How Neurons Do Integrals

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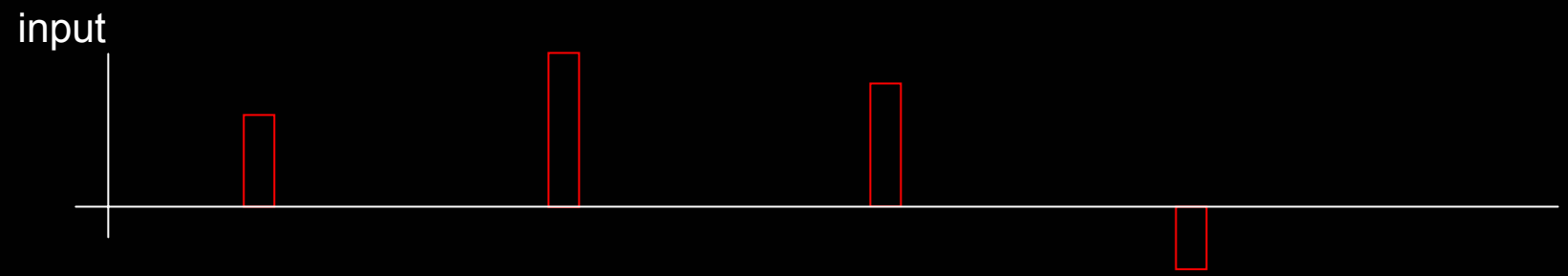
Outline

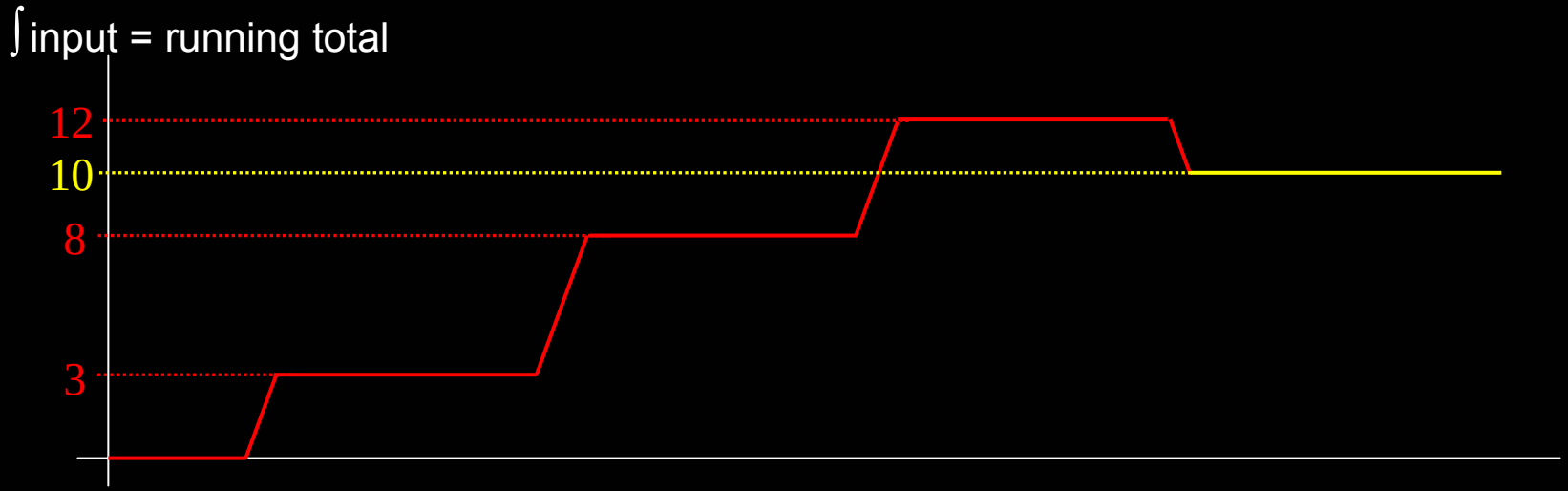
1. What is the neural basis of short-term memory?
2. A model system: the Oculomotor Neural Integrator
3. Neural mechanisms of integration: Linear network theory

[4. Next lecture: Model critique – robustness in integrators and other neural systems]

Add up the following numbers:

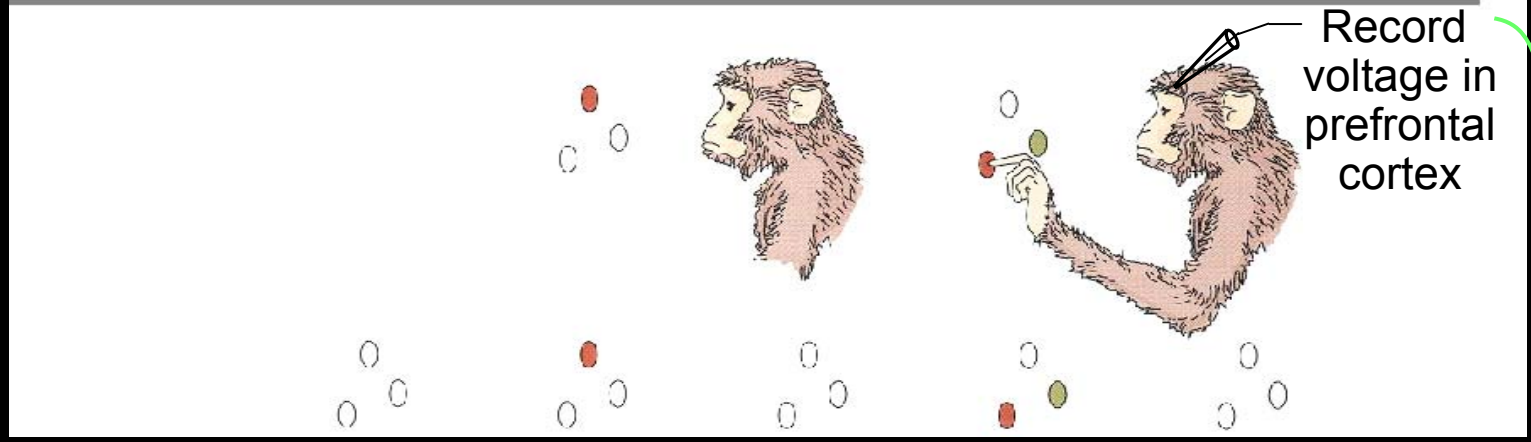
3 +5 +4 -2 =10

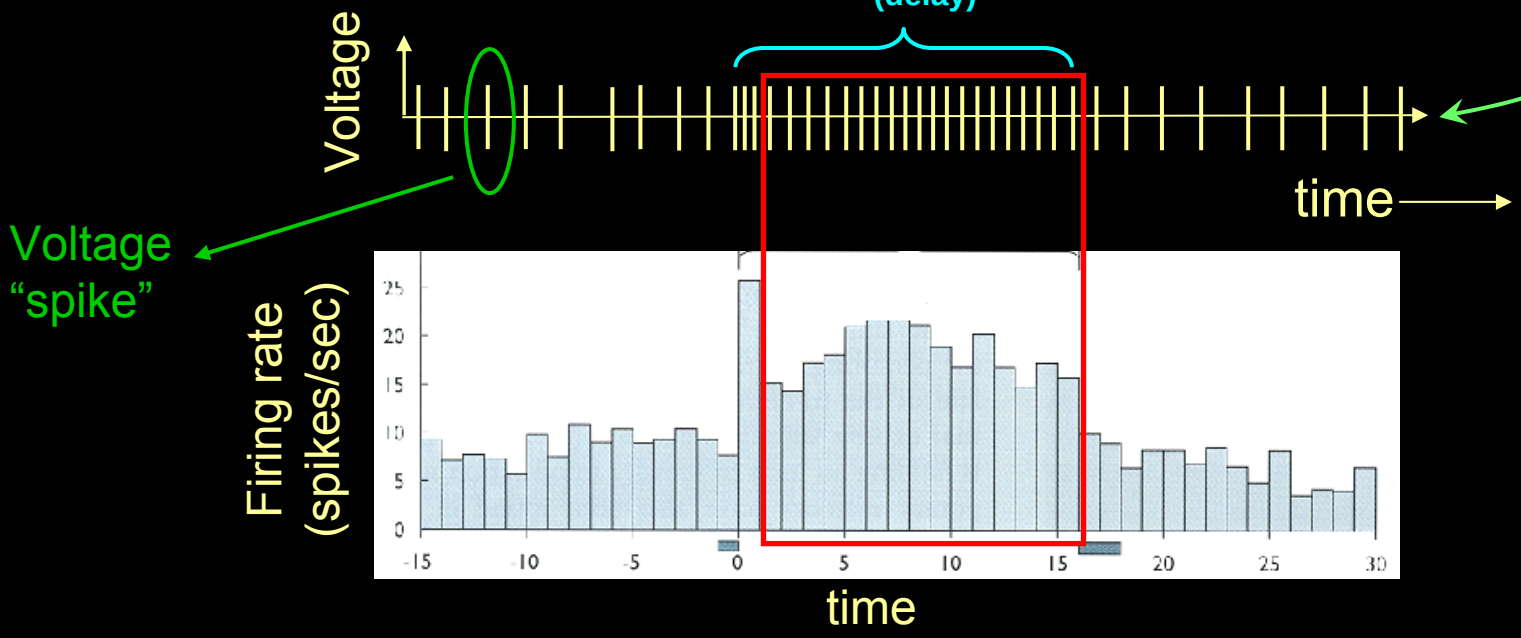




This task involves: 1. Addition
2. **Memory**

Delayed-match-to-sample task





Persistent neural activity is the neural correlate of short-term memory

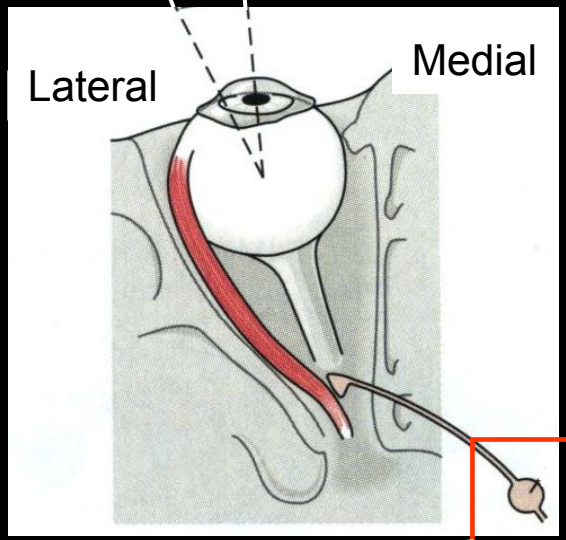
Characteristics of Persistent Neural Activity

- Sustained elevated (or reduced) firing rates lasting up to ~10's of seconds, long outlasting the stimulus
- Rapid onset, offset
- Mean firing rate an analog variable – a neuron can sustain any of many different levels of activity
- Stable *pattern* of activity among many neurons

Model system: eye fixation during spontaneous horizontal eye movements

Carassius auratus (goldfish)

The Oculomotor Neural Integrator



Eye position E (degrees)

Lateral (+)

