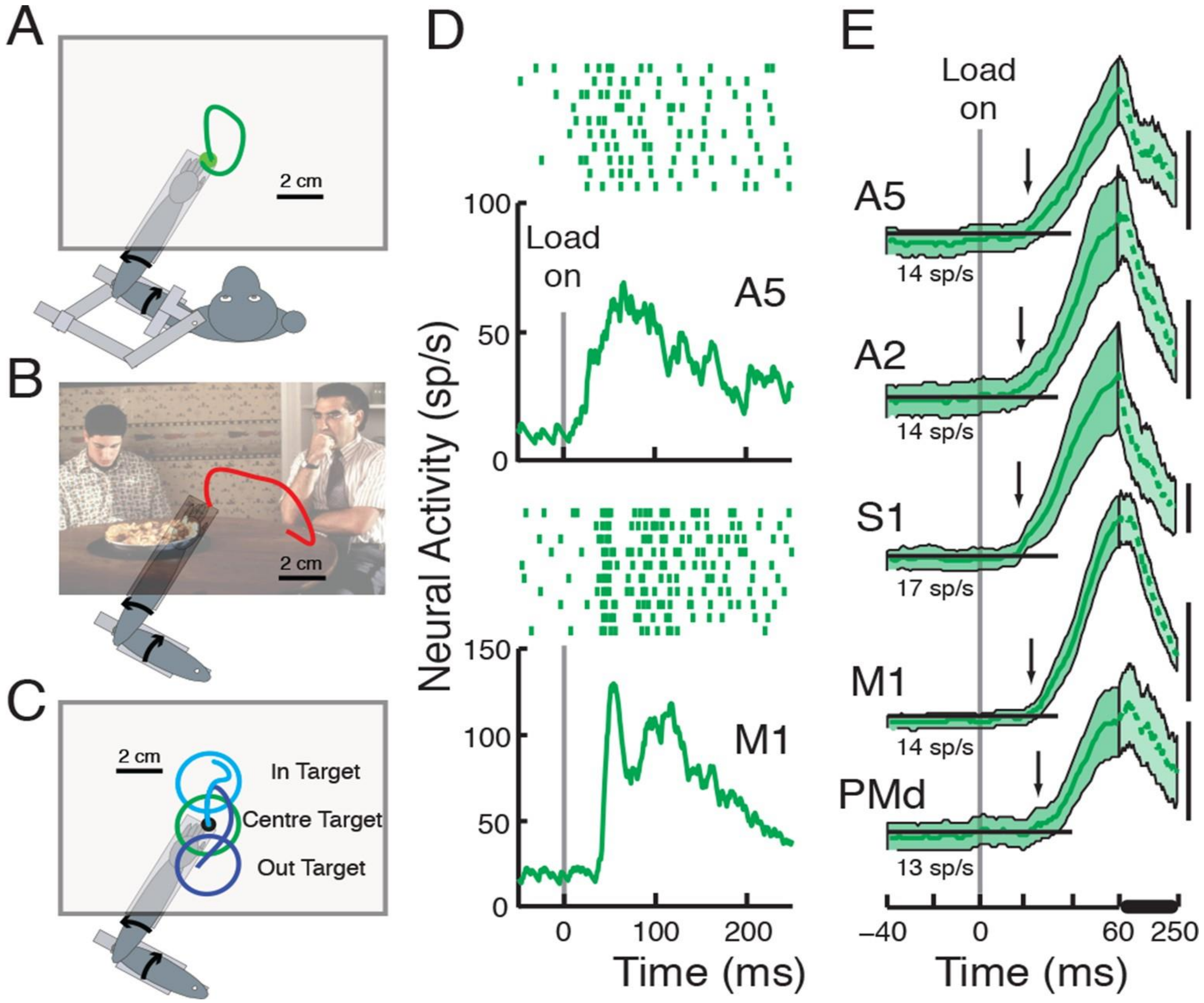
Brain receives large amount of sensory projections





Difficult to interpret how the brain motor areas can have a simpler role in online movement control when it receives very dense sensory projections

Cerebral EEG response to mechanical loads - supports a complex brain signal hypothesis



Different brain regions fire vigorously response to mechanical perturbations

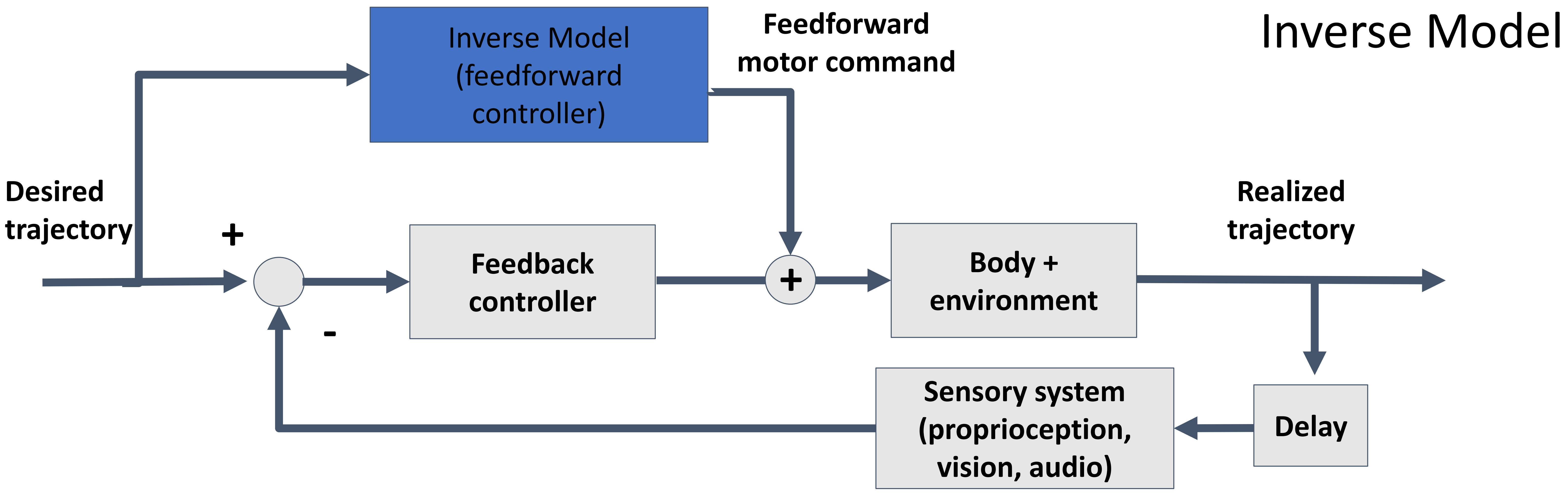
This argues against a lesser involvement of cortical regions and hence against the equilibrium-point hypothesis

Some kind of internal model/estimation about the state of the body and the world must be actively helping online motor control

Internal models can be used to deal with delays and disturbances

Two types of internal models

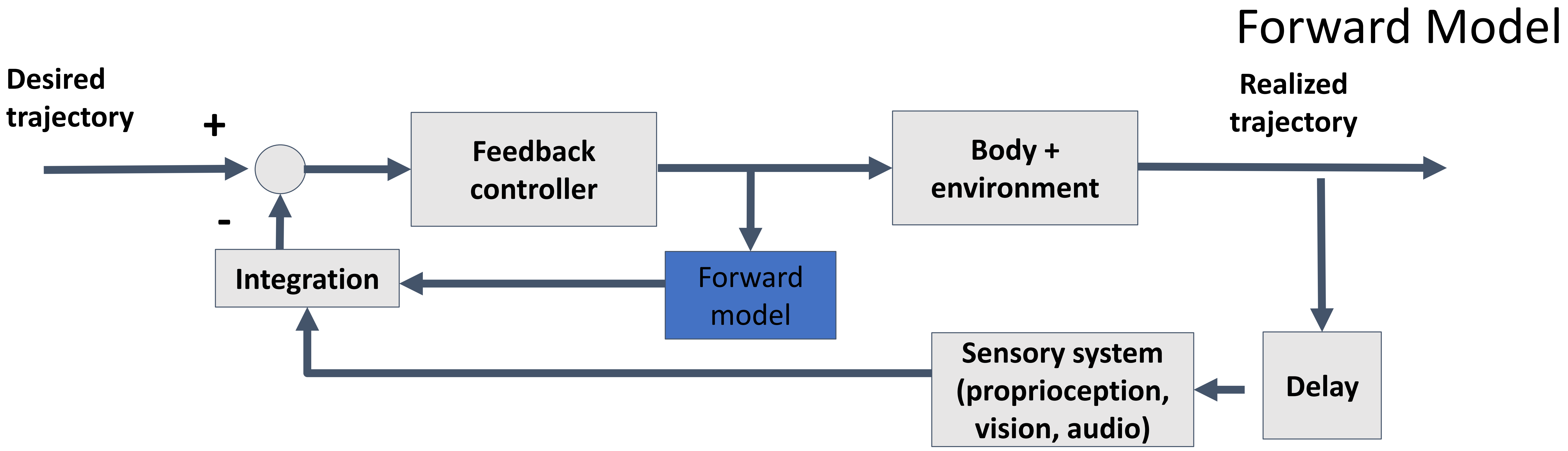
<u>Inverse model</u> – Takes the desired state trajectory as input and produces the muscle/motor commands that are necessary to move the body accordingly



Internal models can be used to deal with delays and disturbances

Two types of internal models

Forward model – takes the copy of muscle commands that the body receives from motor centres as input and generates the prediction of the current/future state of the body



Internal models can be used to deal with delays and disturbances

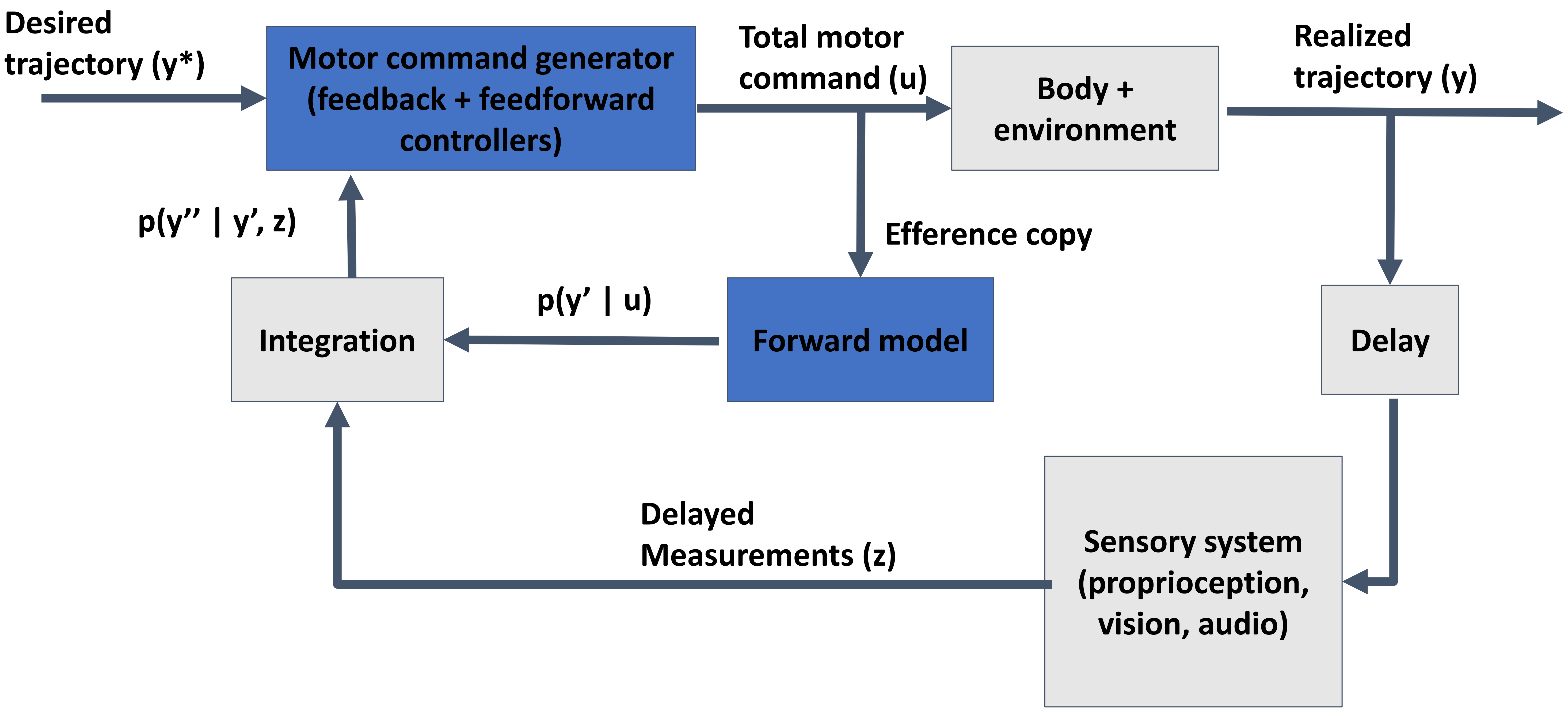
Two types of internal models

<u>Forward model</u>

<u>Inverse model</u>

Further, an **integrator** region should continuously integrate the predictions of the internal models with the respective delayed sensory feedback and produce an estimate of the most likely body state.

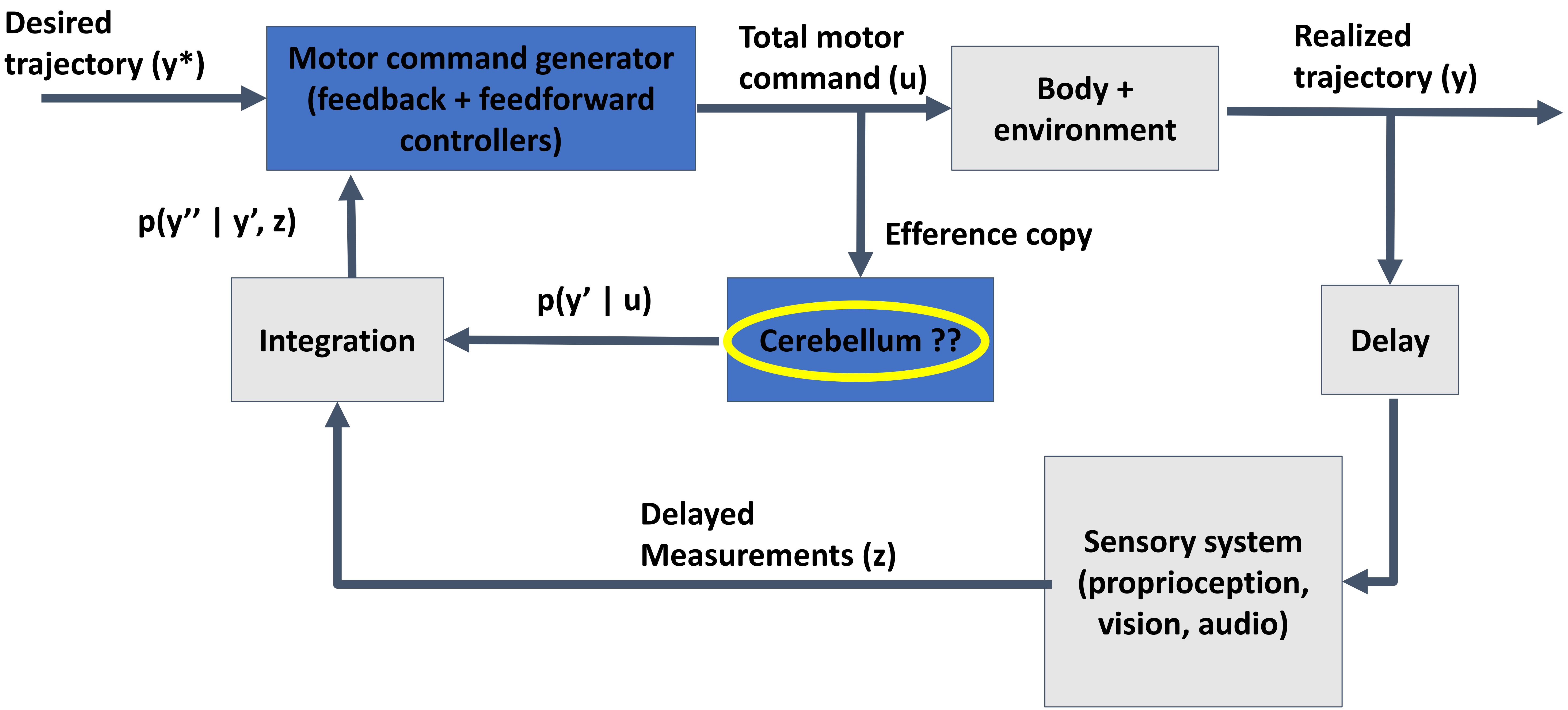
The summary of sensorimotor control with delays and variability



p(y' | u) - likelihood/internal-belief of the original state 'y'

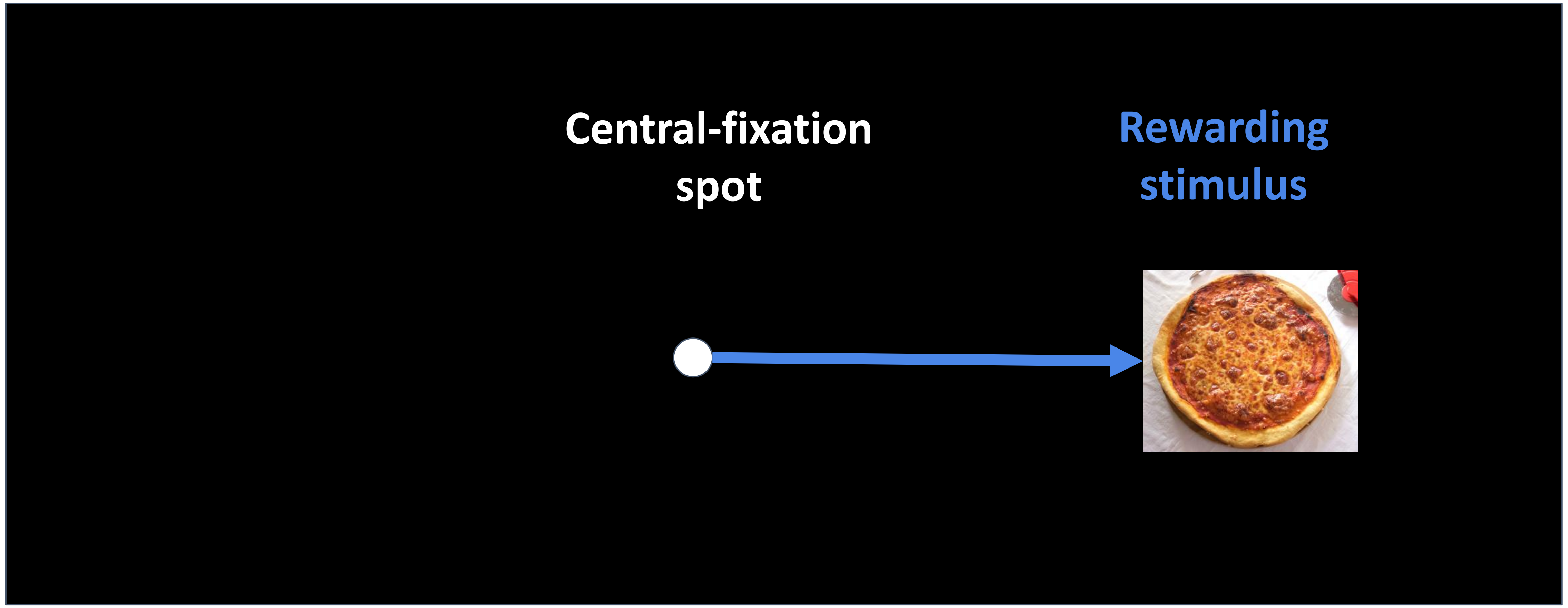
p(y'' | y', z) - posterior estimate of the original state 'y'

The summary of neural sensorimotor control



The brain region that houses internal models should display <u>1. movement prediction</u> and <u>2. plasticity</u>

