

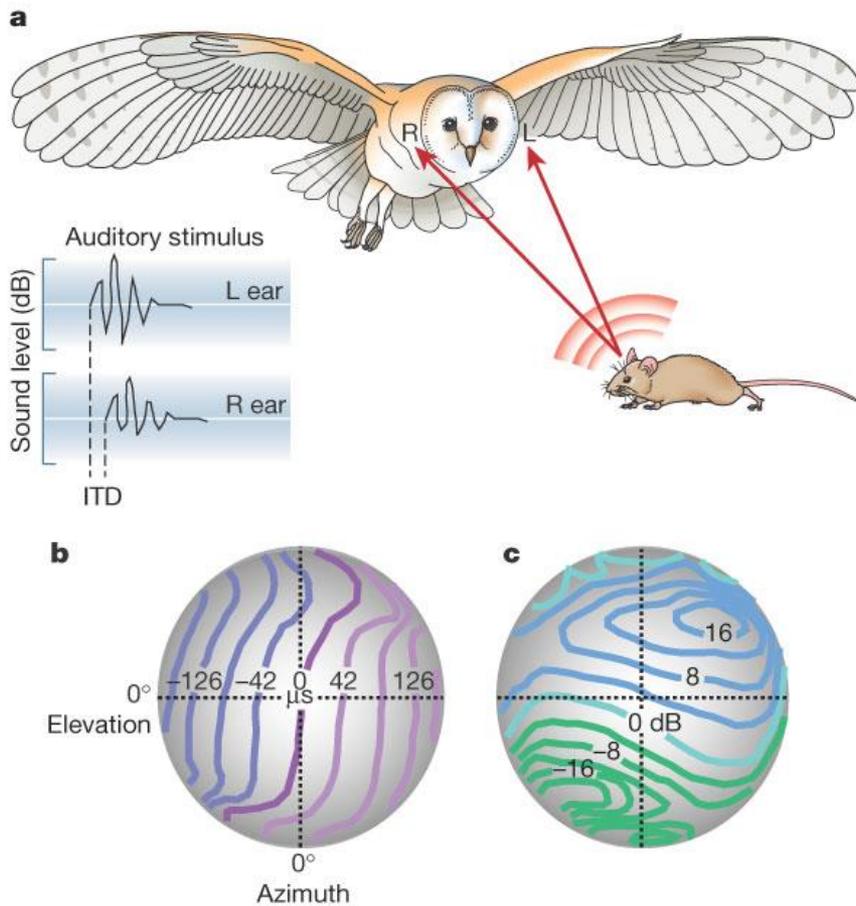
A neuronal learning rule for sub-millisecond temporal coding

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Barn owl (*Tyto alba*) locates prey with precision of 1-2 degrees

that requires time precision of less than 5 μ s.

How?



Phase locking





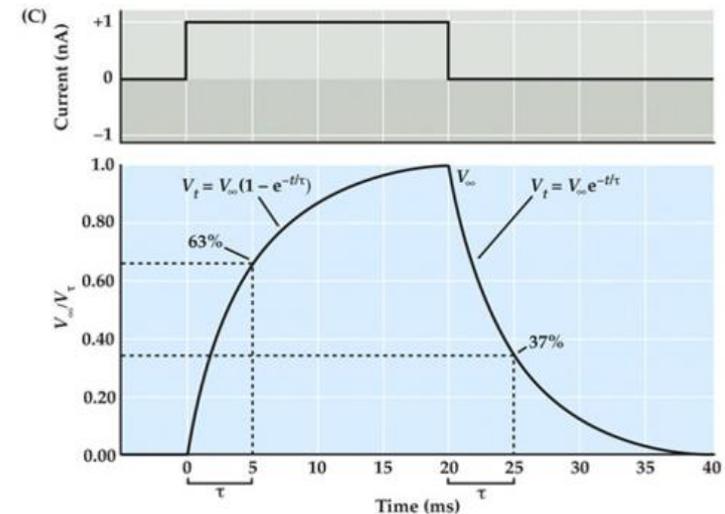
Time-coding

Very precise

Synaptic input current τ_s

Membrane time constant $\tau_m = r_m C_m$

e.g. width of single **excitatory postsynaptic potential** at half maximum (63%) amplitude





Time-coding



Synaptic input current $\tau_s = 200 \mu\text{s}$
Membrane time constant $\tau_m = 2 \text{ ms}$



PARADOX

Neurons are 10x slower than behavioral sensitivity to time differences

Can neuronal firing be more precise than the neuronal processes involved?