Medial (–)

time

Motor neurons (position signal)

readout

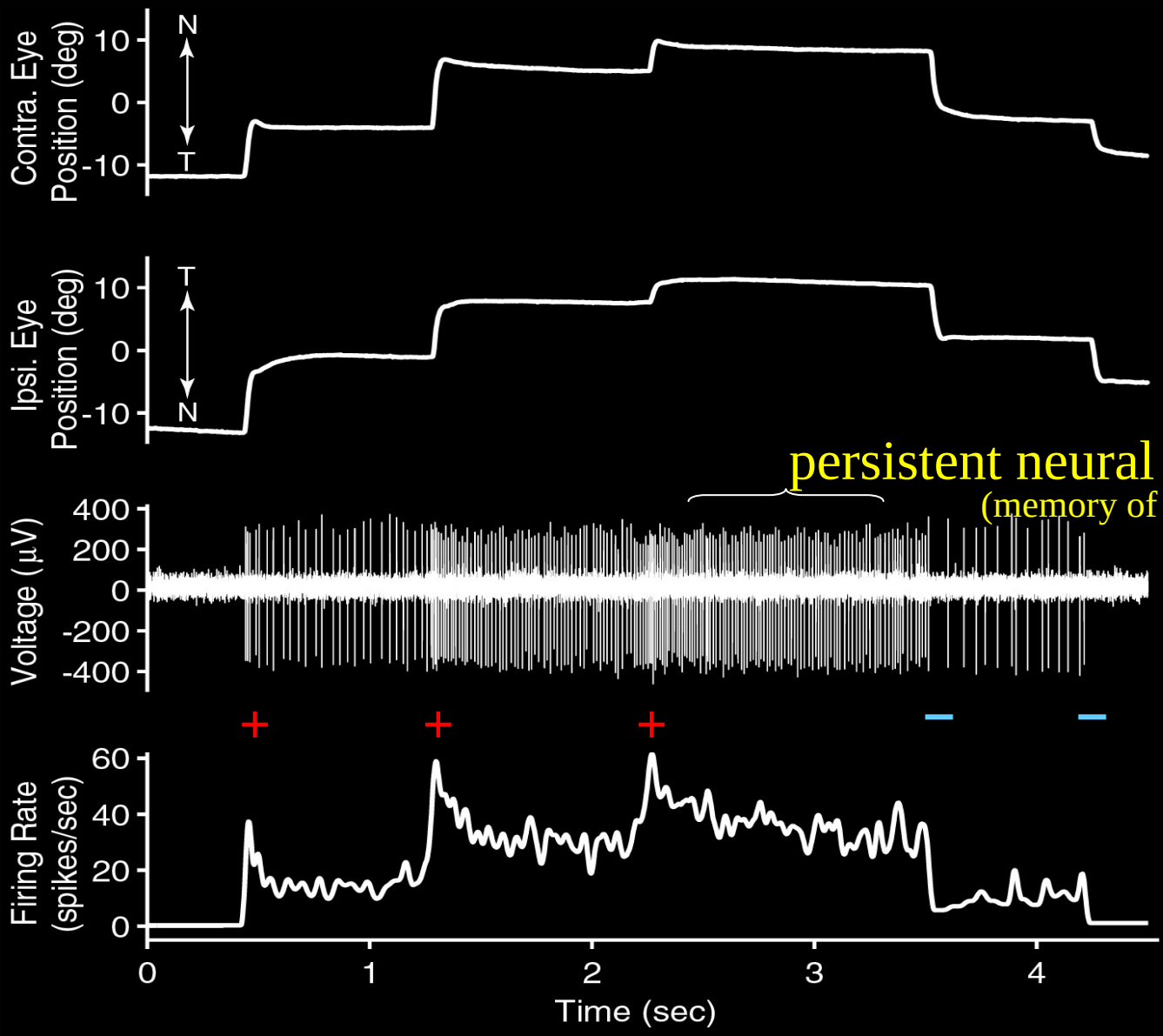
Integrator neurons

Eye movement "burst" neurons (velocity signal)