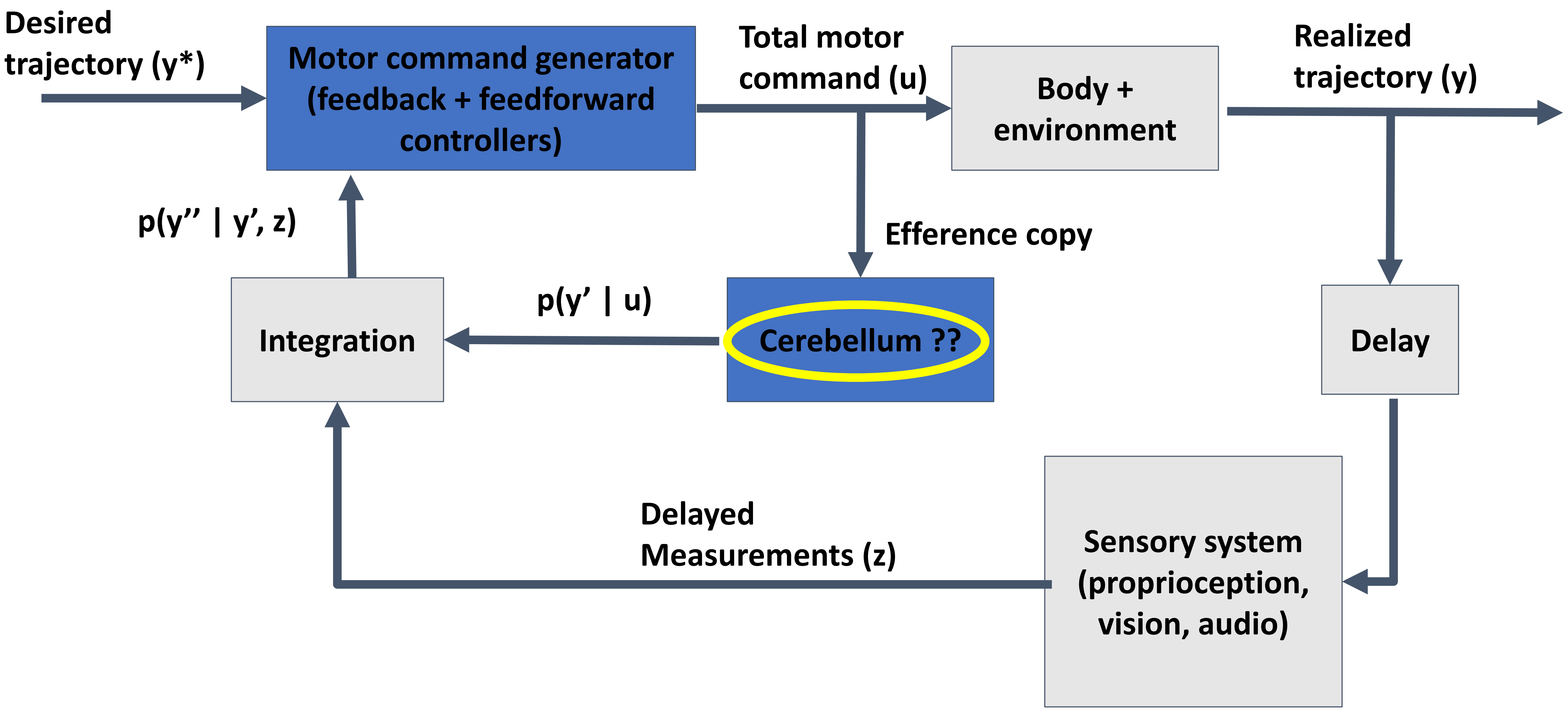
Evidence of cerebellum as forward model – saccadic eye movements



- Saccades are ballistic eye movements that can reach speeds 500-1000 deg/sec, and take place within 20-200 milli-seconds

- Sensory feedback is completely absent during the movement

Feedback effects can be neglected during saccades



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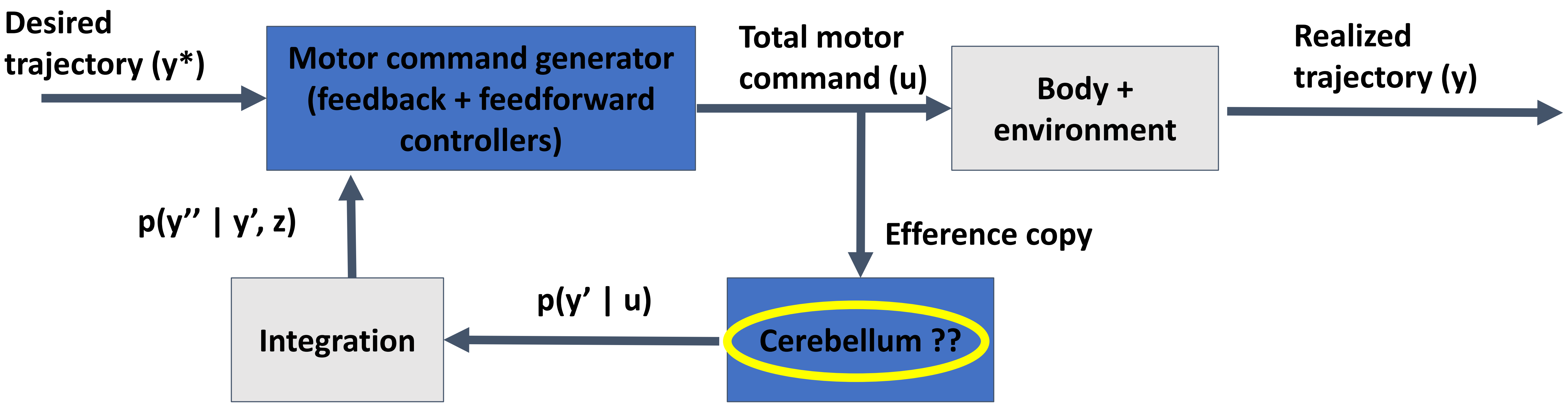
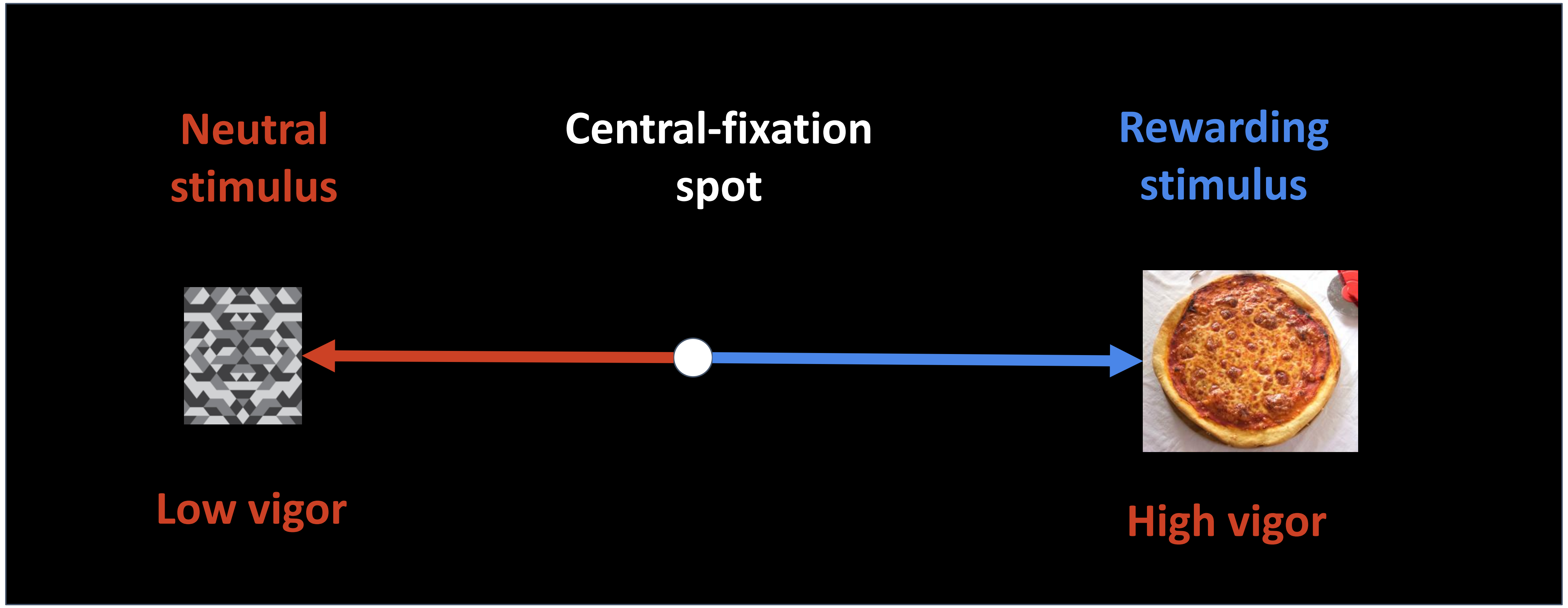
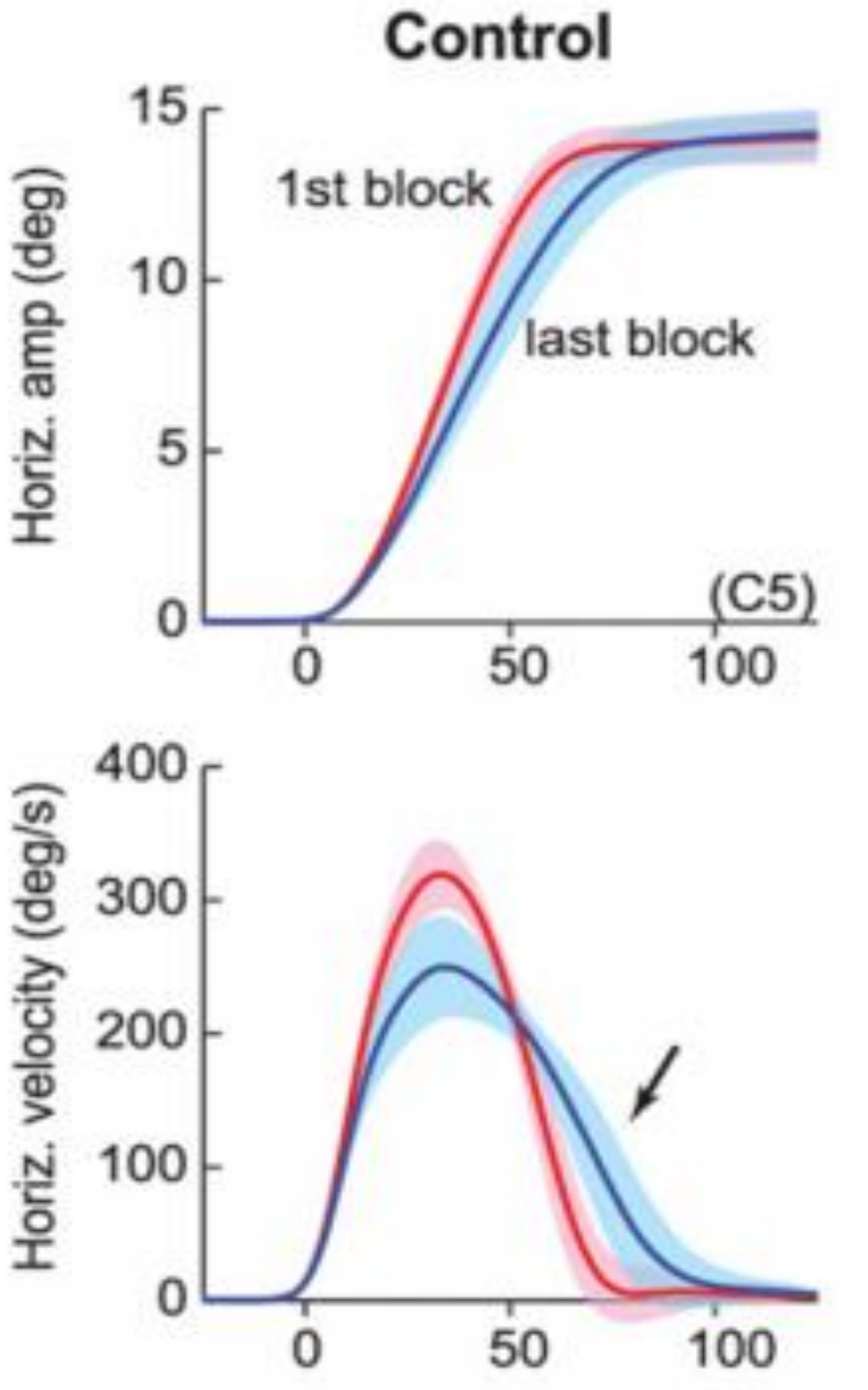


Movements to similar distances are highly variable

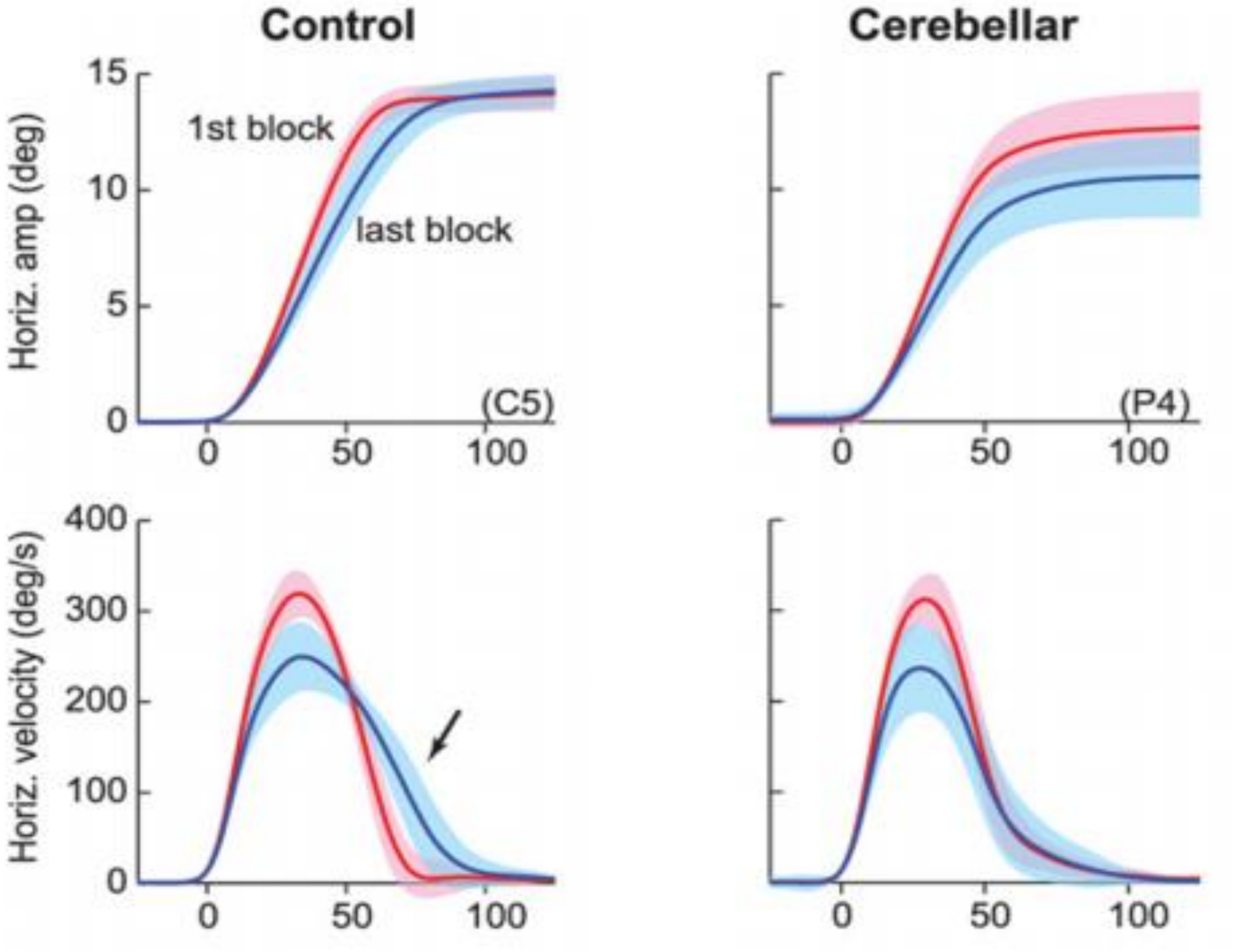


High vigor means low reaction-time and high velocity, which indicates a high motivation to reach the target