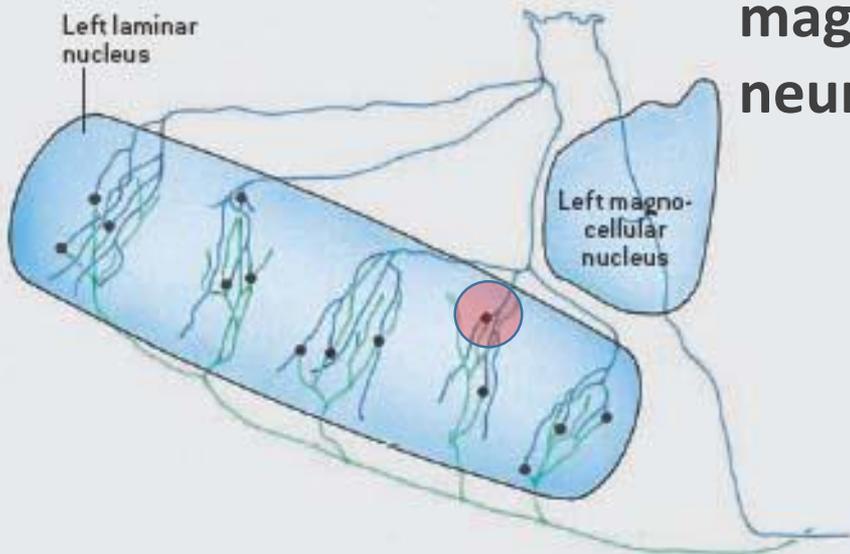


Model: 'integrate-and-fire' neuron

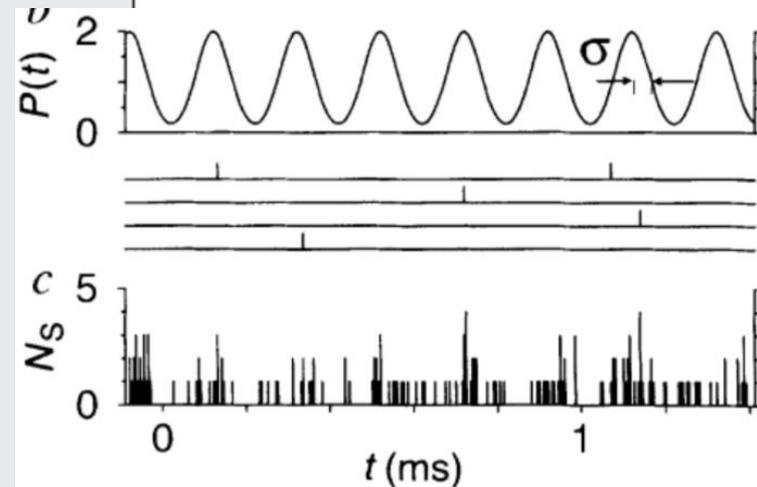
Input from
154 presynaptic
magnocellular
neurons

Single frequency pure tone
e.g. 5kHz, $T=200\mu\text{s}$

Input as sequence of spikes



Fibers from the magnocellular nucleus serve as delay lines, and neurons in the laminar nucleus act as coincidence detectors in the owl's brain. When impulses traveling through the left (blue) and right (green) fibers reach laminar neurons (black dots) simultaneously, the neurons fire strongly.