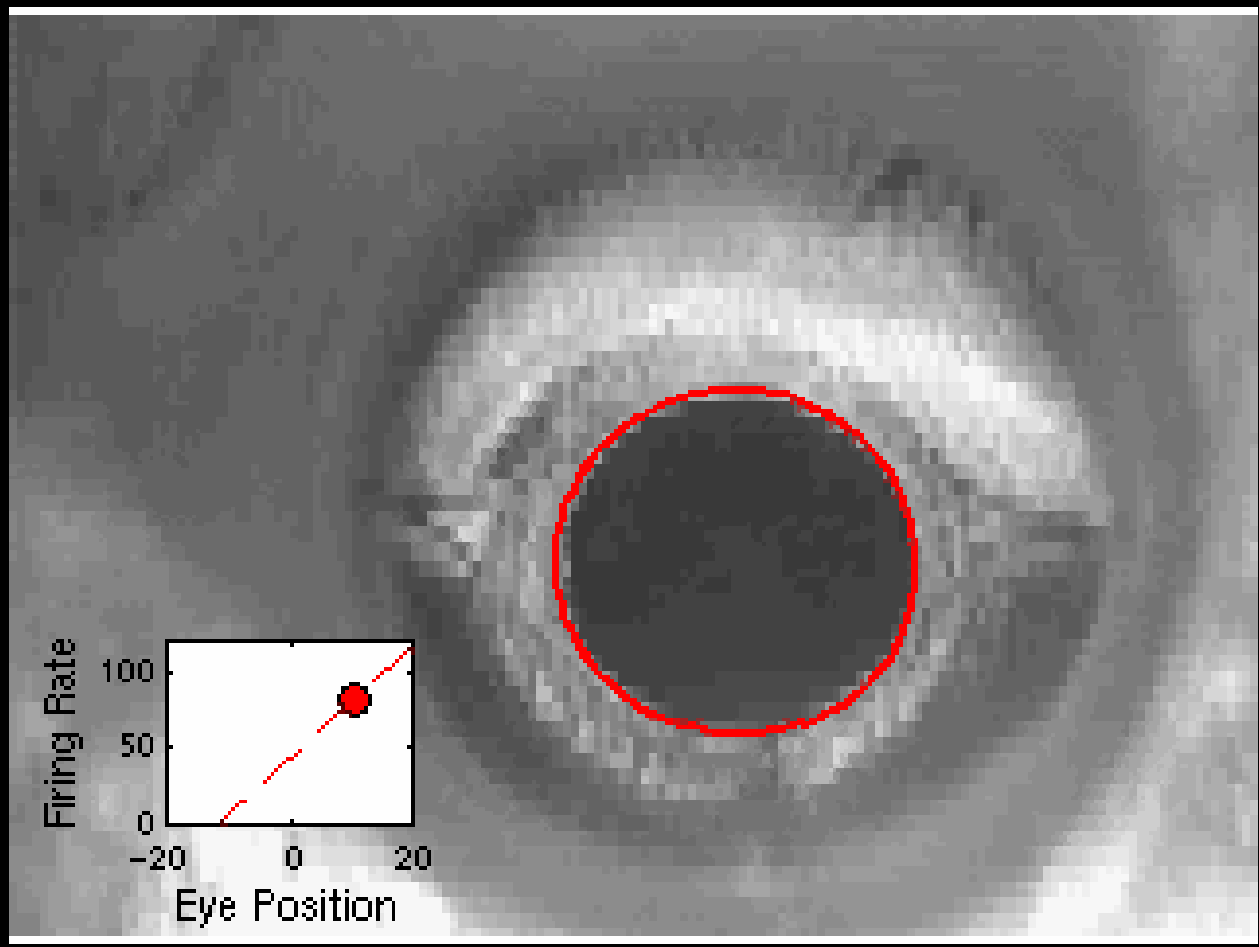
(+) direction

(–) direction

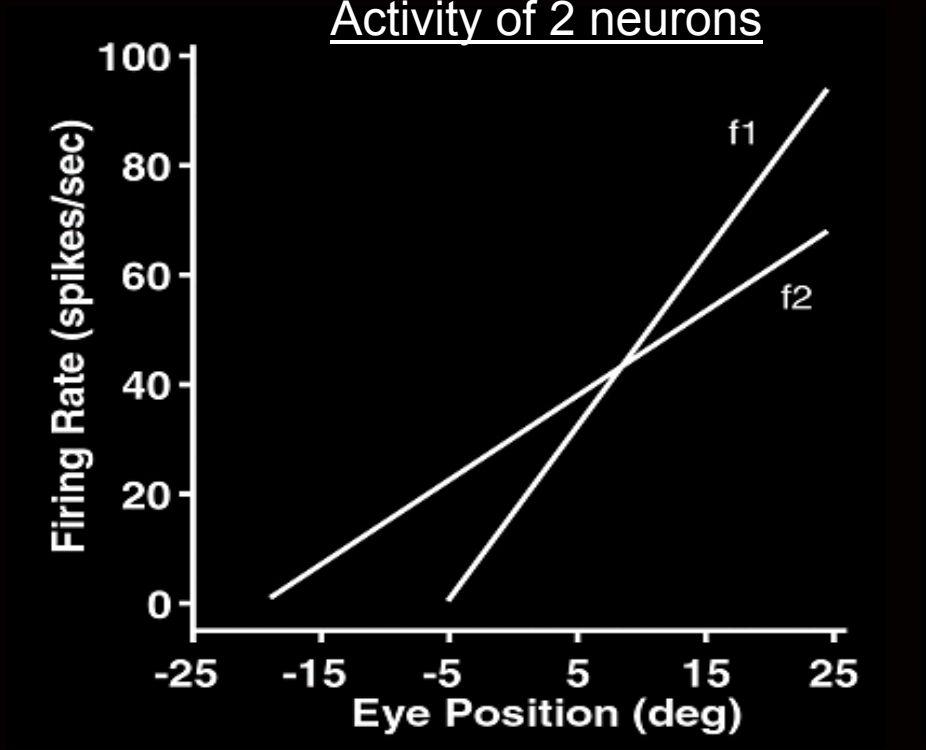
Neural Recording from the Oculomotor Integrator

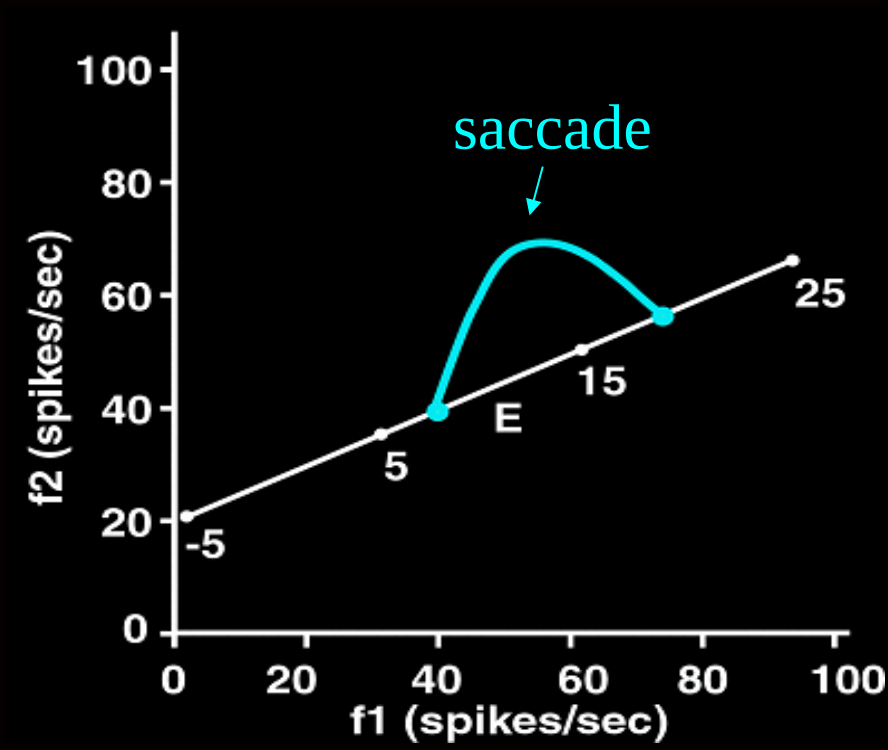


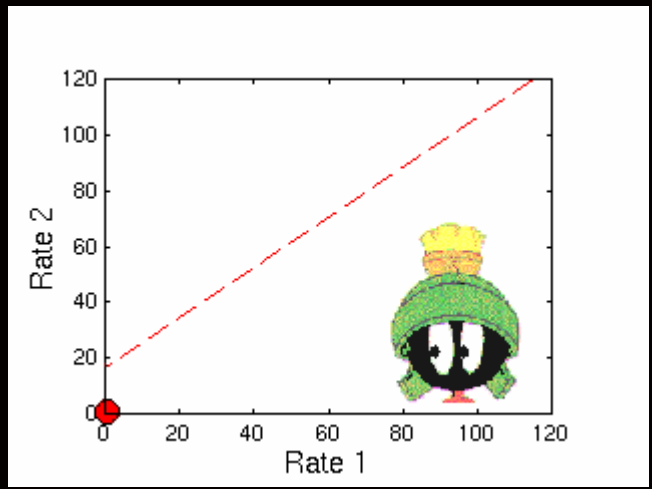
Integrator Neurons:
Firing Rate is Proportional to Eye Position