Brain lesion studies / abnormalities



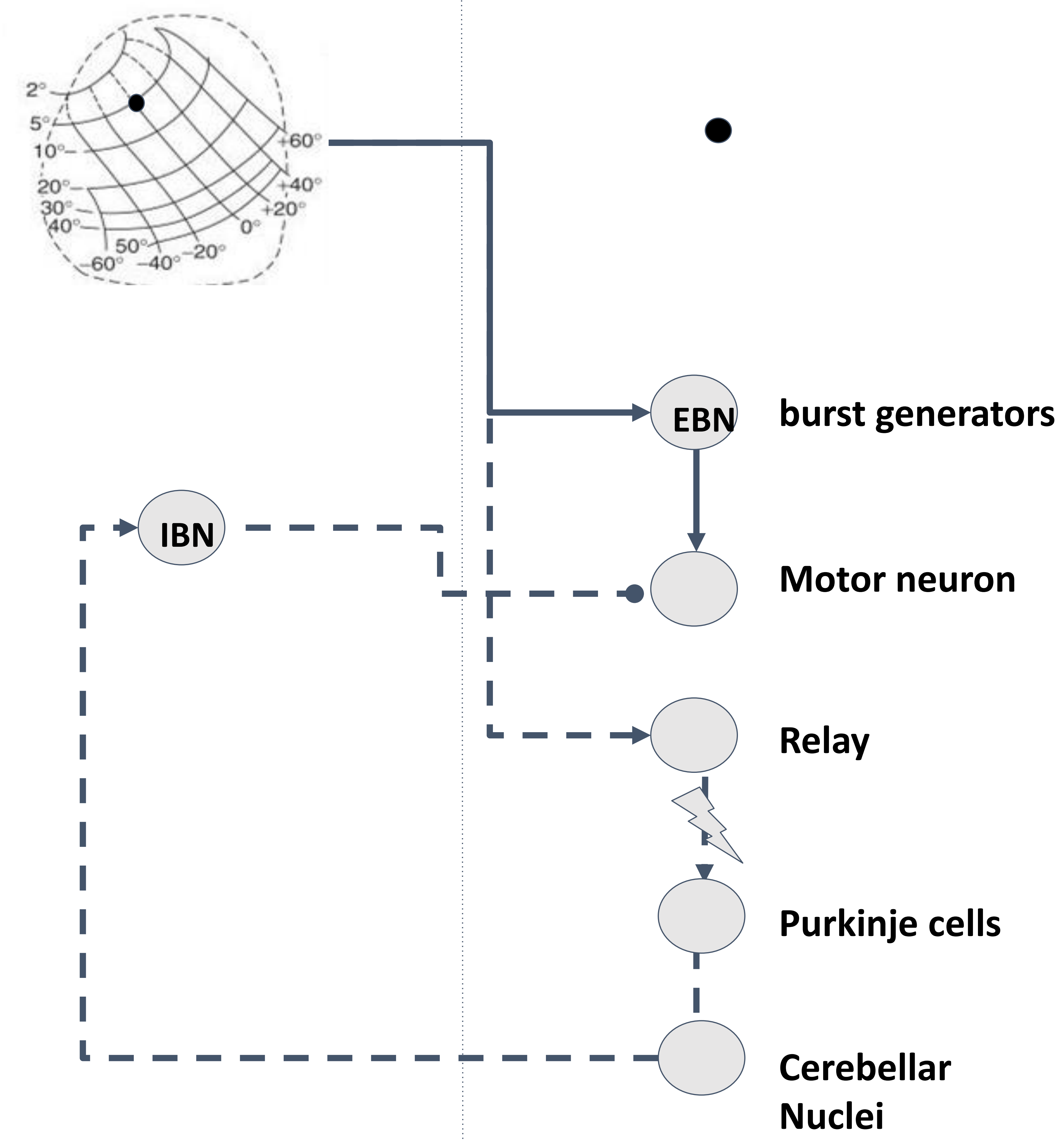
Brain lesion studies / abnormalities



Xu-Wilson & Reza Shadmehr, J.Neuro 2009

Summary

- Saccades are faster to more valuable stimuli
- Stimulus value acts as a source of variability during saccades
- In cerebellar patients the value-induced variability in the motor commands is poorly compensated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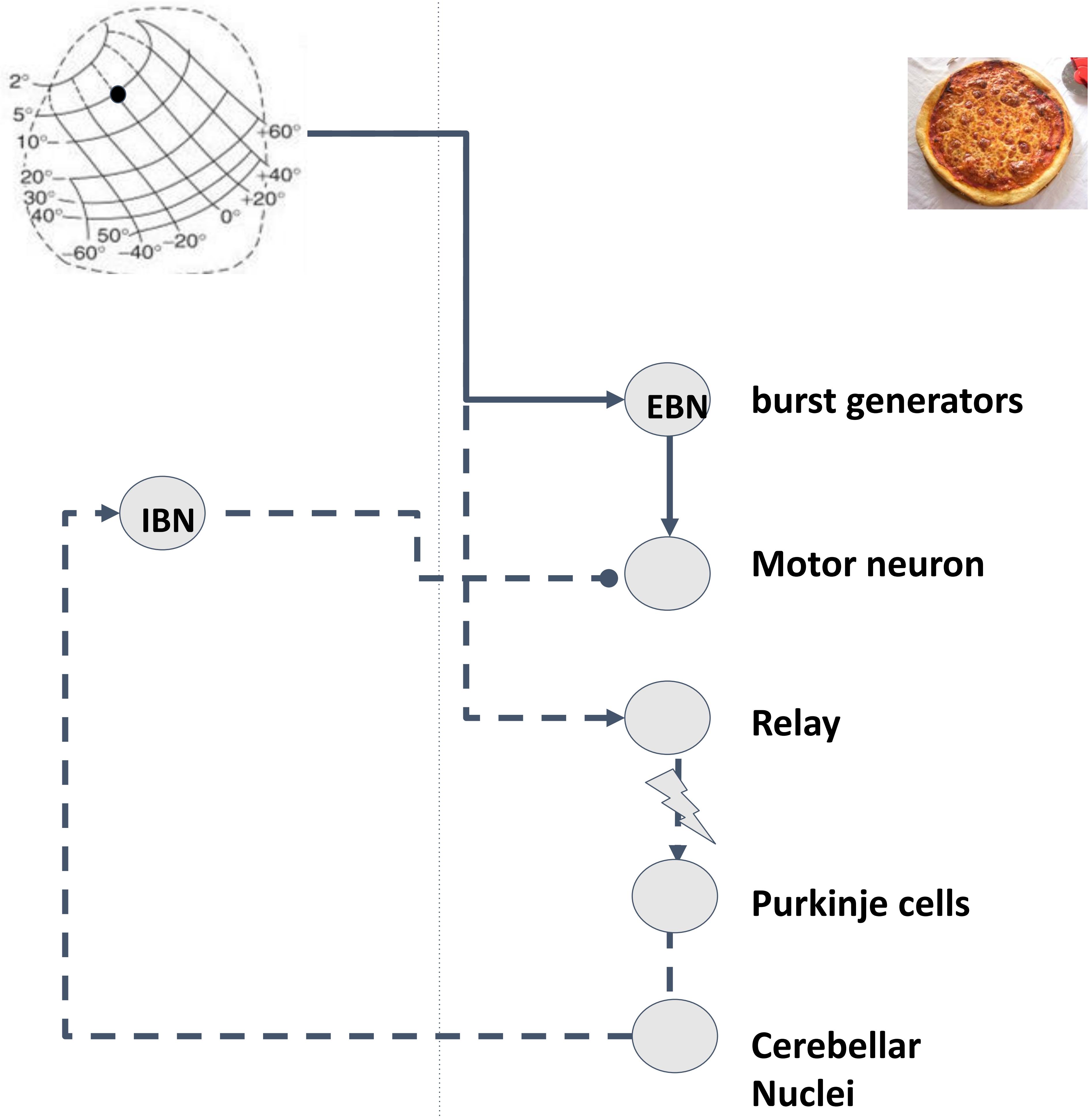
burst generators
IBN
Motor neuron
Relay
Purkinje cells
Cerebellar
Nuclei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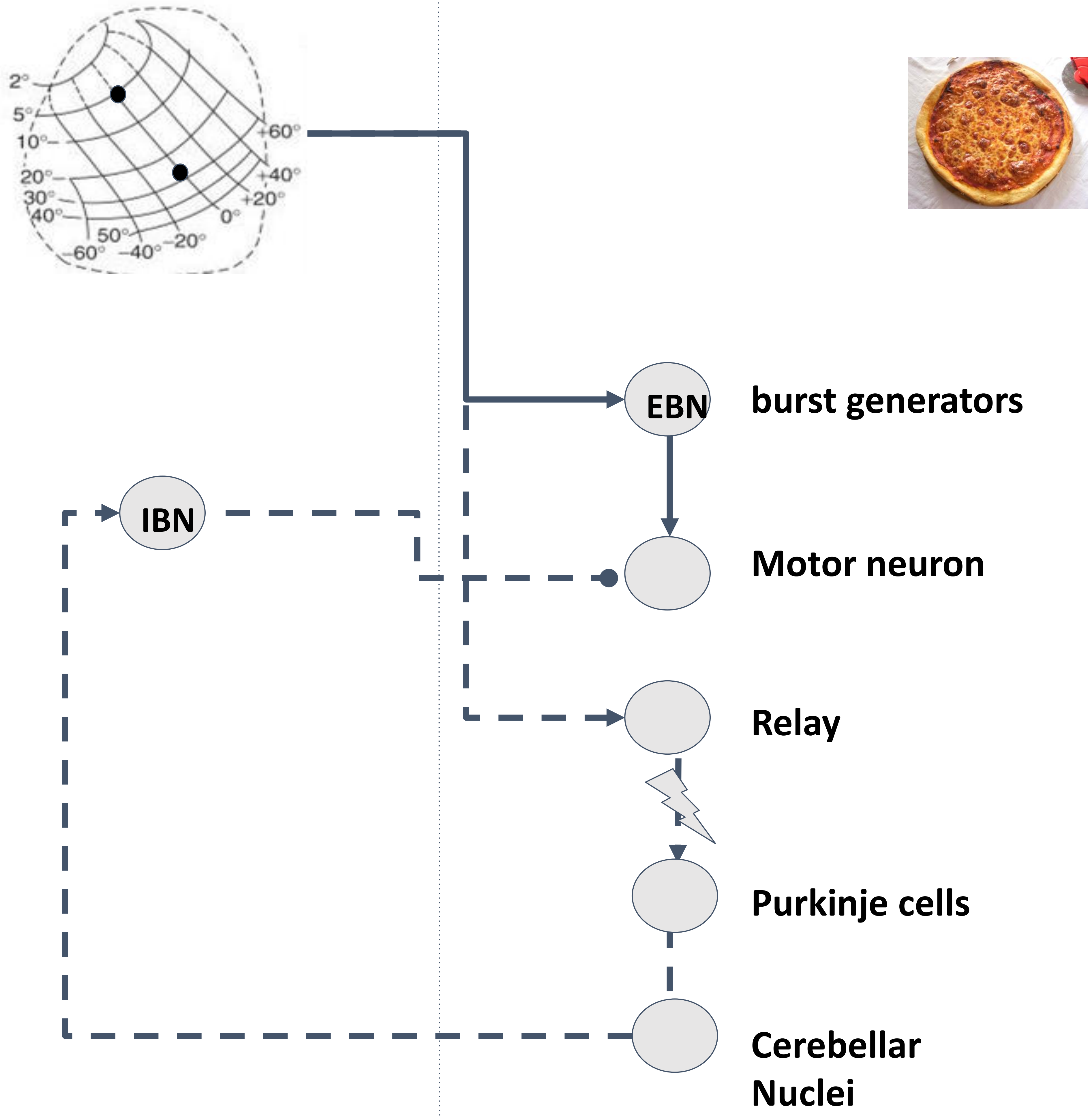
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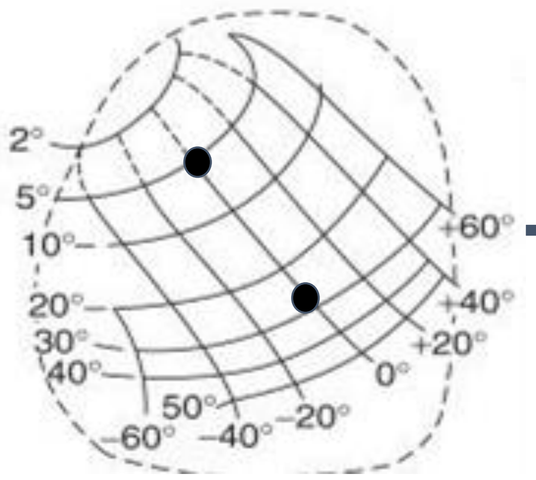
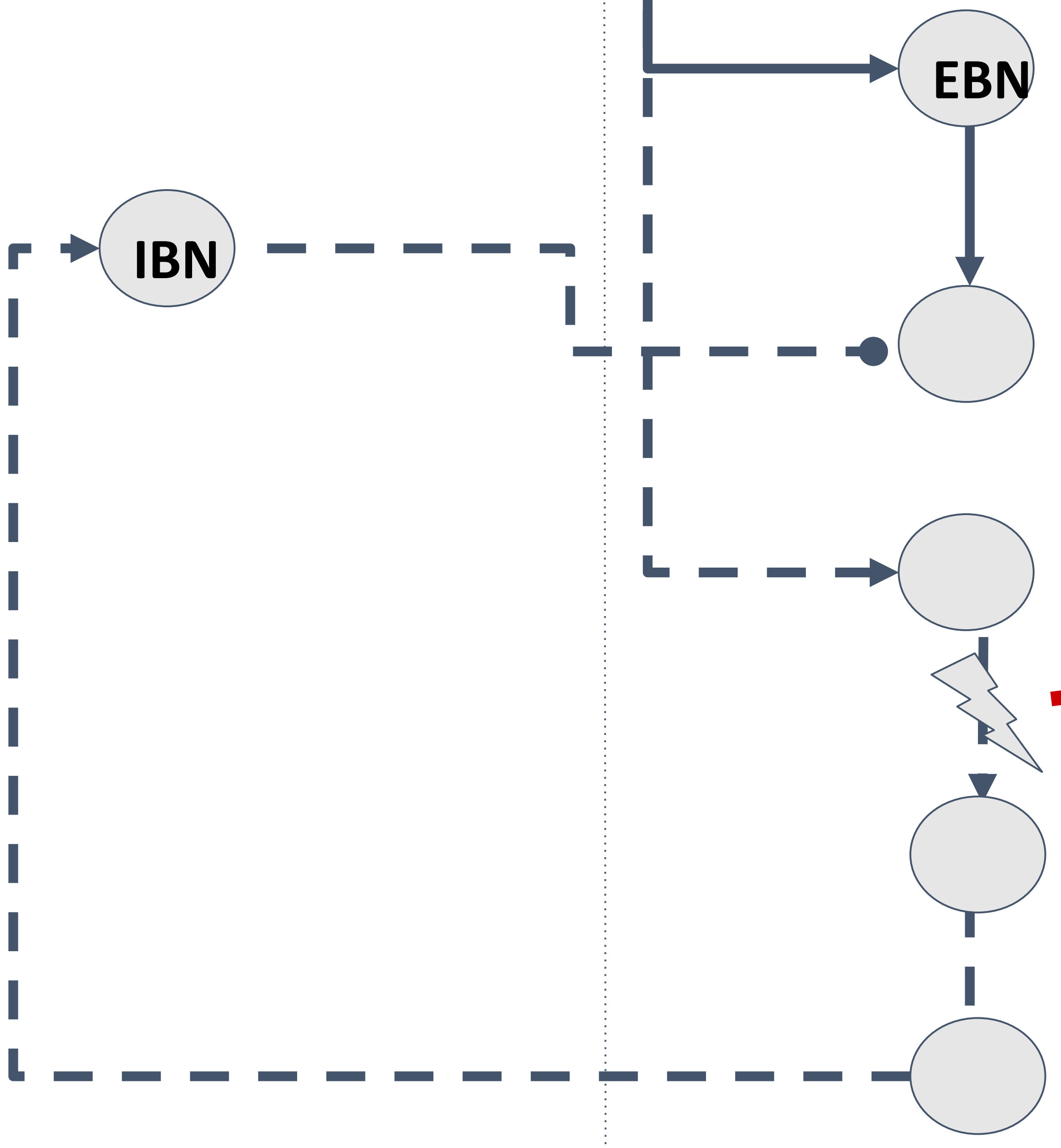




burst generators

Motor neuron

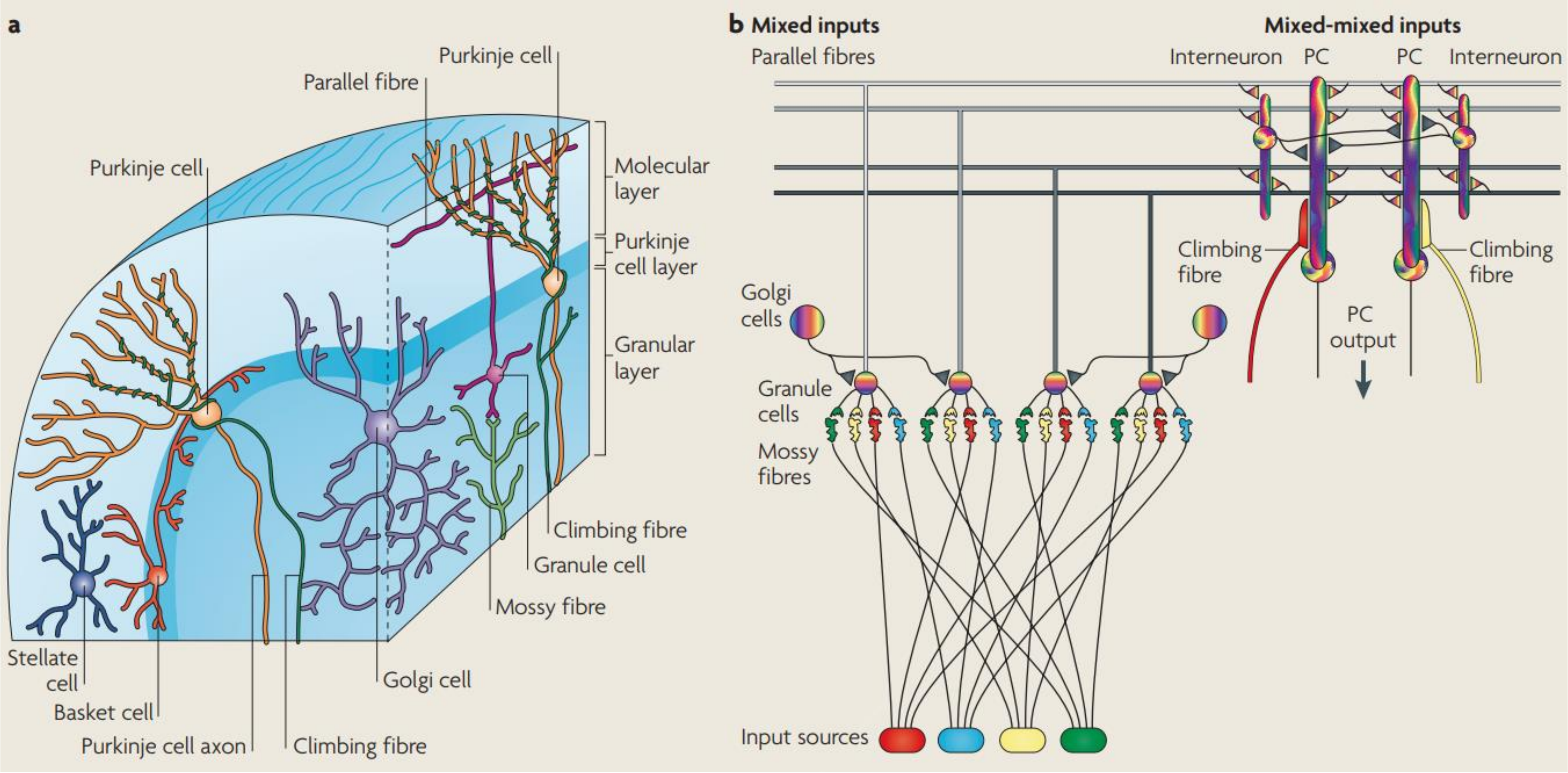
Relay

What is cerebellum computing?

Purkinje cells

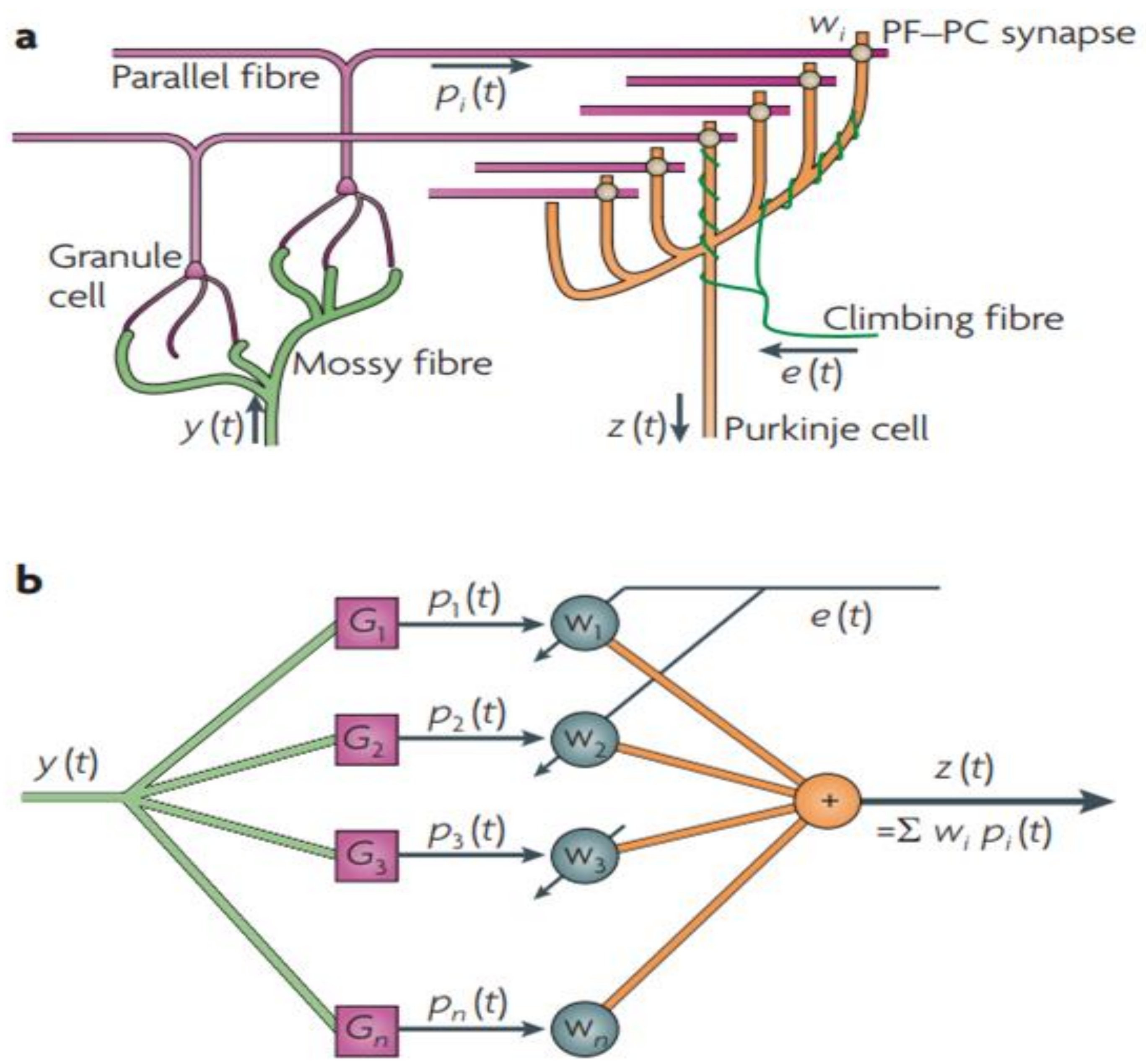
Cerebellar Nuclei

The computational circuit of cerebellum



P.Dean et al., Nature reviews neuroscience 2010

The computational circuit of cerebellum - adaptive filter approximation



How is the output adjusted to produce desired response??

Organization

Repetitive crystal like

Operation

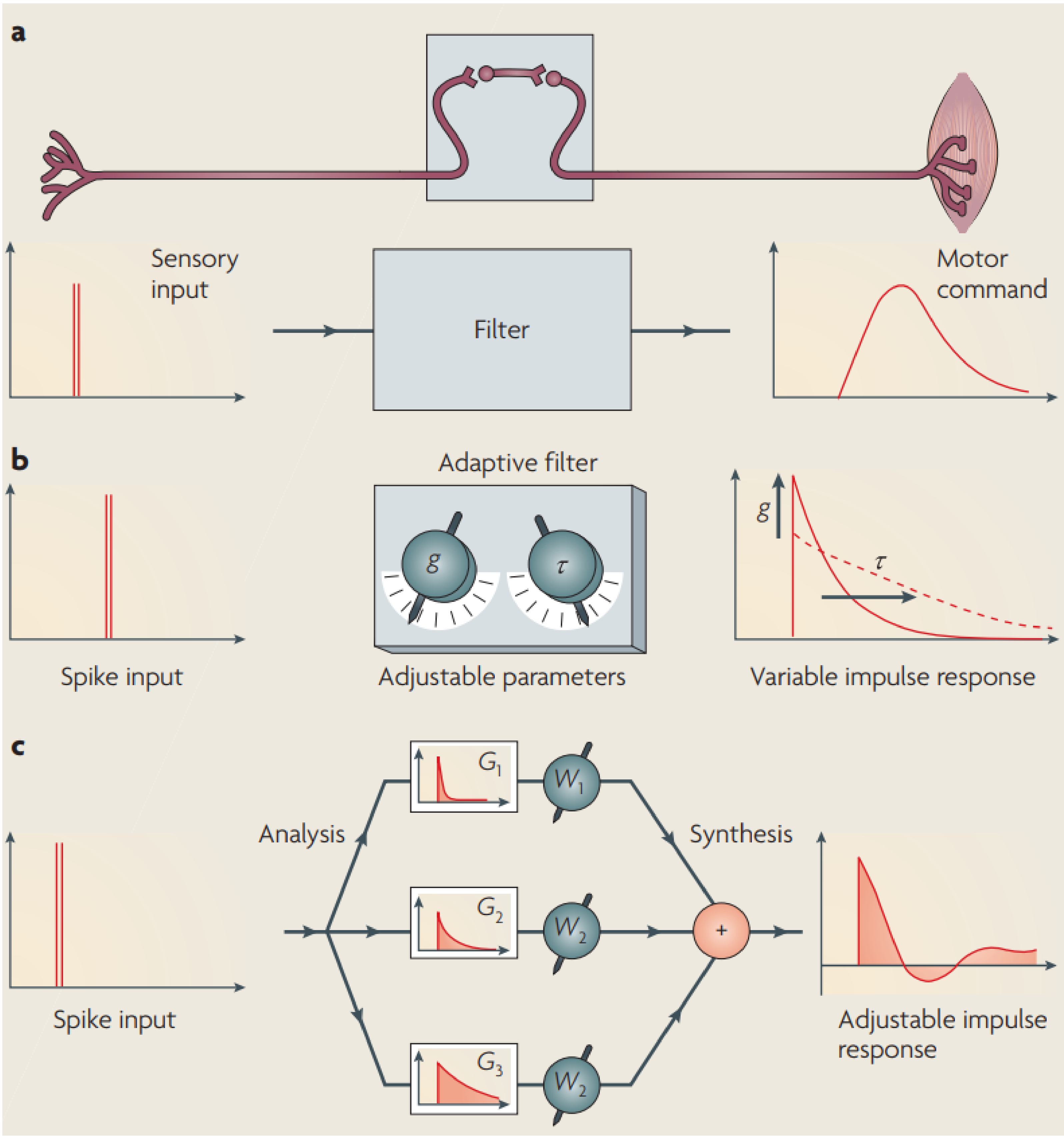
1.Receives input information 'y(t)'

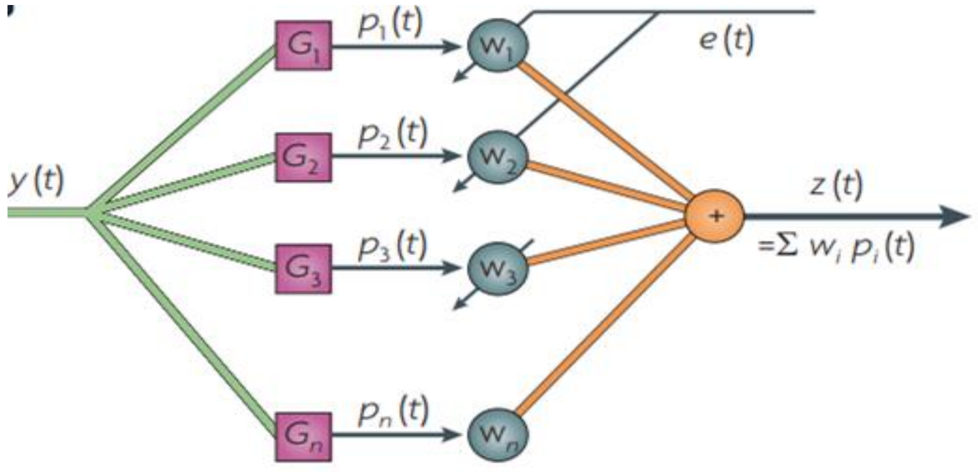
2. Generates a high-dimensional representation p(t) = G*y(t)

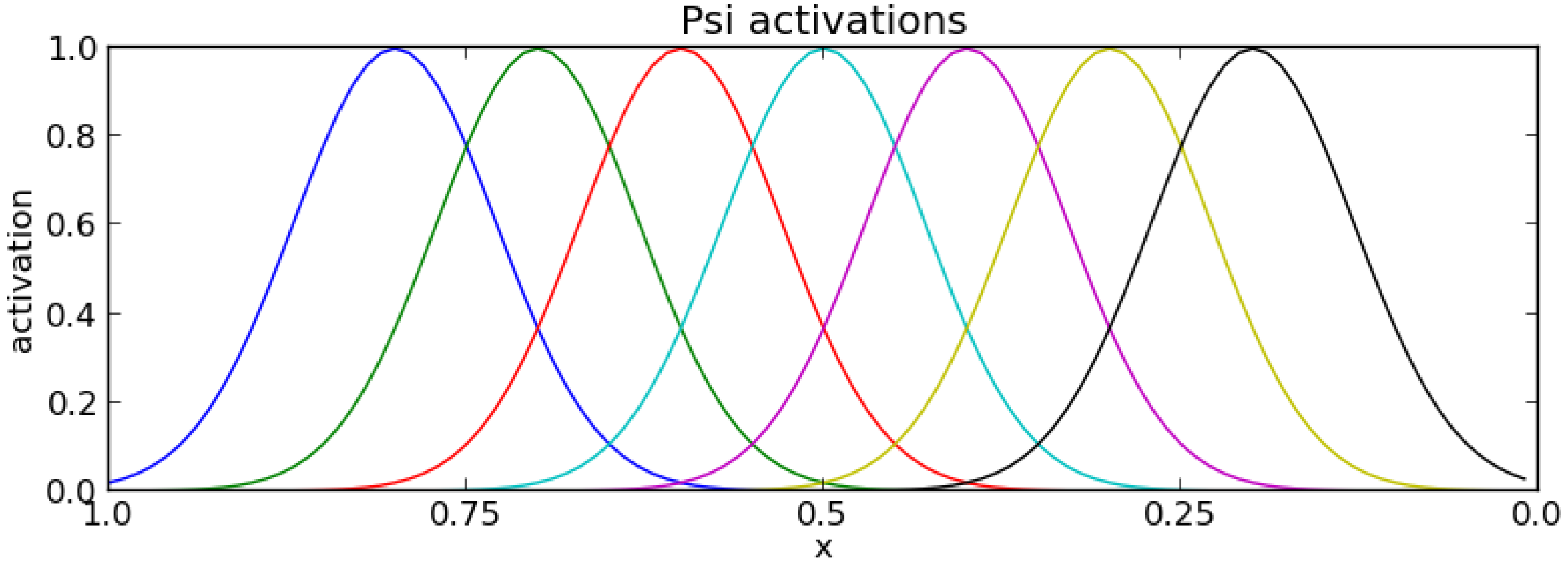
3. Produces a purkinje cell output ***z(t) = w*p(t)***

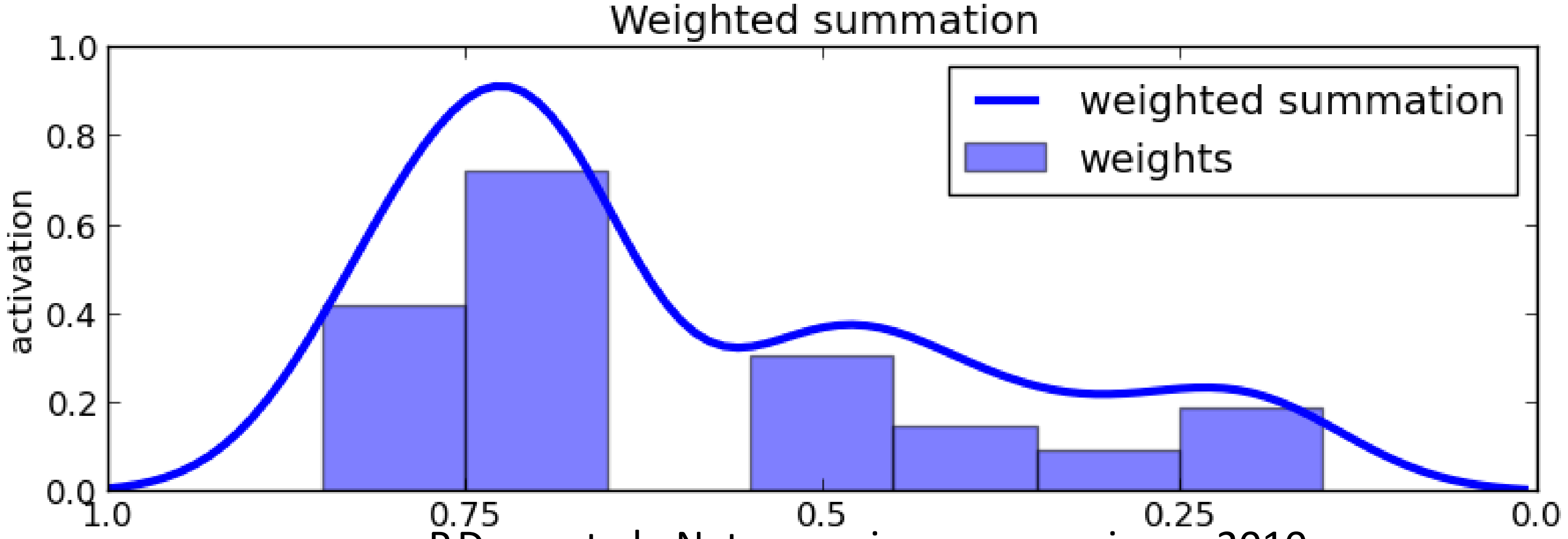
P.Dean et al., Nature reviews neuroscience 2010