Many-neuron Patterns of Activity Represent Eye Position



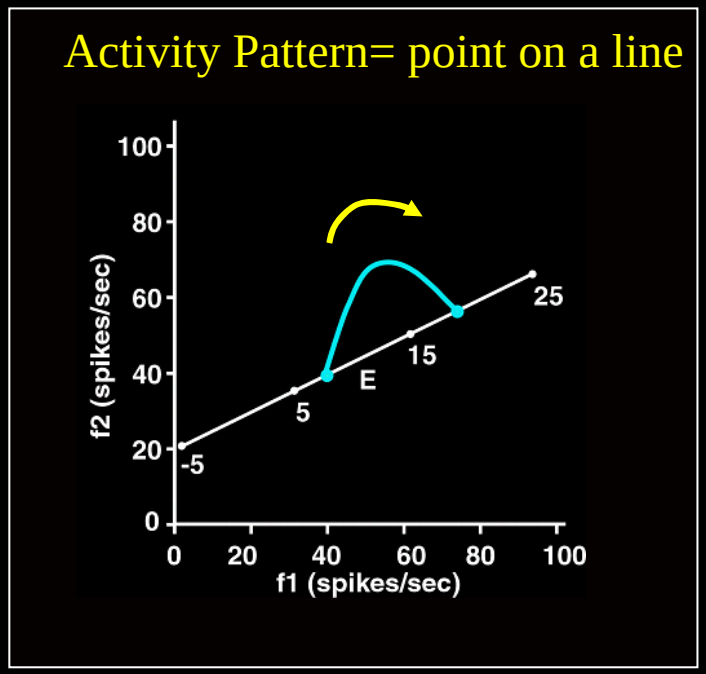




eye position represented by location along a low dimensional manifold ("line attractor")

(H.S. Seung, D. Lee)

General Principle?



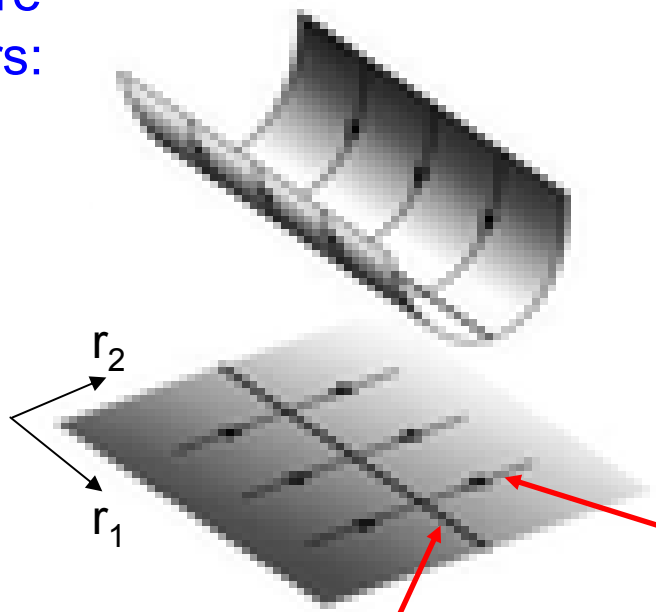
Neural integrators operate by using their input to shift internally-generated patterns of activity along a coordinate (coding) axis.

Persistent activity patterns are the integrator "memory" of previous inputs

Mechanisms and Models of Persistent Neural Activity

Line Attractor Picture of the Neural Integrator

Geometrical picture of eigenvectors:



Axes = firing rates of 2 neurons

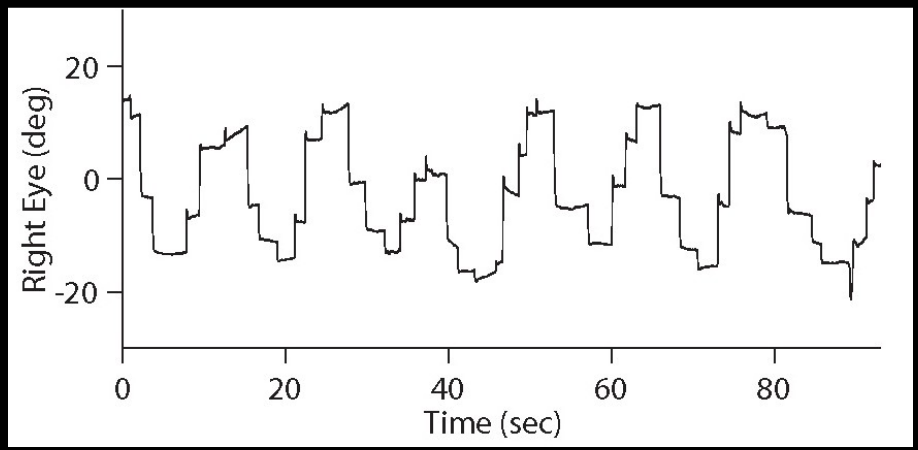
Decay along direction of decaying eigenvectors