The computational circuit of cerebellum - adaptive filter



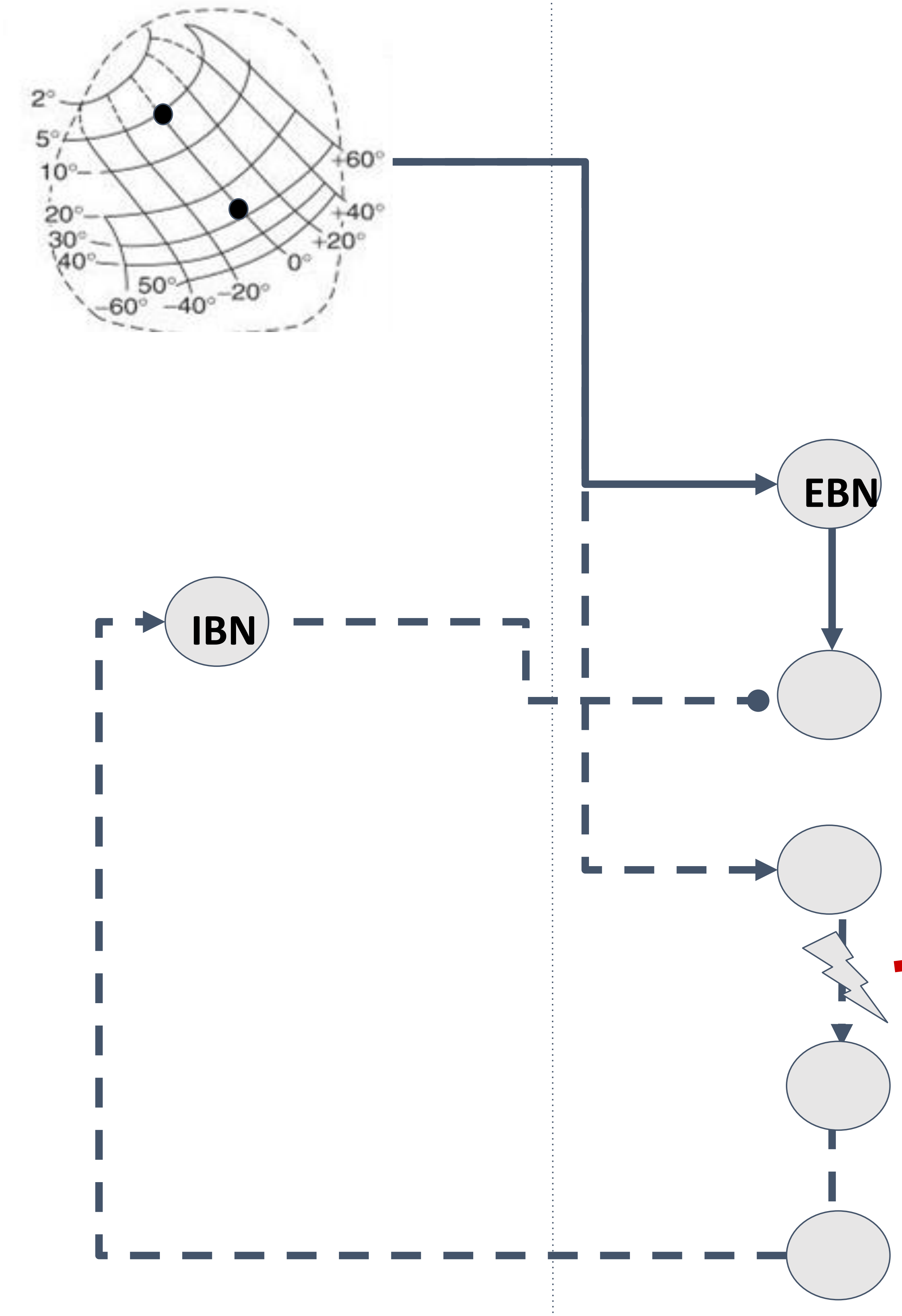






P.Dean et al., Nature reviews neuroscience 2010

StudyWolf blog



burst generators

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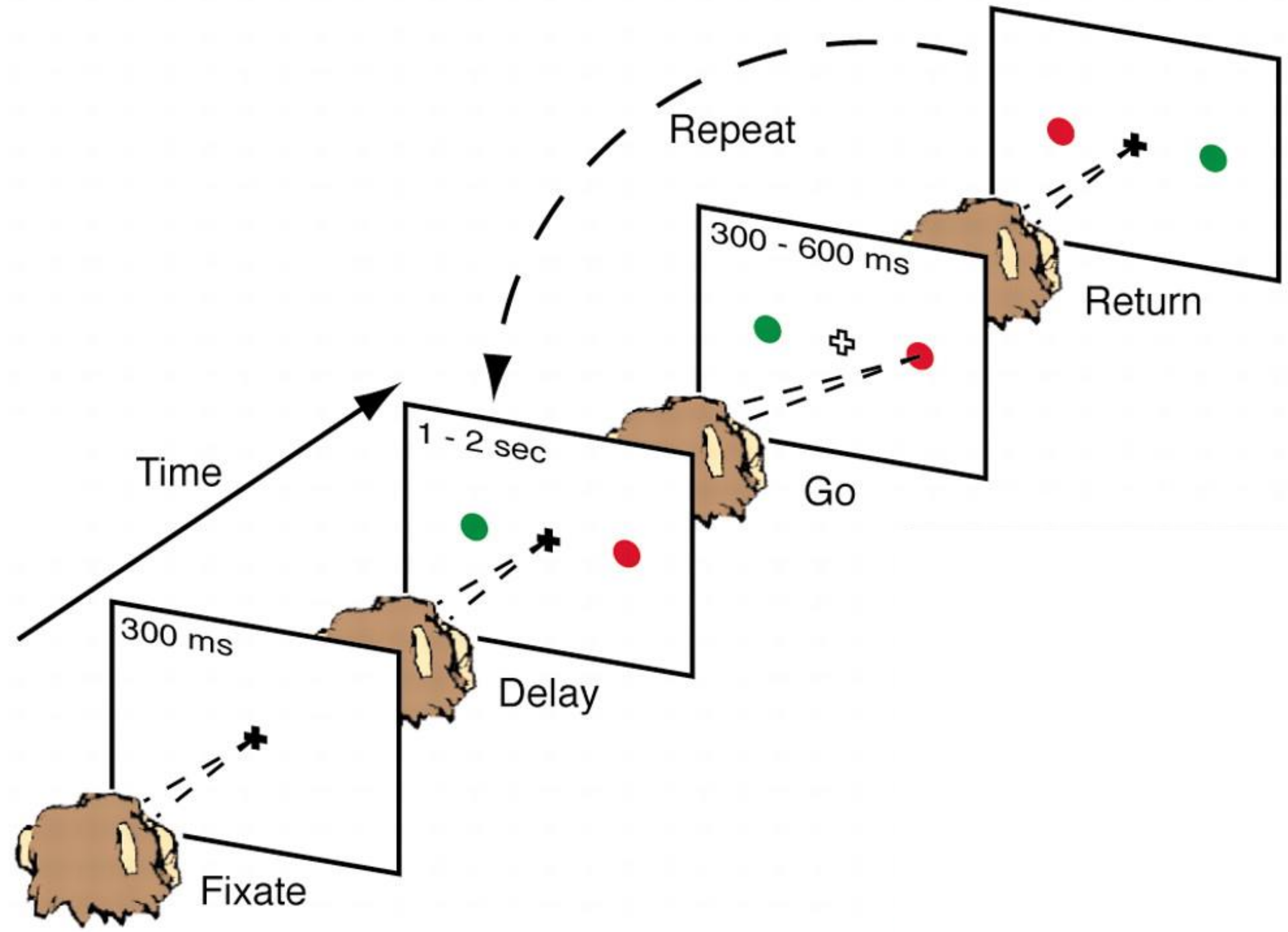
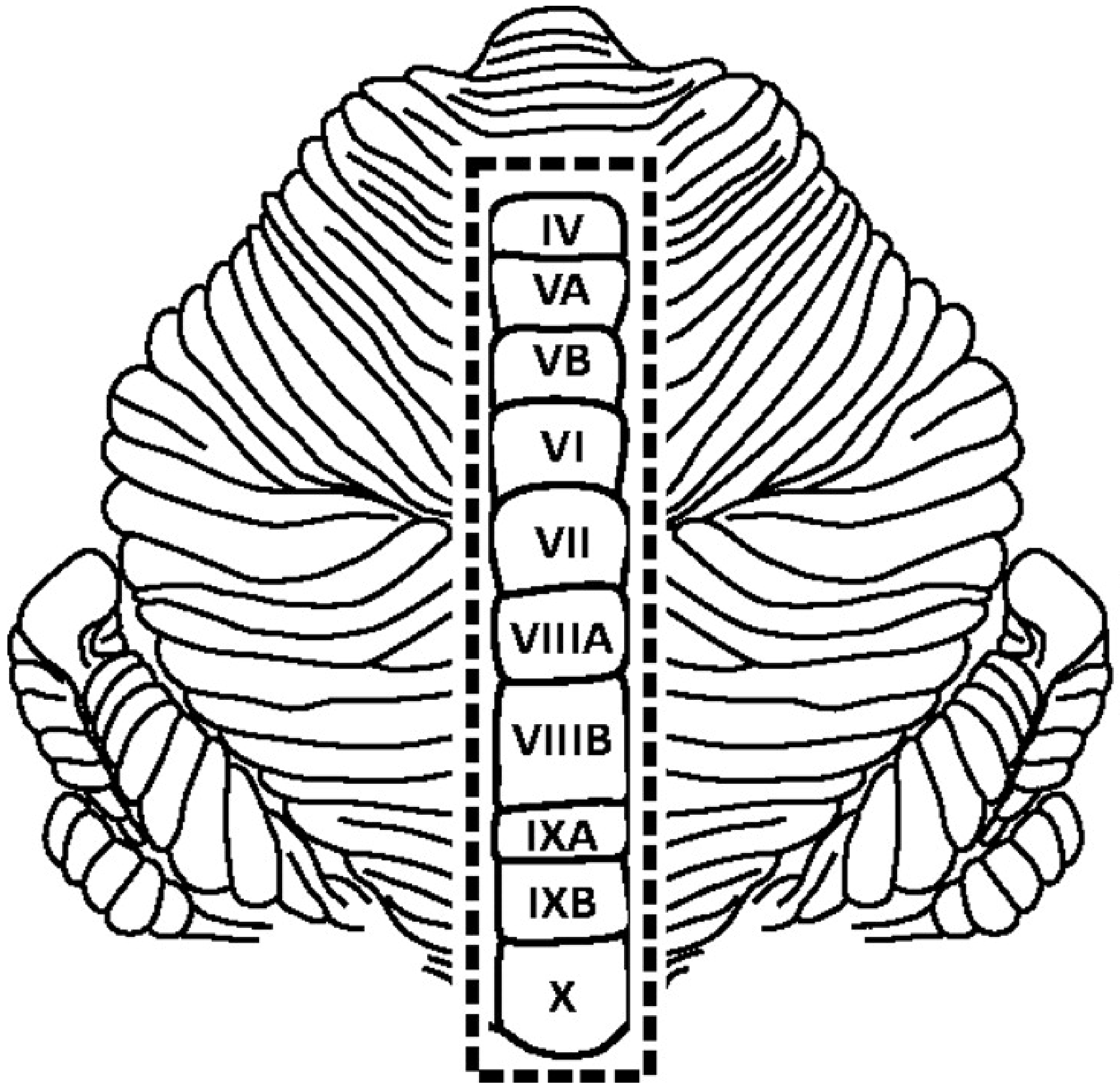
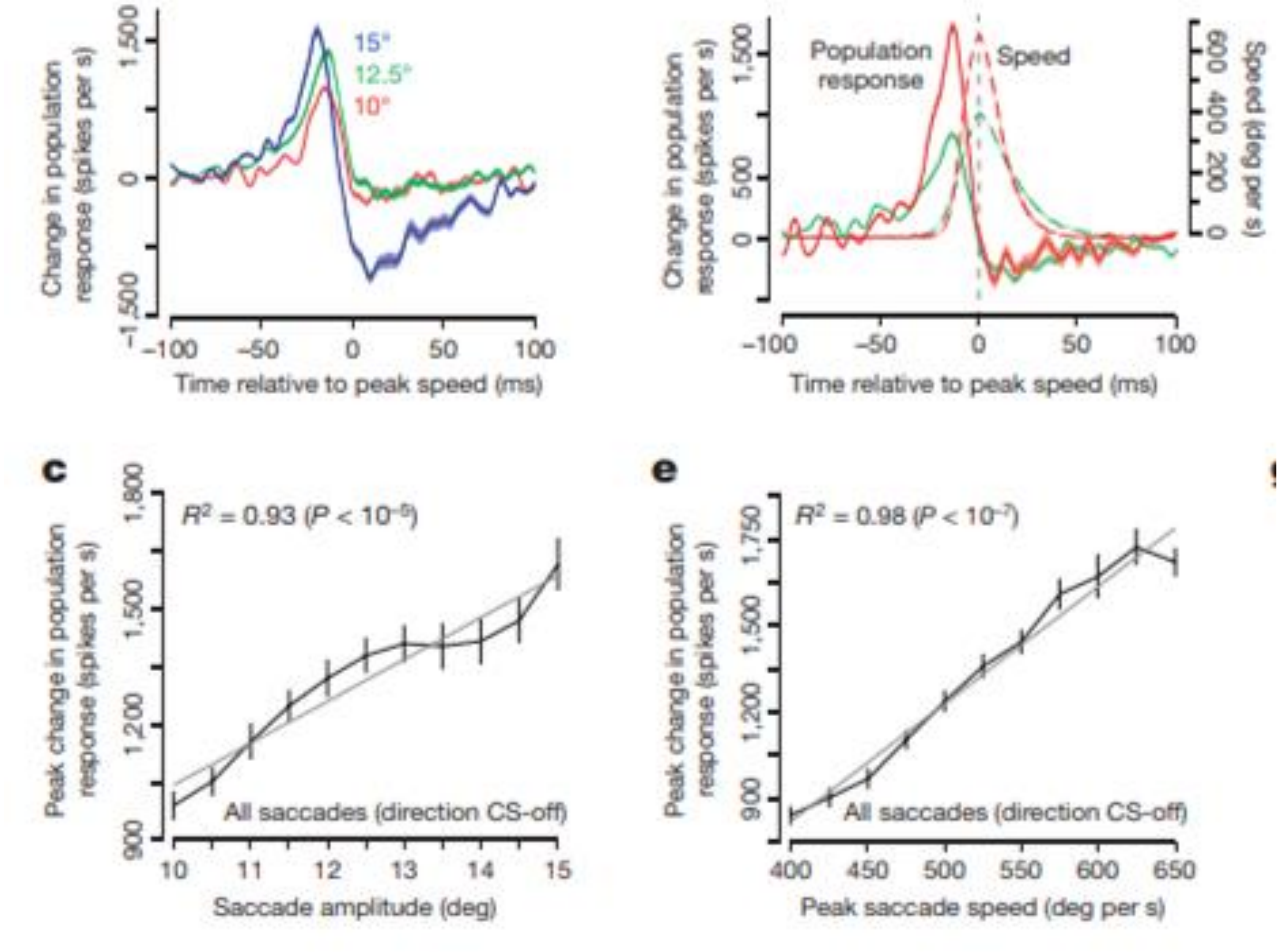
What is cerebellum computing?

Record from cerebellum





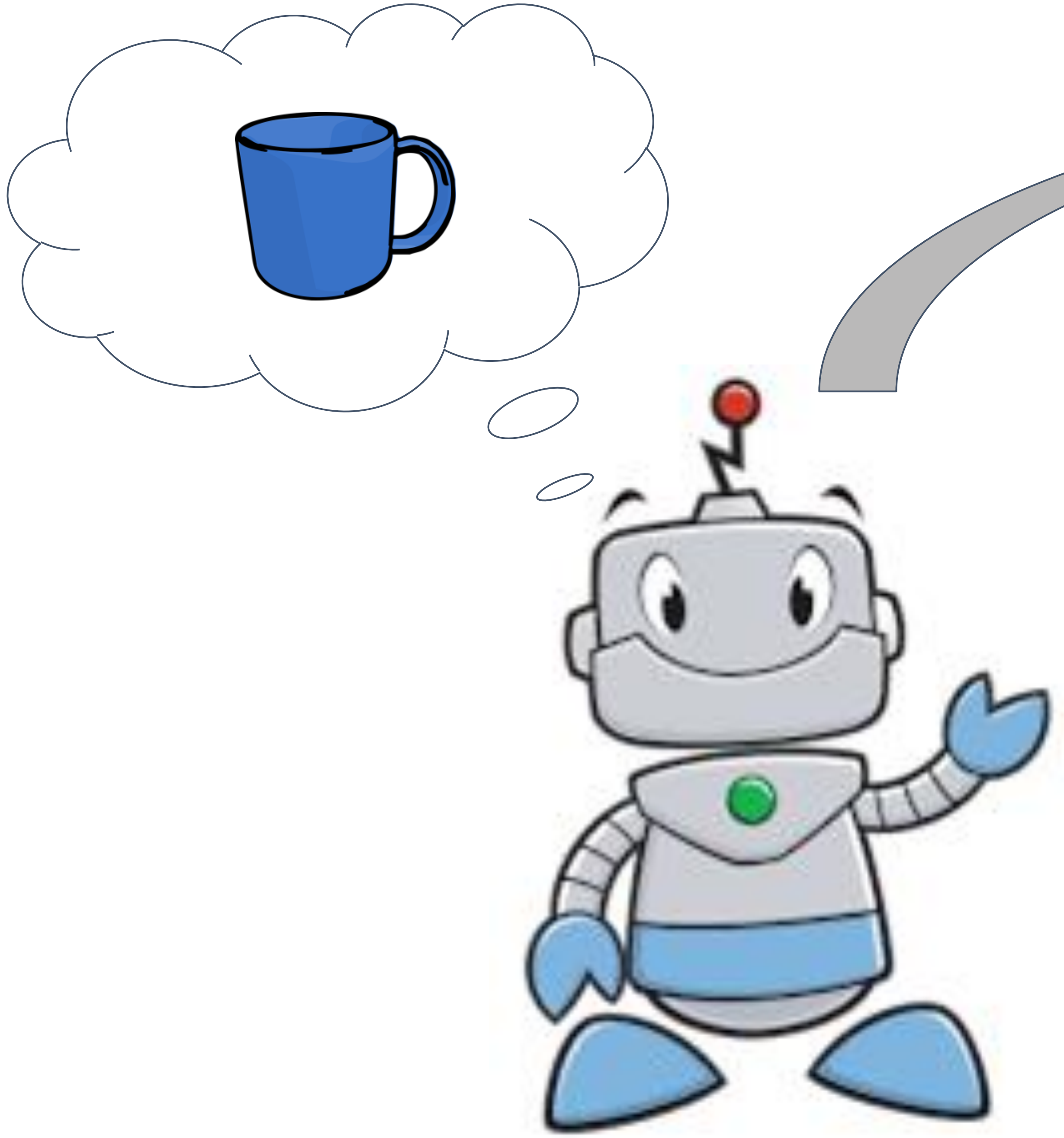
Output of cerebellum precedes the actual eye movement



Purkinje cell firing is correlated with the eye speed, displacement and precedes the eye movement, **predicting** the state of the eye

Herzfeld et al., Nature 2015

Internal models should continuously adapt



$a_t \sim \pi_c(g_t, s_t)$

Context-dependent control policy

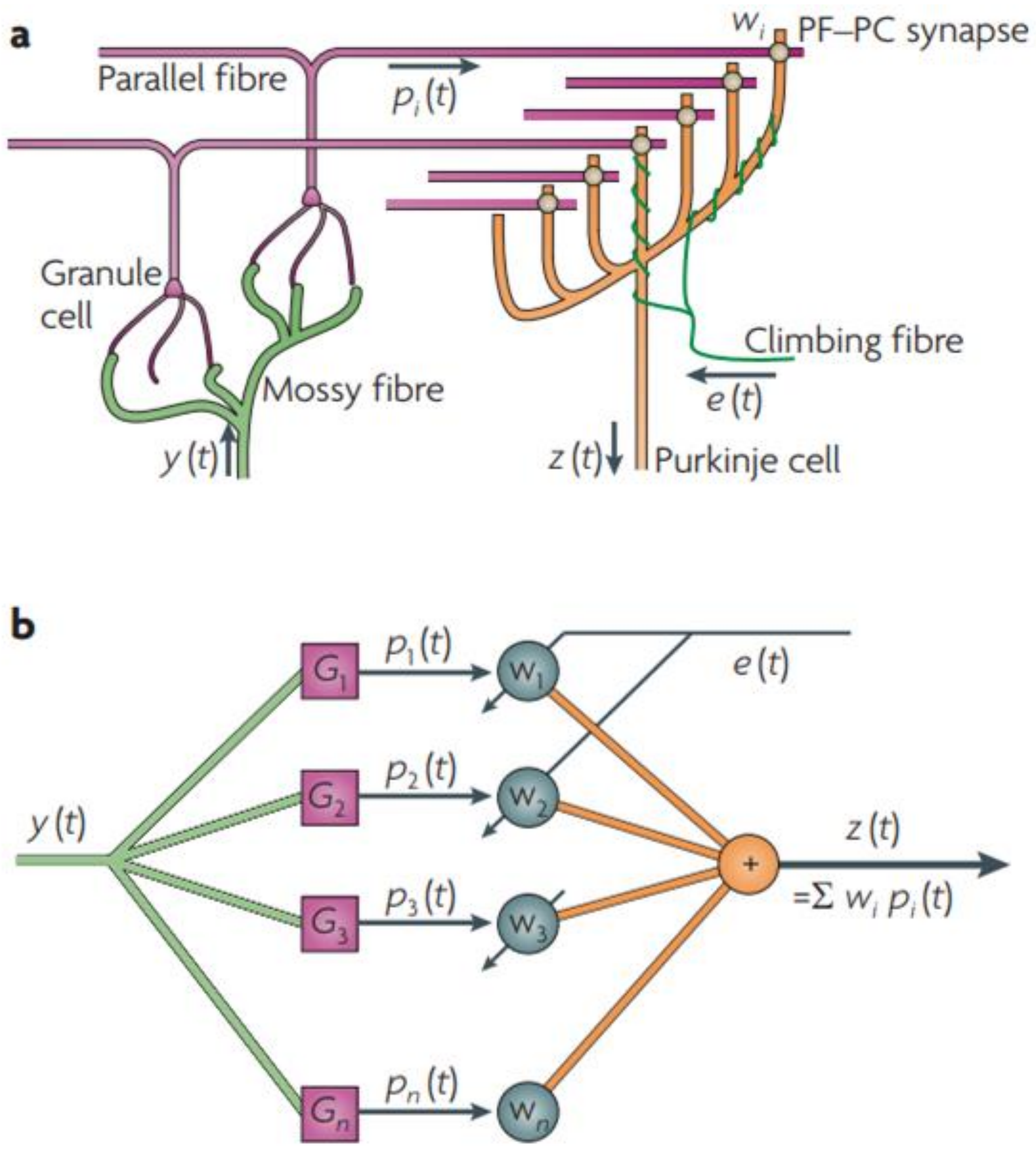
Both 'π' and 'p' are probability distributions over state and actions respectively. 'c' indicates the current context of movement

These distributions should be continuously estimated/inferred from experience

Uncertain body+environment dynamics

$p(s_{t+1} \mid s_t, a_t)$

Decorrelation learning in cerebellum



The PF-PC synapses can be subject to plasticity.

<u>Adaptation</u>

'***e(t)***' be the error between <u>desired cerebellum output and the actual cerebellum output</u>. Then the PF-PC weights can be adjusted based on

$$\Delta \mathbf{w}_i\,(t) \propto -\langle \mathbf{e}(t)\;.\;\Delta \mathbf{p}_i(t)\rangle$$

i.e., occurence of a positive error decreases the weight of PF-PC synapses and vice-versa

This learning rule enables cerebellum to behave as a supervised learning center, that functions to reduce the mean square error between the desired response and actual response.

Can the same learning rule explain movement adaptation?

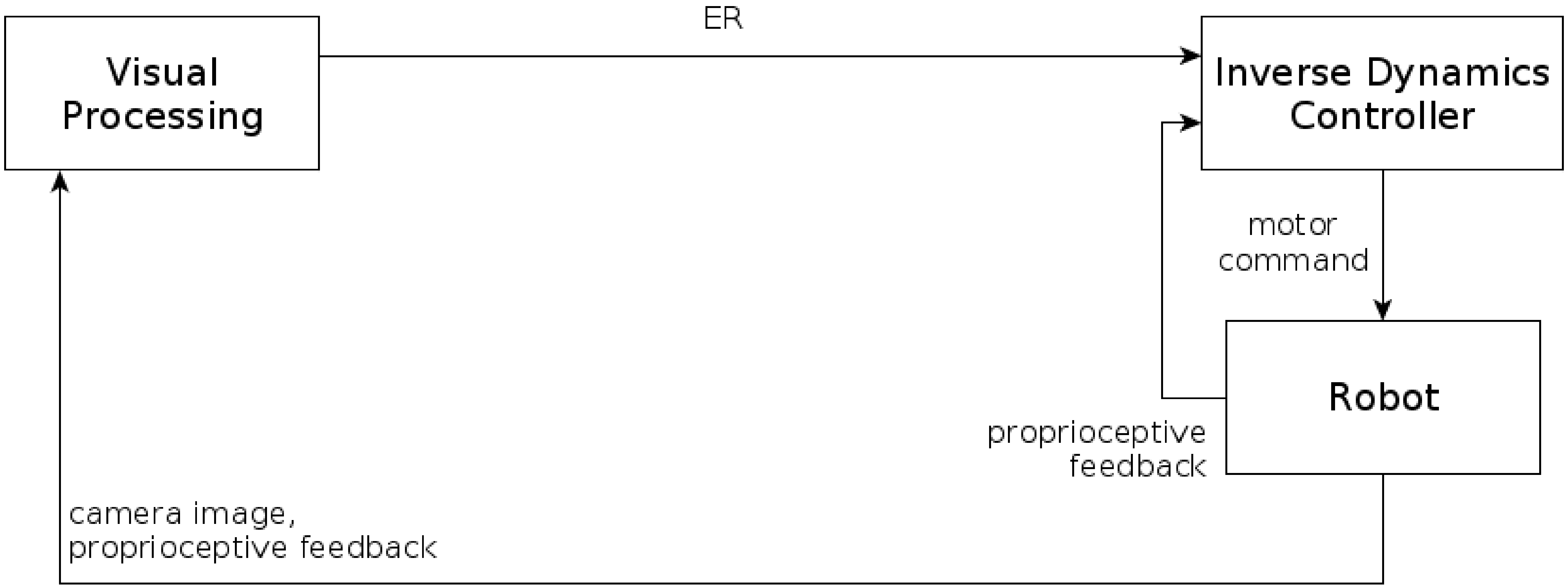
Consider the vestibulo-ocular reflex or head - video

Applications – icub VOR experiment

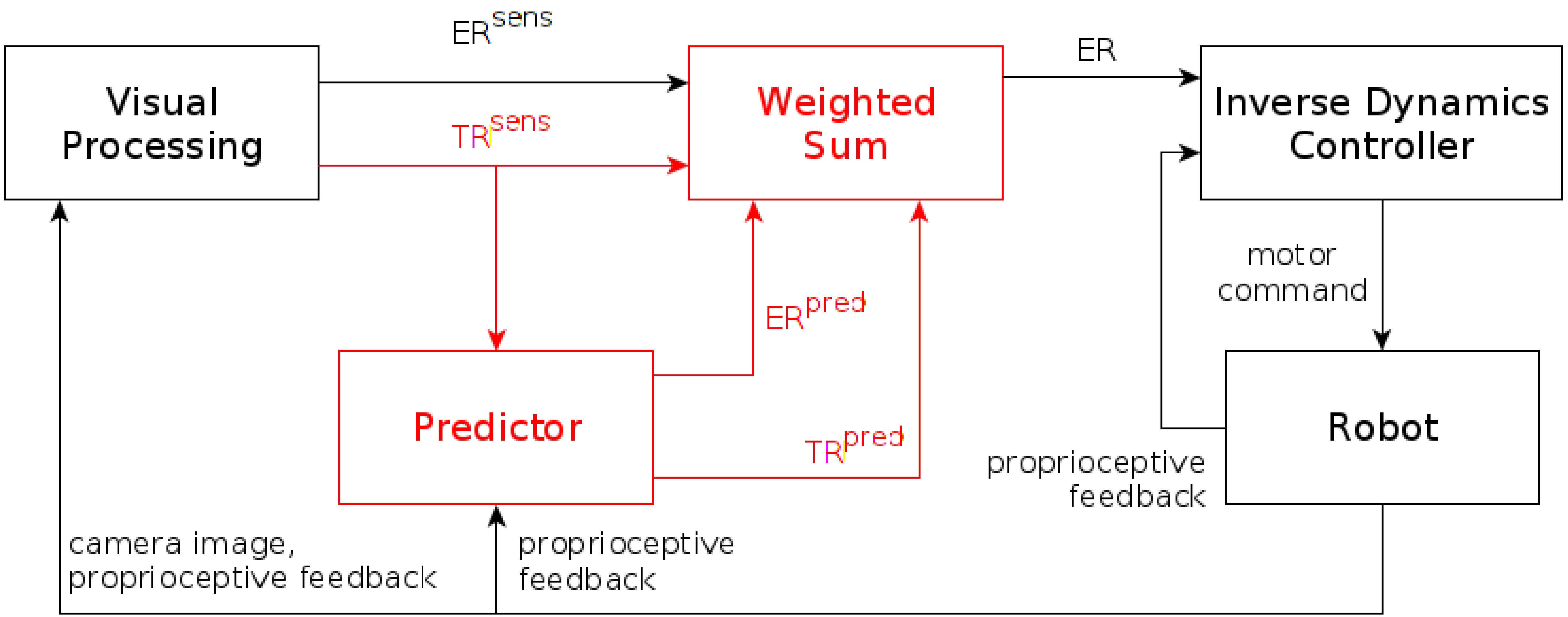
Applications – smooth pursuit gaze control

Humans, in order to follow a moving target with foveal vision, use a combination of eye and head movements in conjunction with prediction of the target dynamics in order to align eye and target motion.

Applications – smooth pursuit gaze control model

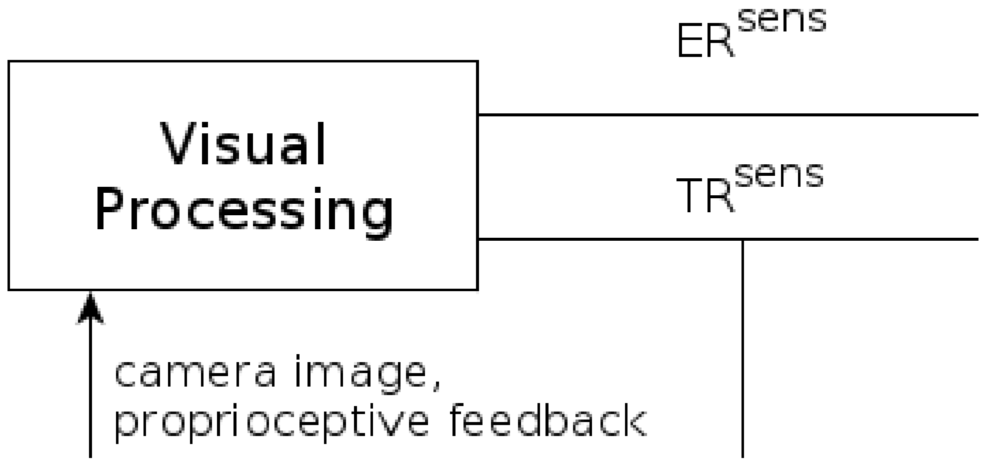


Applications – smooth pursuit gaze control model



Vannucci, L., Falotico, E., Di Lecce, N., Dario, P., & Laschi, C. (2015, July). **Integrating feedback and predictive control in a bio-inspired model of visual pursuit implemented on a humanoid robot**. In *Conference on Biomimetic and Biohybrid Systems* (pp. 256-267). Springer, Cham.

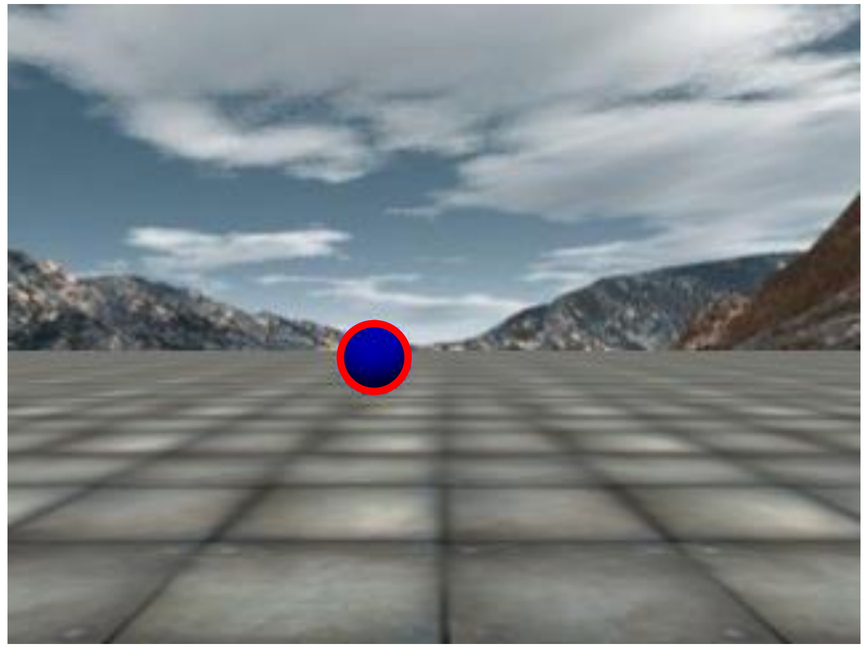
Applications – smooth pursuit gaze control model



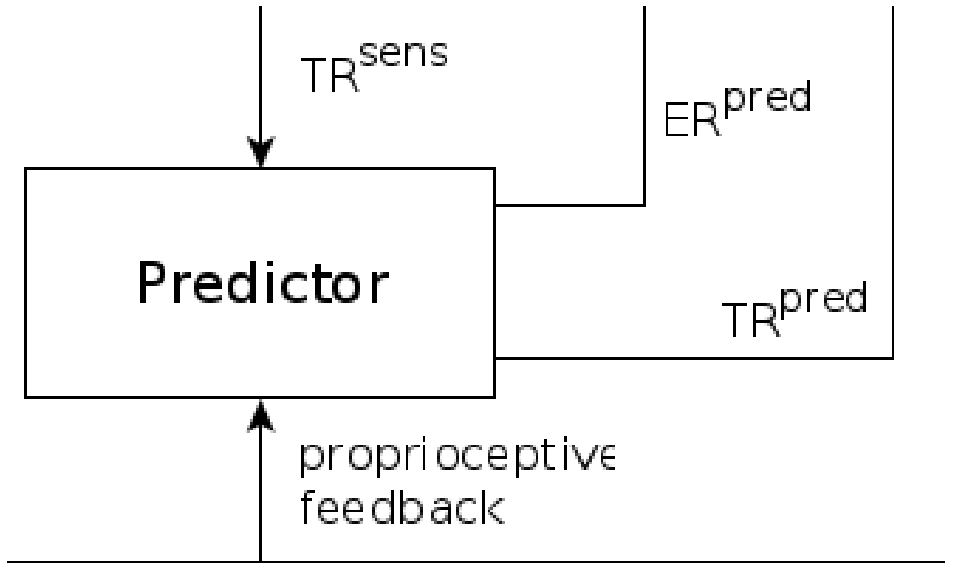
The camera image is processed to get sensory information about the target.

ER^{sens} = error reference (retinal slip, 3D gaze displacement, etc…)

TR^{sens} = target reference (target velocity, target 3D position, etc…)



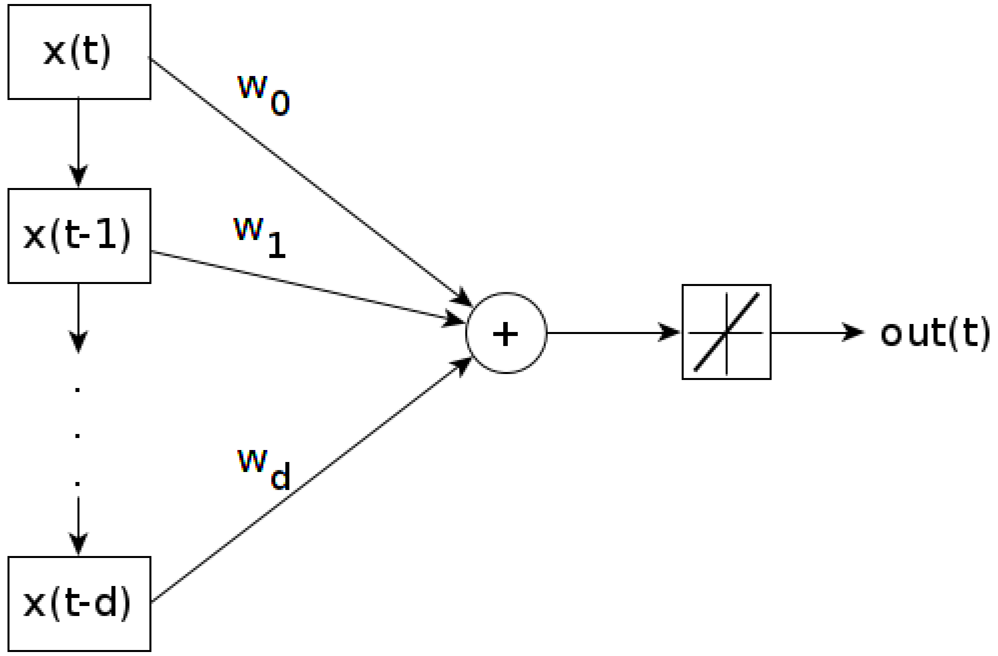
Applications – smooth pursuit gaze control model



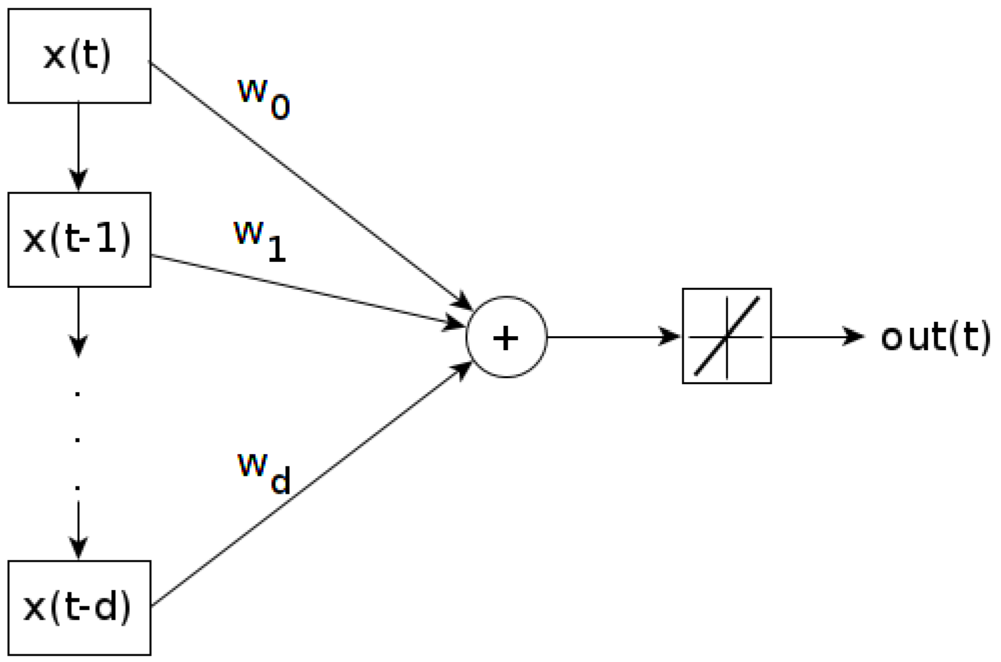
The predictor uses sensory information to predict future states of the target.

Predictor implemented as linear neural model: Rosenblatt's single layer perceptron with a tap delay.

$$out(t) = \sum_{i=0}^{d} x(t-i) \cdot w_i$$



Applications – smooth pursuit gaze control model



Training with an online version of Widrow-Hoff rule: (which is also a **decorrelation learning** rule)

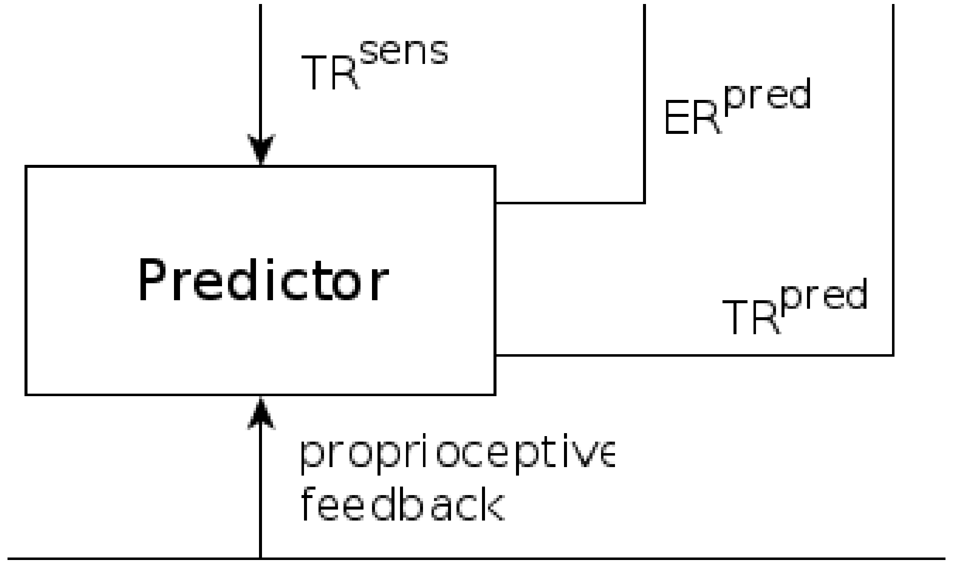
$$\Delta w = \eta \cdot \big(x(t+p) - out(t)\big) \cdot x(t)$$

where p is the number of prediction steps.

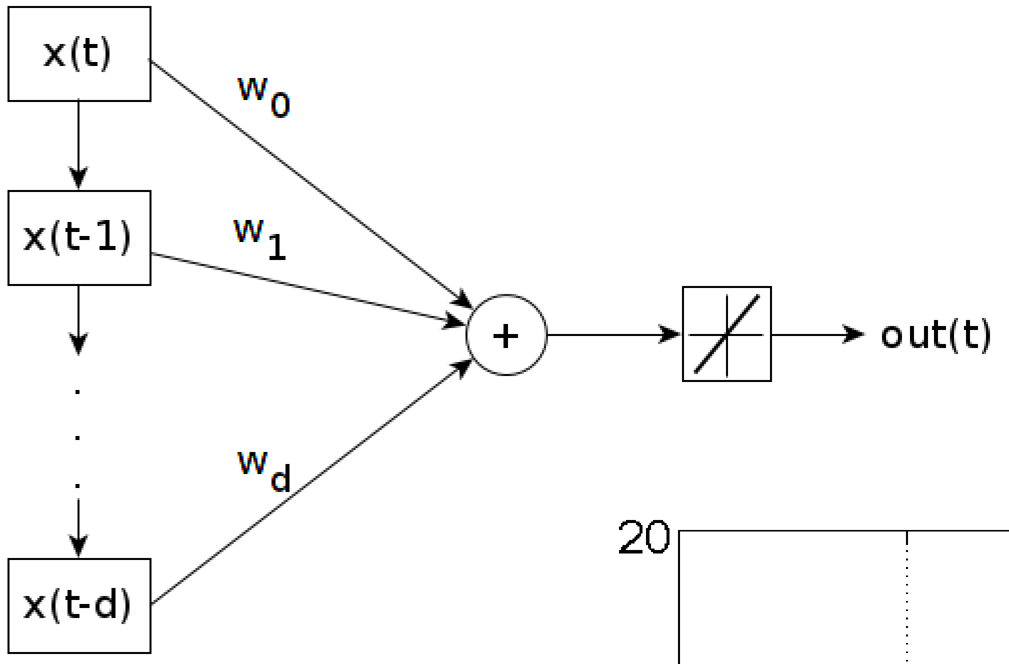
$$x(t) = TR^{sens}(t)$$

$$TR^{pred}(t) = out(t)$$

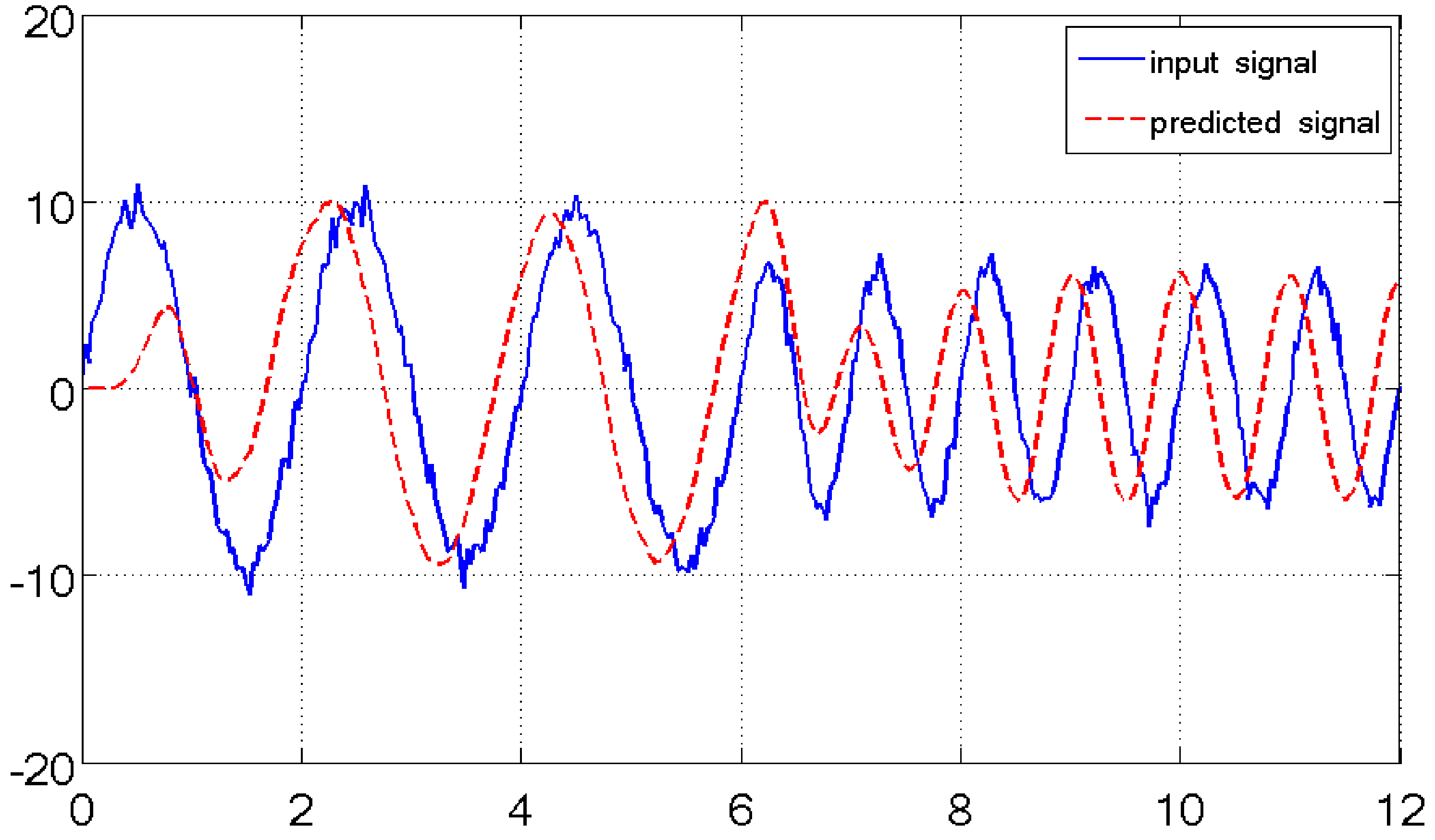
$$ER^{pred}(t) = TR^{pred}(t) - g(sensors(t))$$



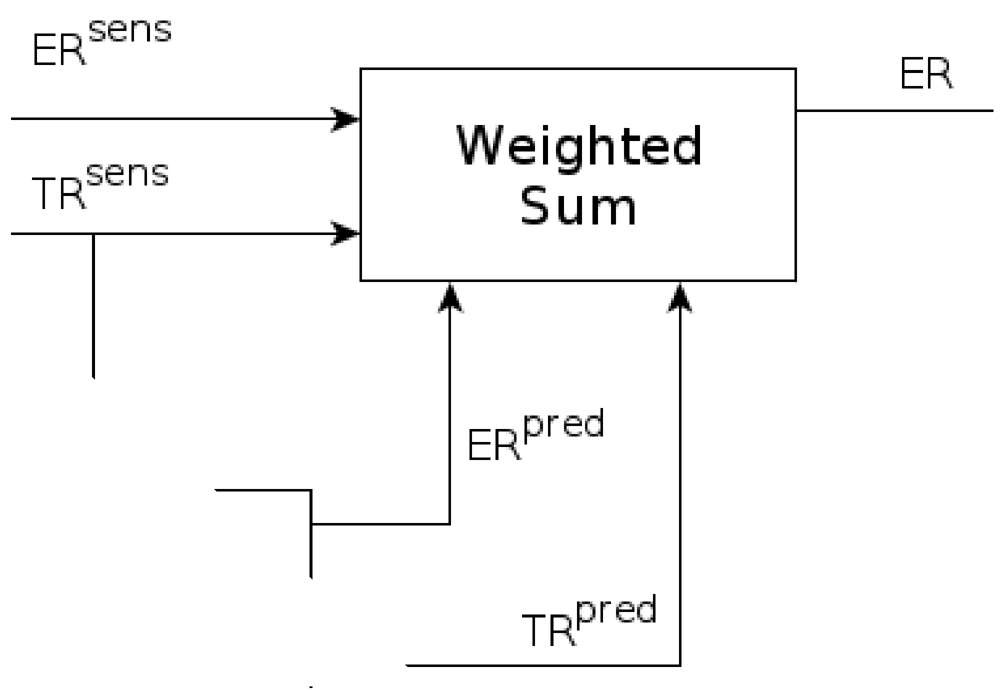
Applications – smooth pursuit gaze control model



Such a linear model is able to predict periodic motions, also in presence of noise.