No decay or growth along direction of eigenvector with eigenvalue = 1

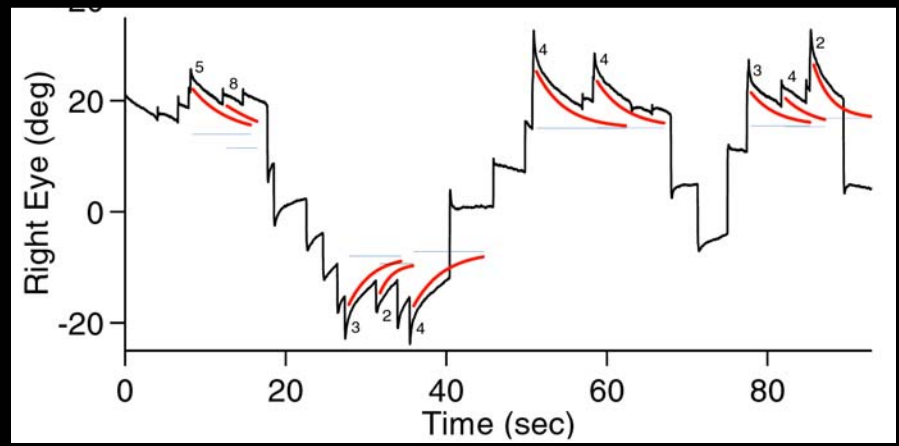
"Line Attractor" or "Line of Fixed Points"

Effect of Bilateral Network Lesion

Control



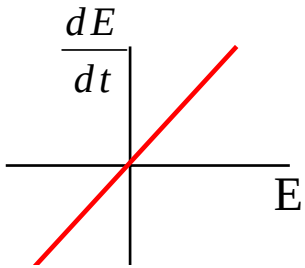
Bilateral Lidocaine:
Remove Positive Feedback

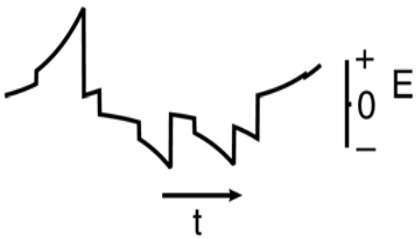


Unstable Integrator

Human with unstable integrator:

$$\frac{dE}{dt} = (w-1)E$$

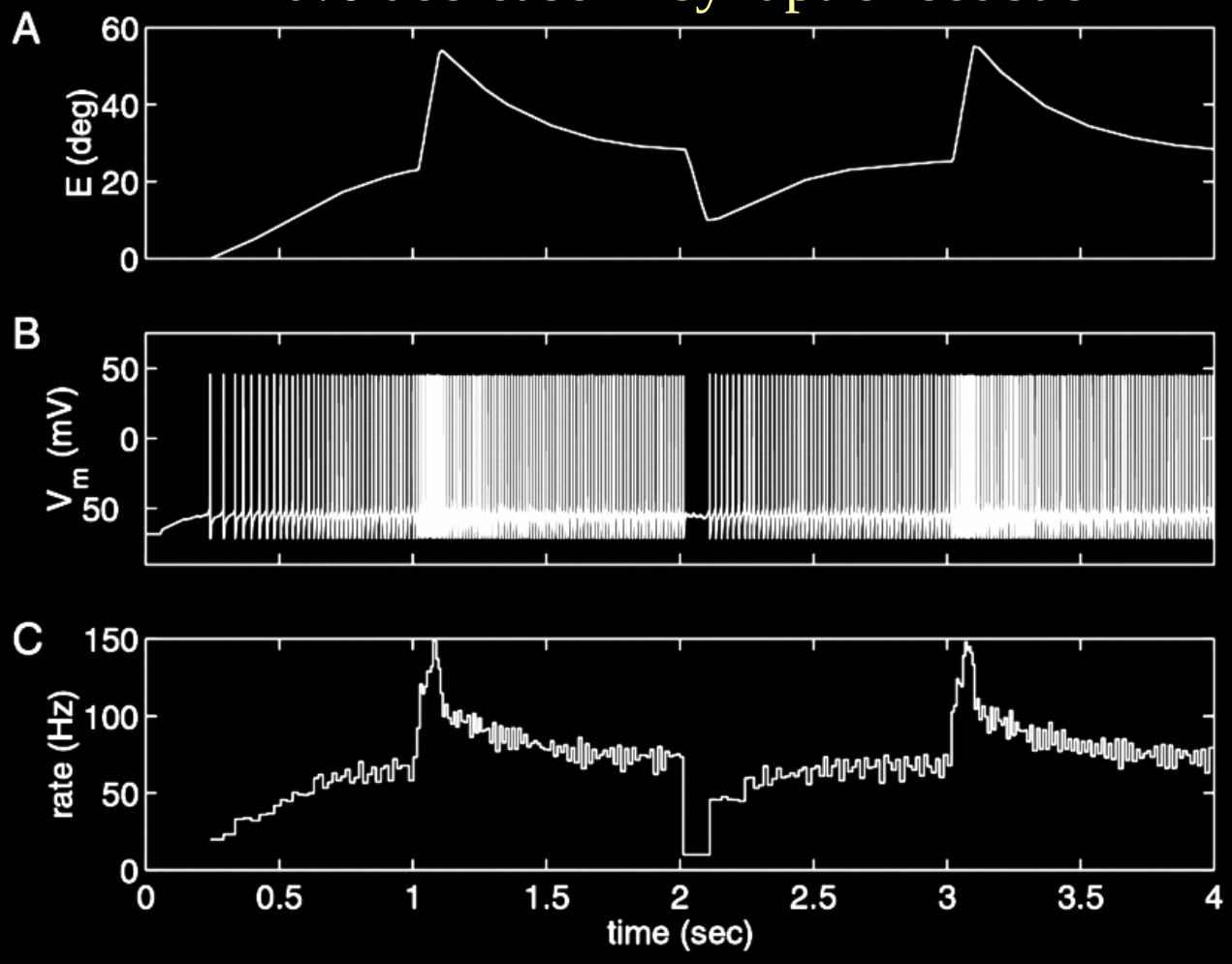




Weakness: Robustness to Perturbations

Imprecision in accuracy of feedback connections severely compromises performance (memory drifts: leaky or unstable)