Applications – smooth pursuit gaze control model

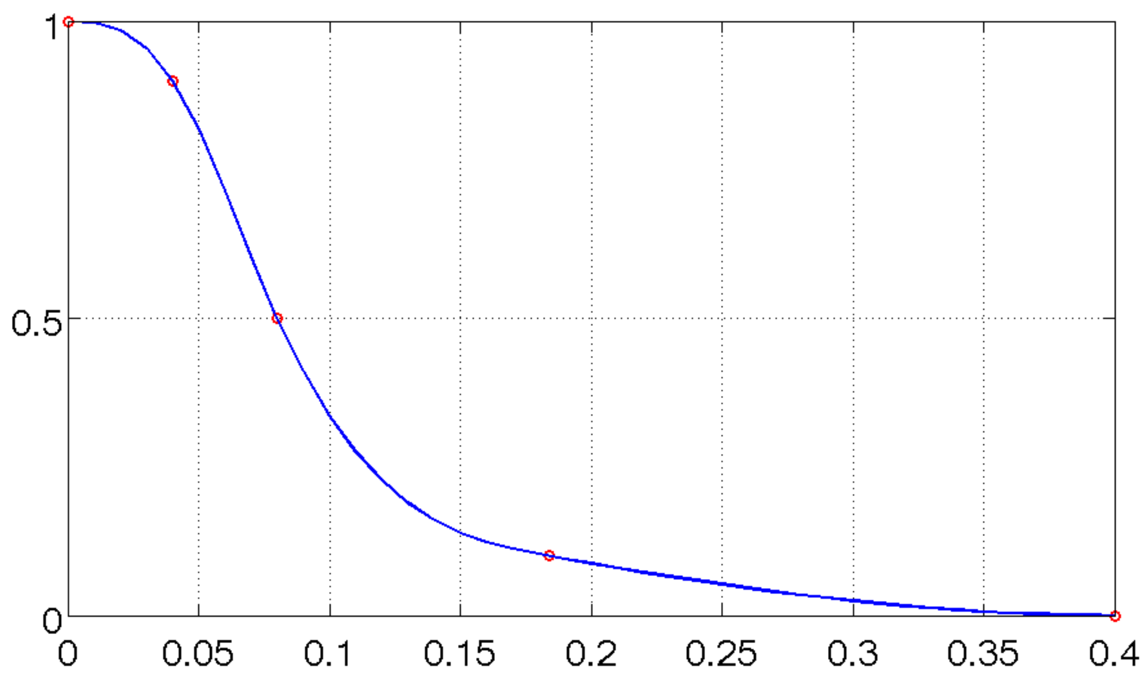


In order to automatically switch between the sensory and predictive pathways, a weighted sum of the error references coming from the two pathways is performed:

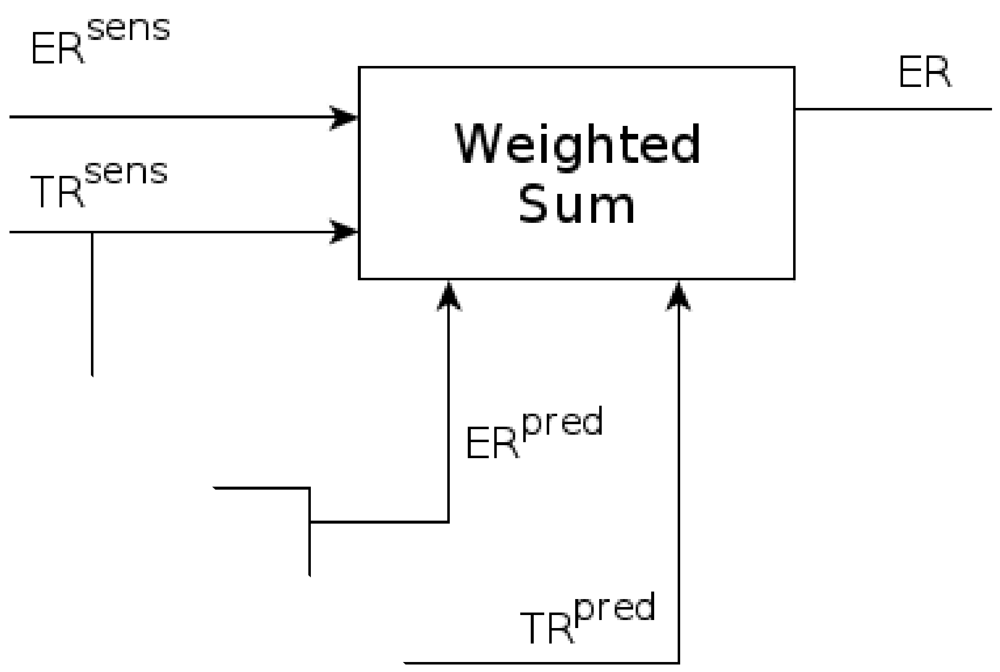
$\alpha \in [0,1]$ is a measure of the accuracy of the prediction and it is computed as follows:

$$\alpha(t) = f(\max\{err(t), \dots, err(t-100)\})$$

$$err(t) = \frac{\left|TR^{sens}(t) - TR^{pred}(t-p)\right|}{maxTR - meanTR}$$



Applications – smooth pursuit gaze control model

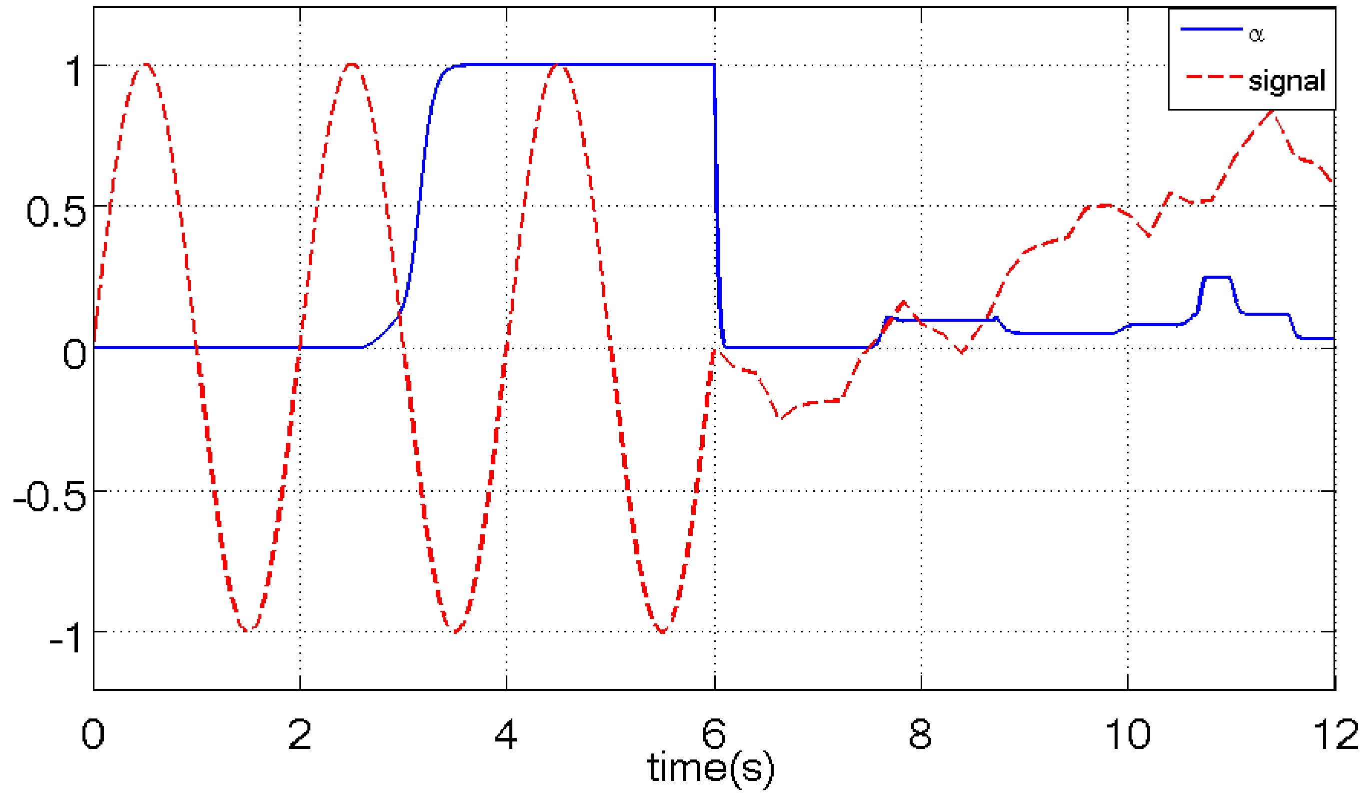


The selection performed by α works in two directions:

- Its value increases when prediction becomes accurate enough
- it suddenly decreases when the signal changes

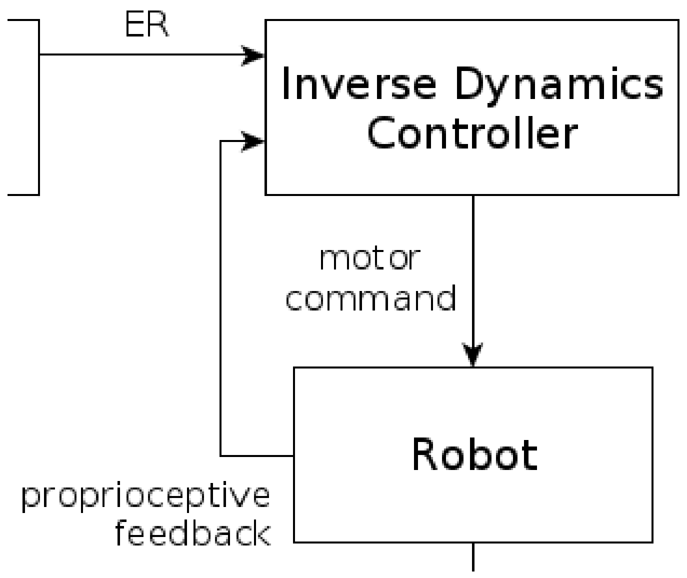
The accuracy measure α actually performs the selection between the predictive and sensory pathways:

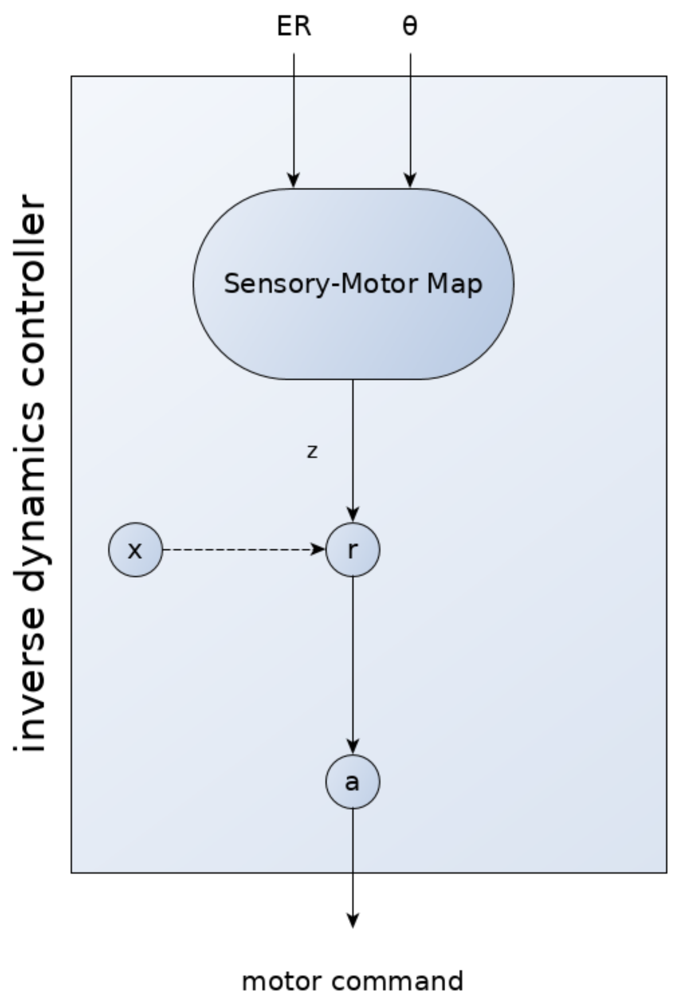
$$\alpha(t) \cong 1 \rightarrow ER^{pred} \ \ will\ be\ used$$
$$\alpha(t) \cong 0 \rightarrow ER^{sens} \ will\ be\ used$$



Applications – smooth pursuit gaze control model

The objective of the IDC is to move the target robot plant towards the target reference. This can be in principle any kind of controller.





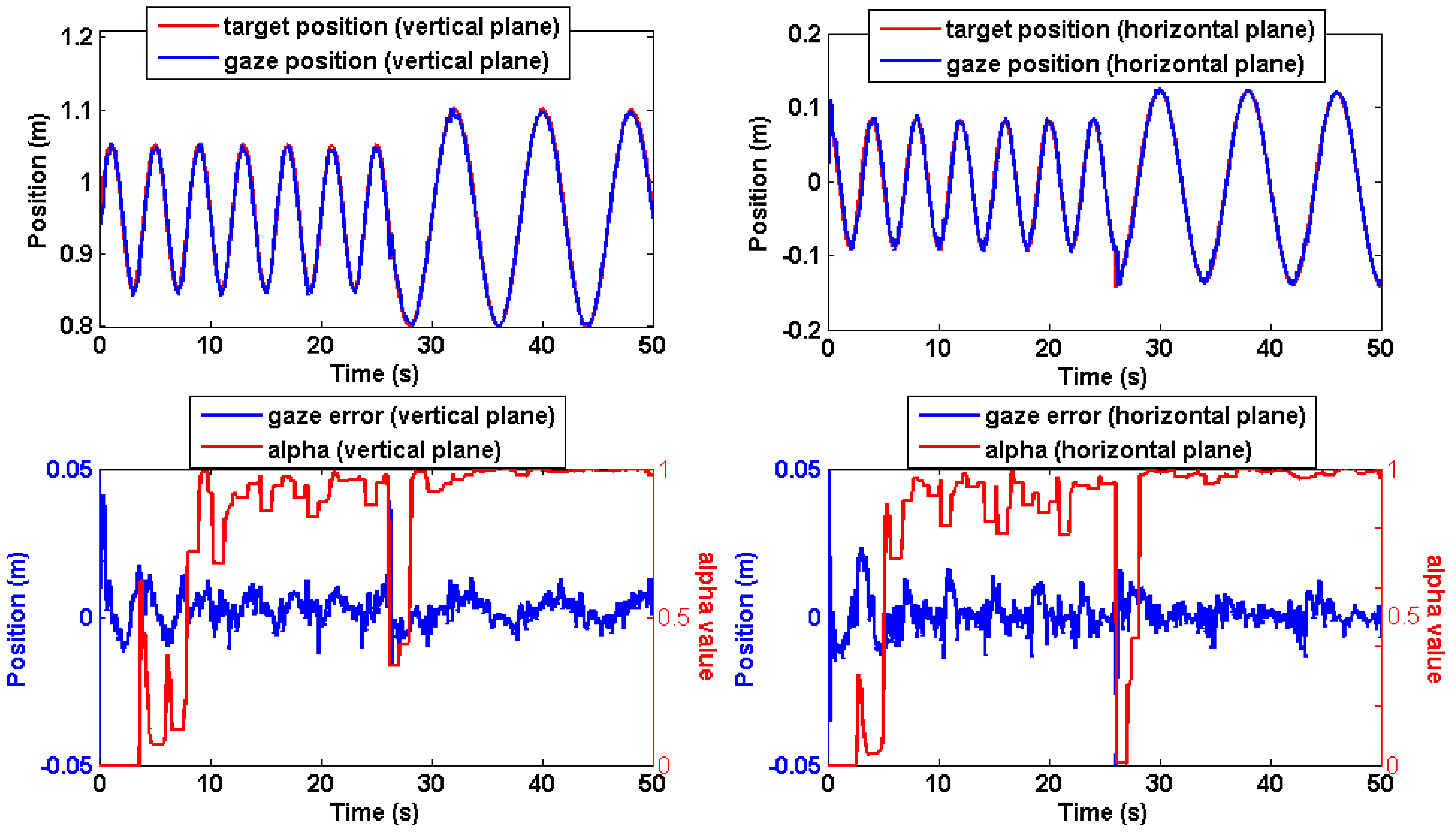
Two implementations were given:

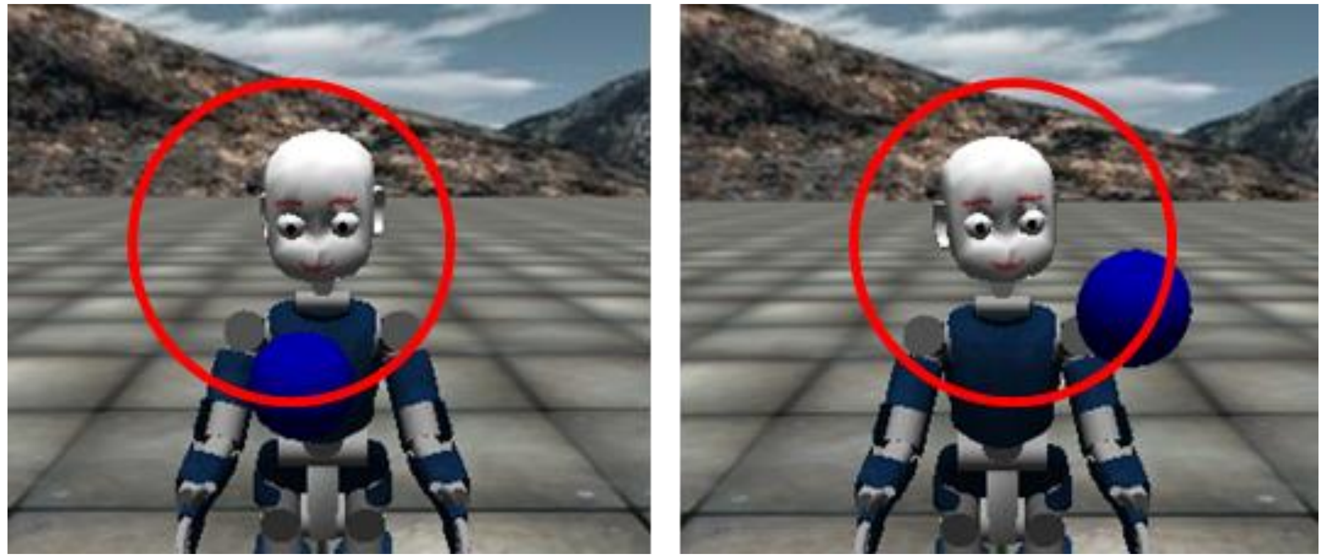
- an adaptive backstepping-based controller

- a neurocontroller, inspired by cortical sensory-motor associations, capable of learning how to perform coordinated gaze movements

Applications – smooth pursuit gaze control model

Same movement on both axes: from (0.25Hz, 0.1m) to (0.125Hz, 0.15m) after 26 seconds (in a 50 seconds trial), neurocontroller as IDC.

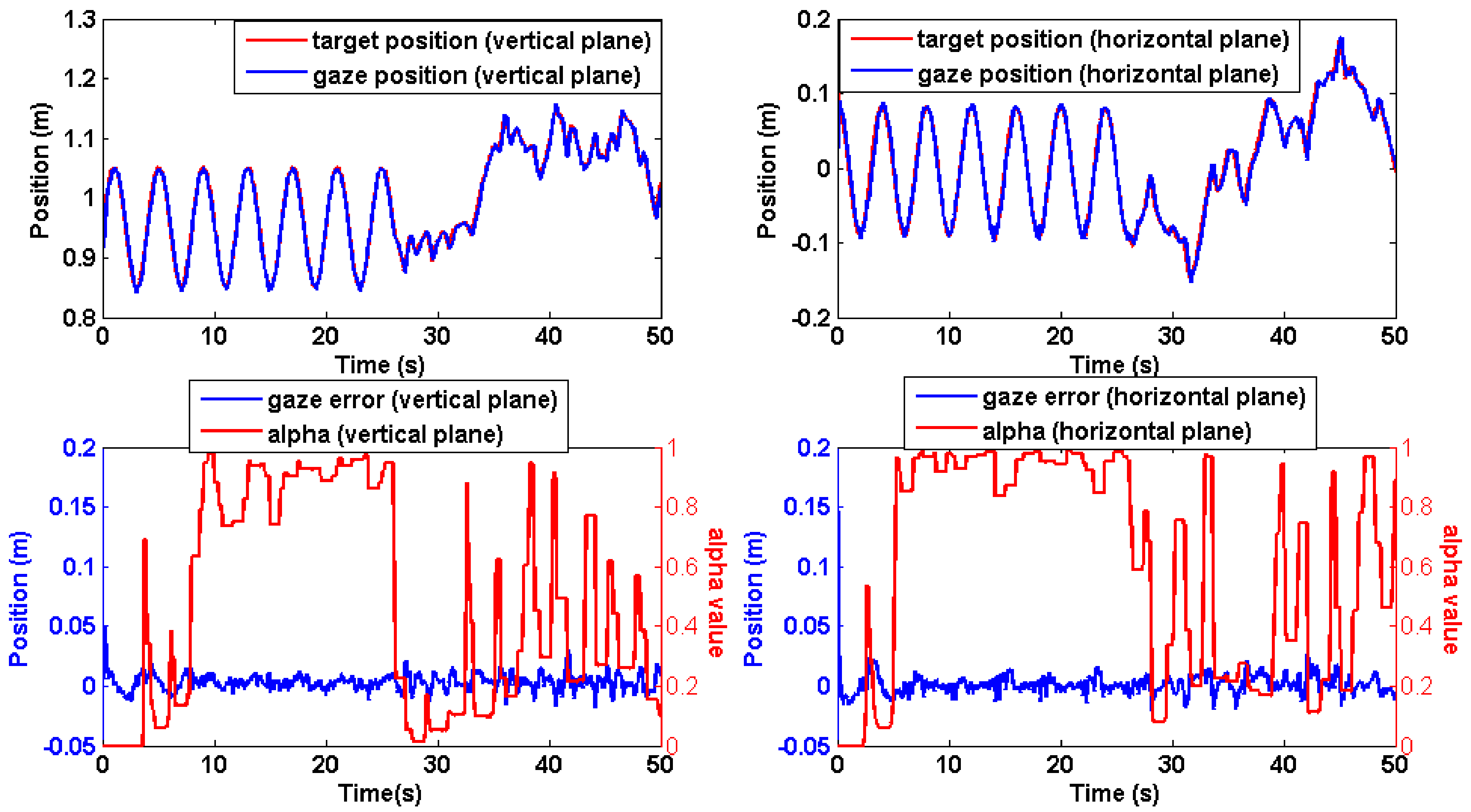




When α increases, the peak-to-peak retinal slip decreases from 0.04m to 0.02m, on both axes. After the switch, the value of α suddenly decreases, only to raise up again after a few seconds.

Applications – smooth pursuit gaze control model

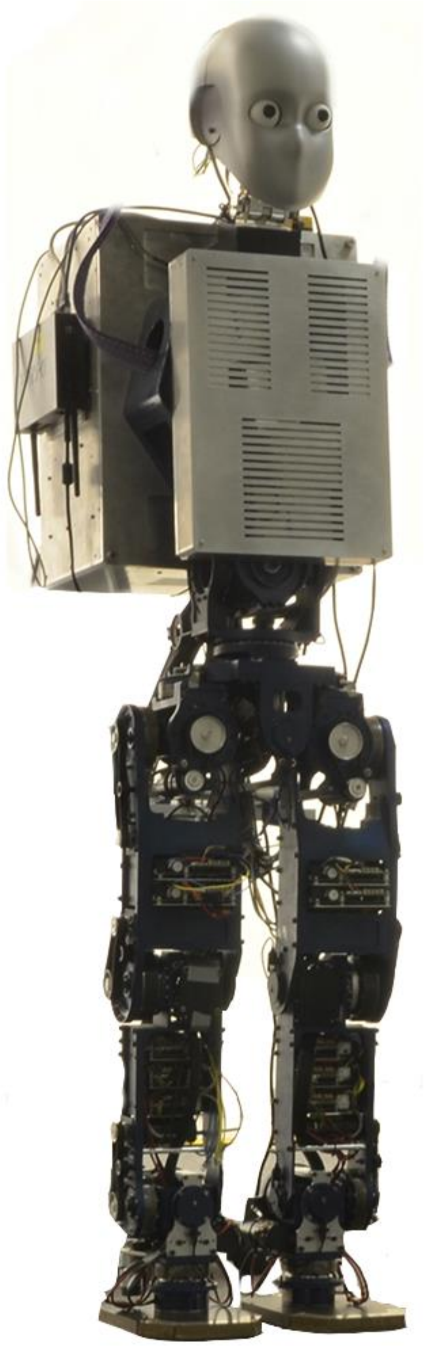
Switching from a sinusoidal motion (0.25Hz, 0.1m) to a random one after 26 seconds (in a 50 seconds trial).

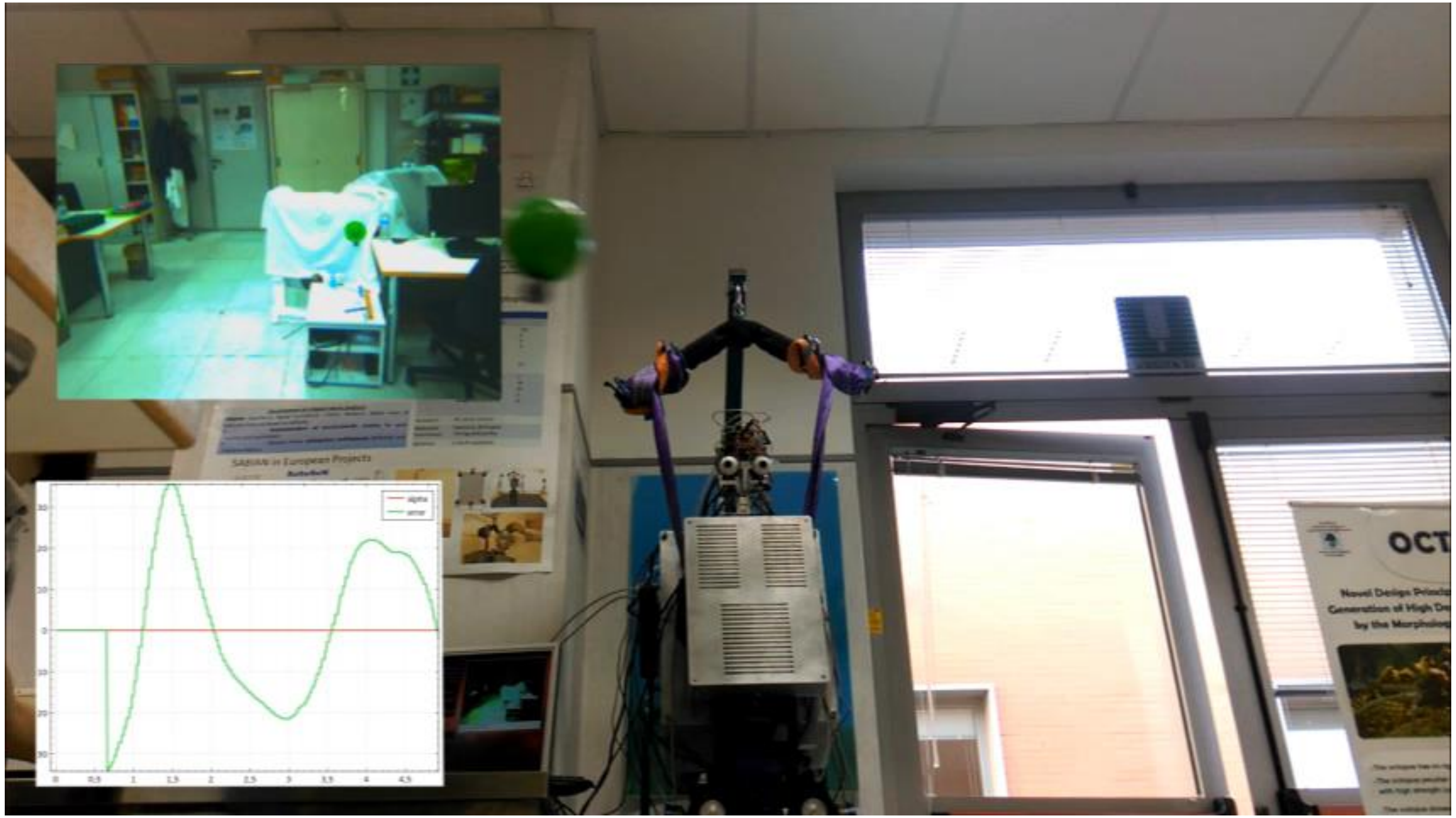


When the signal switches to the random motion, the value of α suddenly drops. Nevertheless, the model is still able to follow a moving target with a maximum error amplitude of 0.05m.

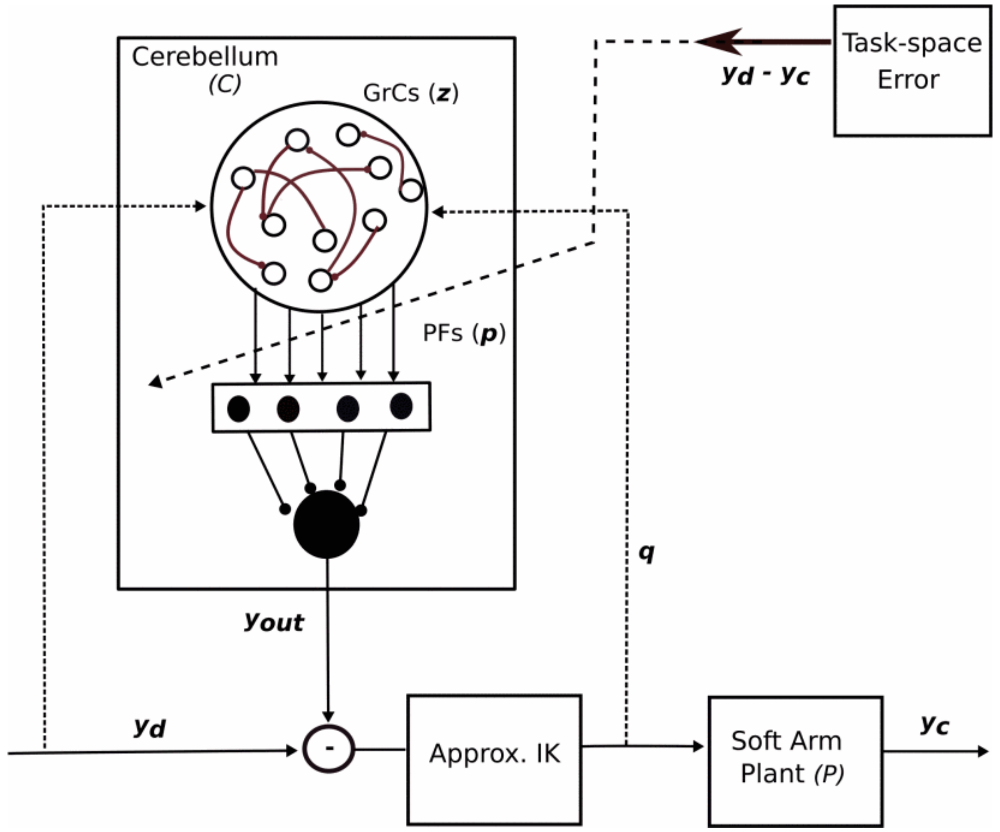
Applications - Lorenzo’s videos on icub smooth pursuit

This model was also implemented on the SABIAN robot (backstepping-based version).

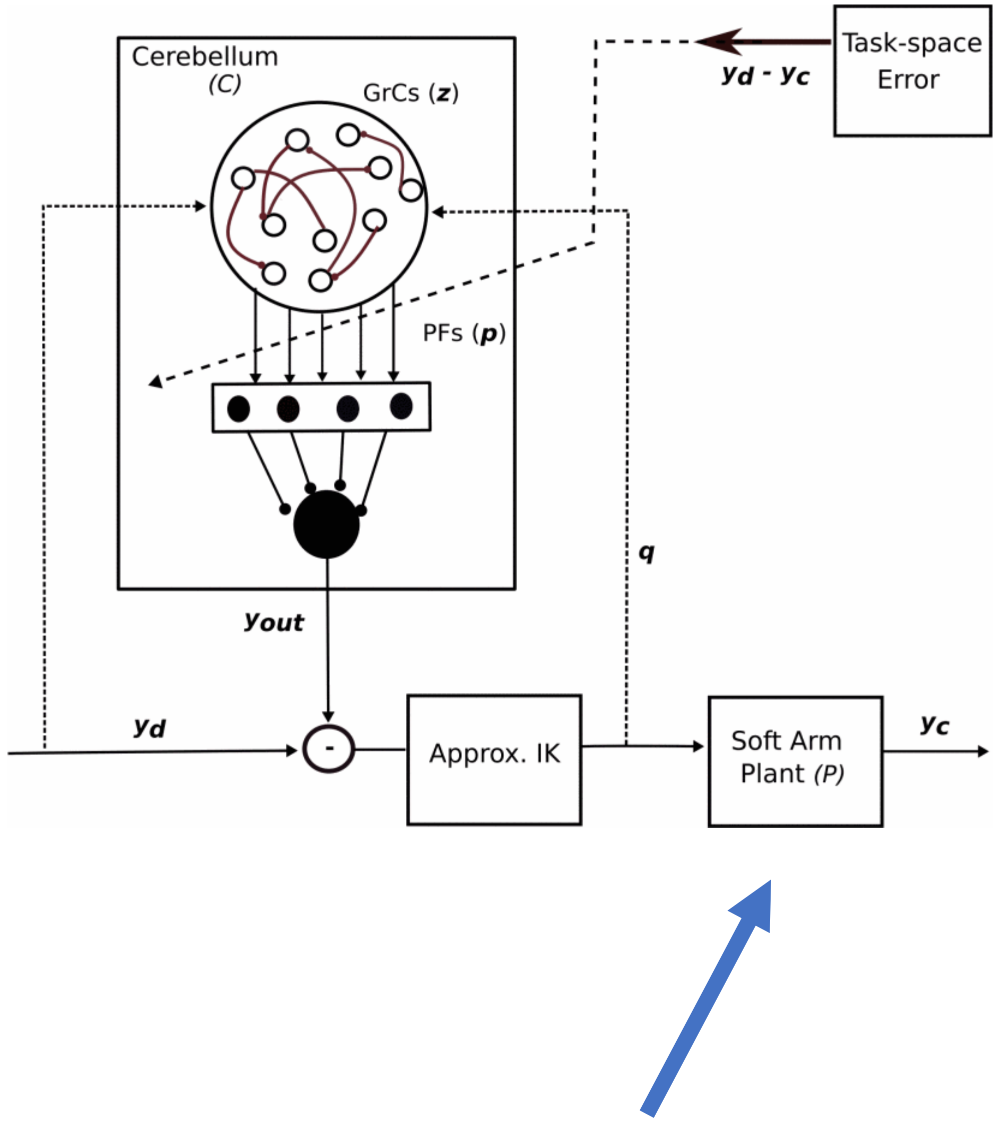




Applications - Soft robot simulation video

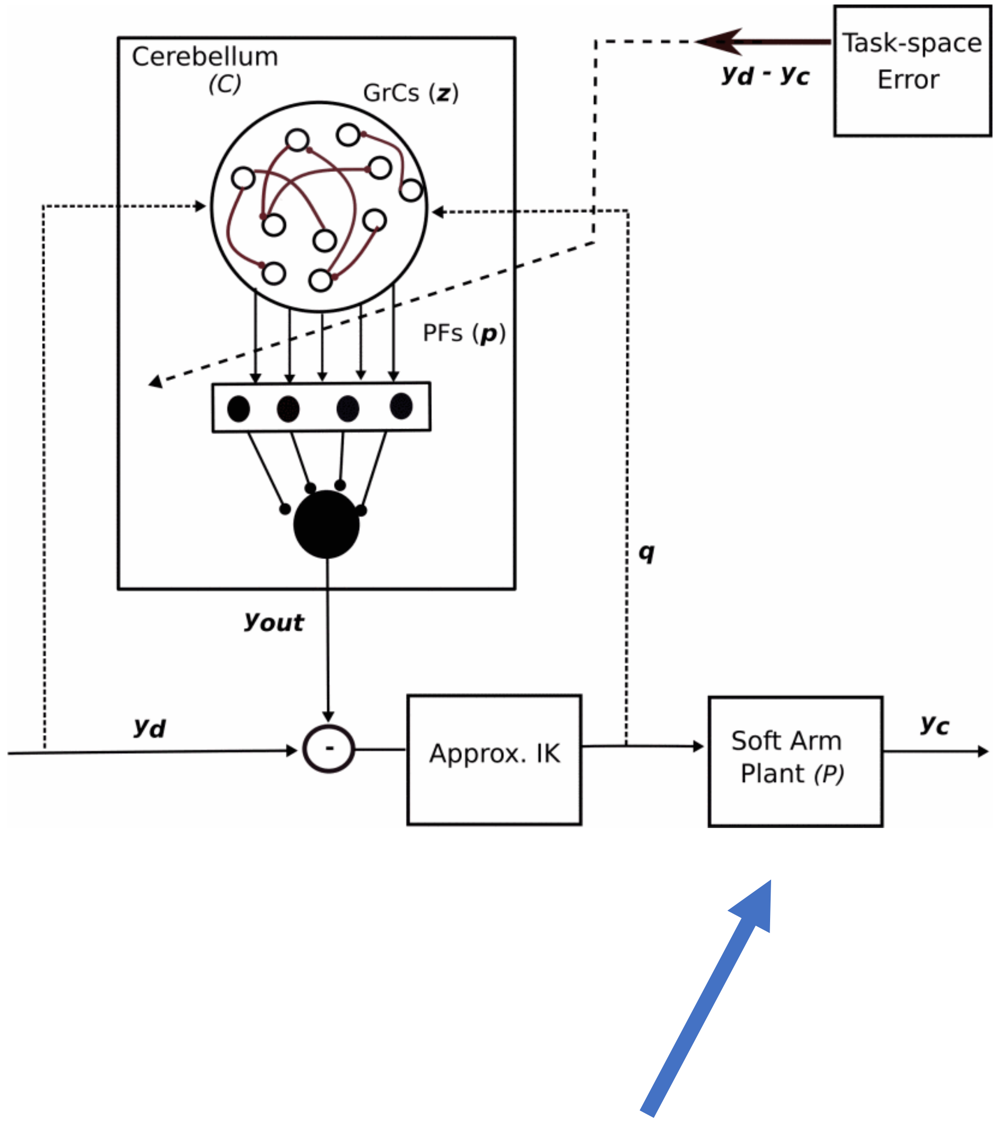


Applications - Soft robot simulation video



Can the cerebellum forward model compensate for changes in the soft arm dynamics?

Applications - Soft robot simulation video



Can the cerebellum forward model compensate for changes in the soft arm dynamics?