10% decrease in synaptic feedback



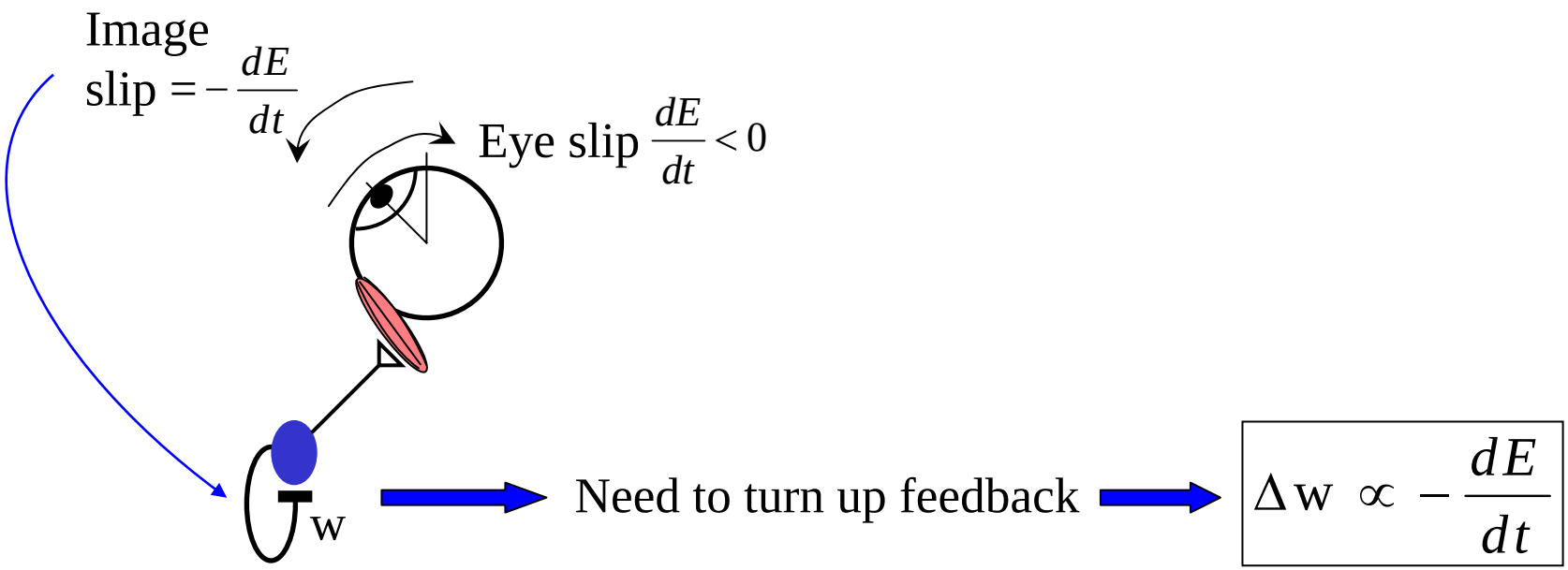
Learning to Integrate

How accomplish fine tuning of synaptic weights?

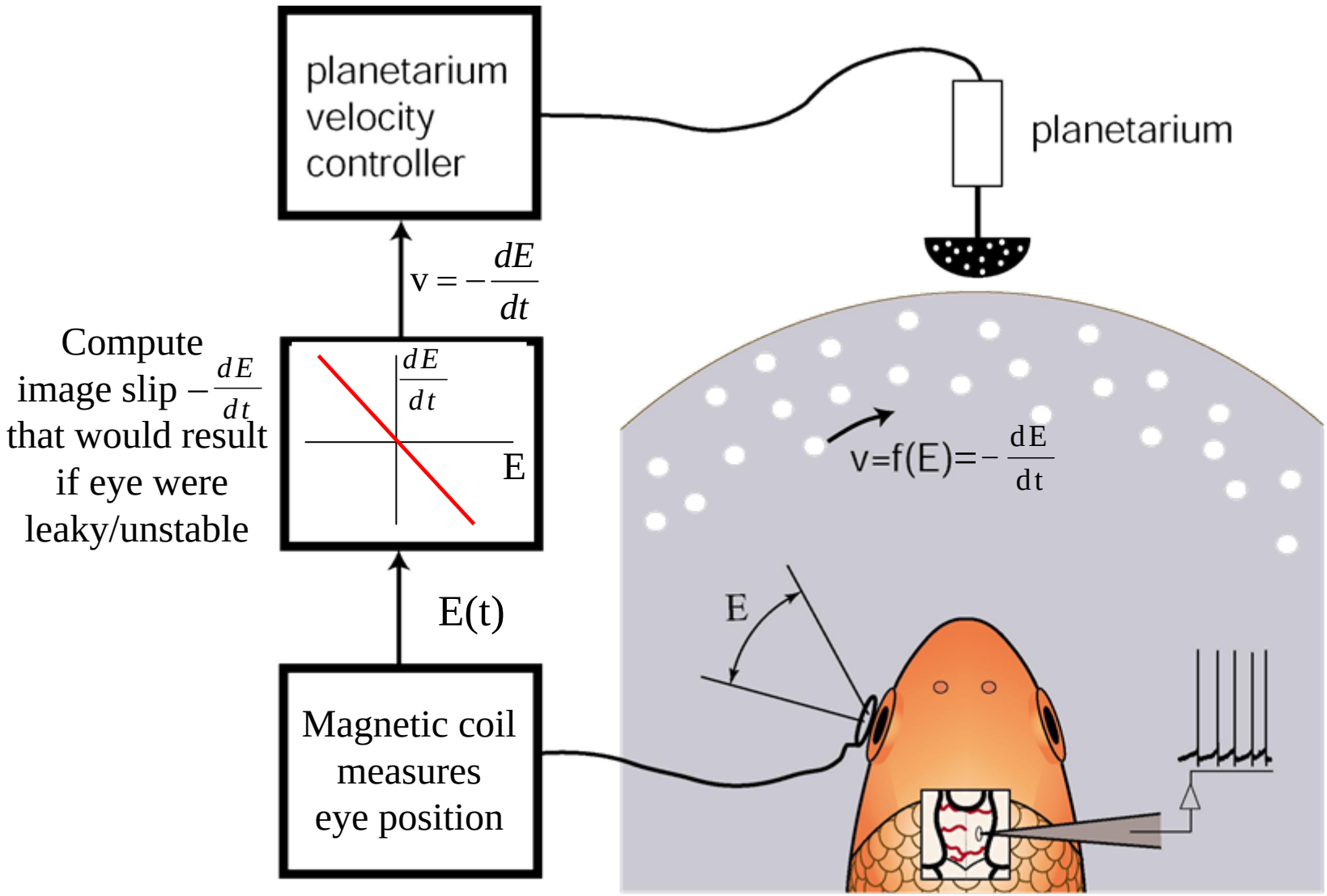
→ IDEA: Synaptic weights w learned from "image slip"

(Arnold & Robinson, 1992)

E.g. leaky integrator:



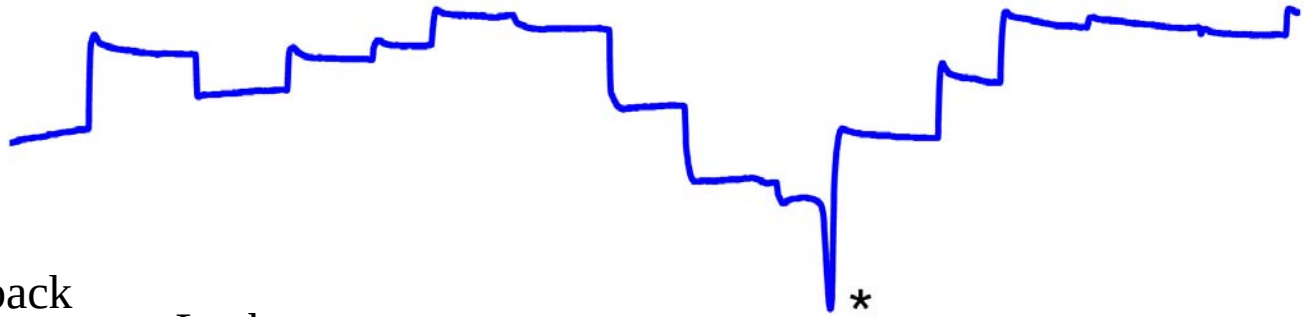
Experiment: Give Feedback as if Eye is Leaky or Unstable



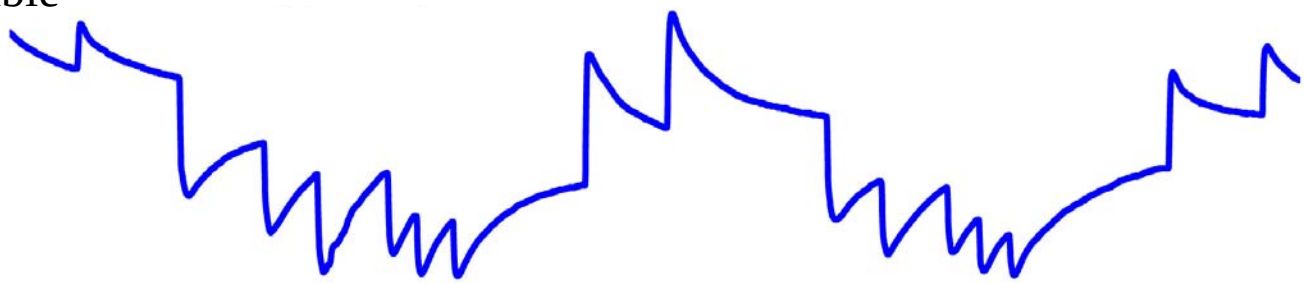

LOOK
HERE
Planetarium
Search
Coils
z-axis
rate table

Integrator Learns to Compensate for Leak/Instability!

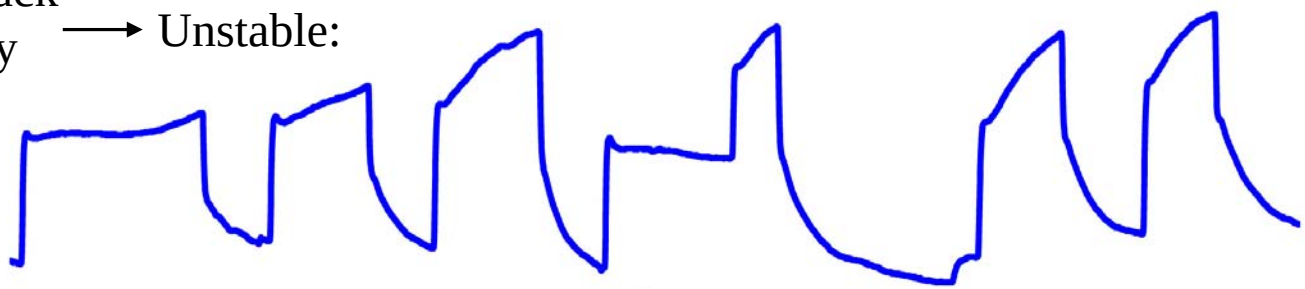
Control (in dark):

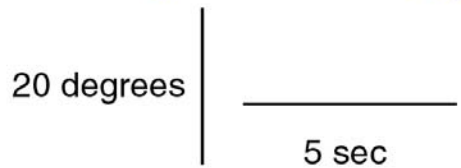


Give feedback as if unstable → Leaky:



Give feedback as if leaky → Unstable:





Summary

Persistent neural activity: activity which outlasts a transient stimulus

Neural integrator: outputs the mathematical integral of its inputs
-in the absence of input, maintains persistent neural activity

Oculomotor neural integrator:
-converts eye-velocity encoding inputs to eye position outputs
-Mechanism:
-Anatomy and physiology suggest network contribution
-Issue of Robustness:
Simple models are less robust to perturbations than the real system
But: -Plasticity may keep the system tuned on slow time scales
-On faster time scales, intrinsic cellular processes may provide a “friction-like” slowing of network decay