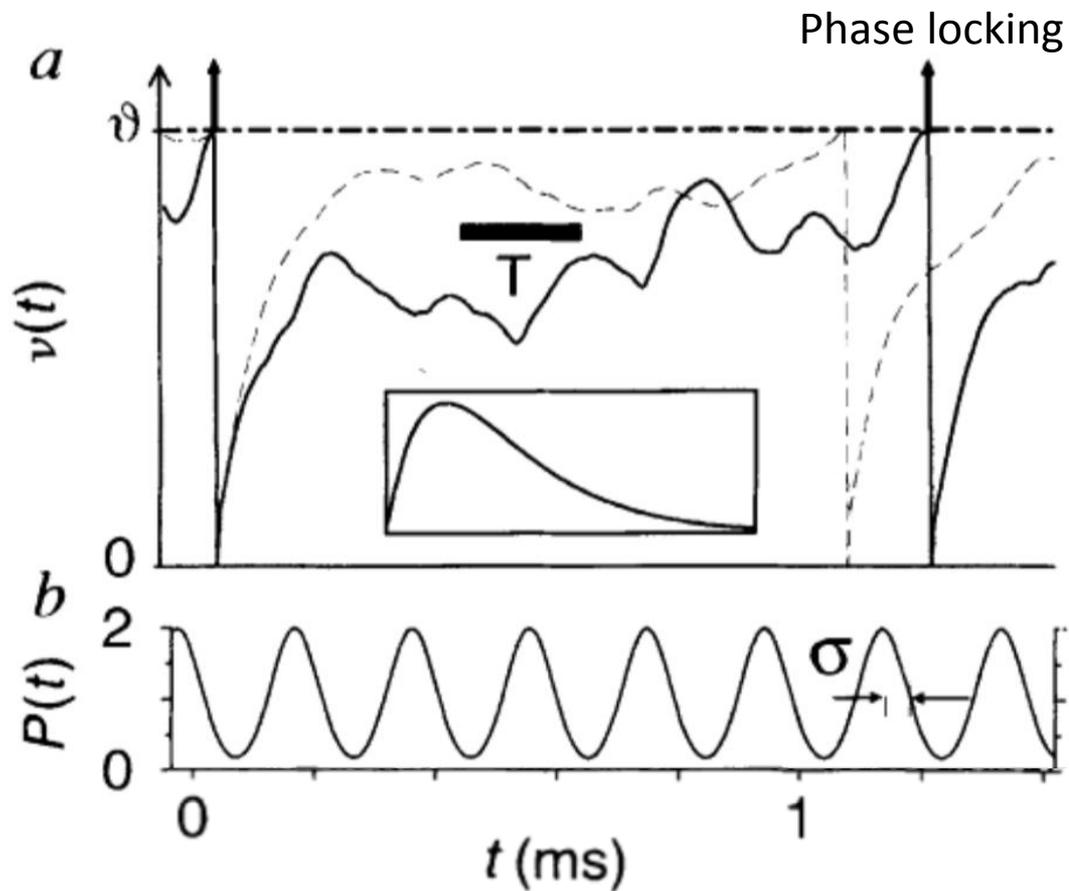


Specific mean phase of tone

40 μs 'jitter' as noise



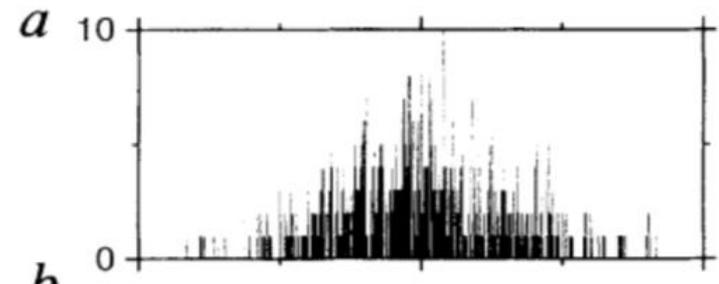
Accurate phase locking



Input with a **coherent common mean phase** leads to oscillating membrane potential

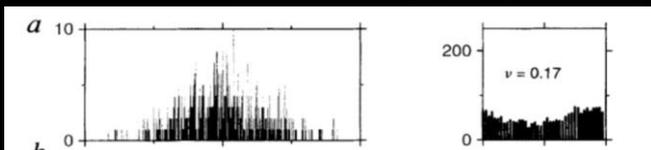
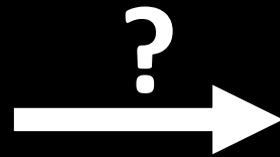
Random phase input leads to aperiodic fluctuations,

i.e. the output spikes have uniform distribution:





For adults
signal
transmission
delay from ear
to laminar
nucleus differs
greatly



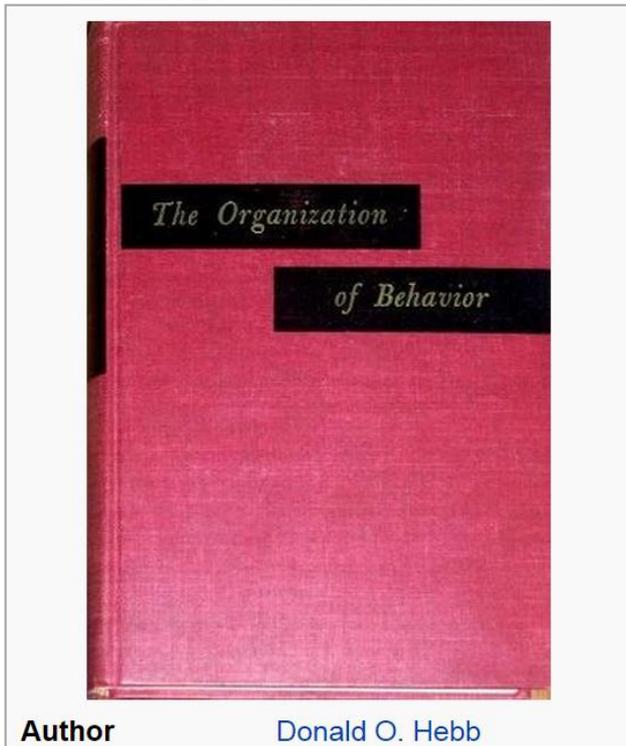
Left: Signal transmission delay for 600 synapses

Right: Output phases



Hebbian learning rule

The Organization of Behavior



‘Cells that fire together, wire together’

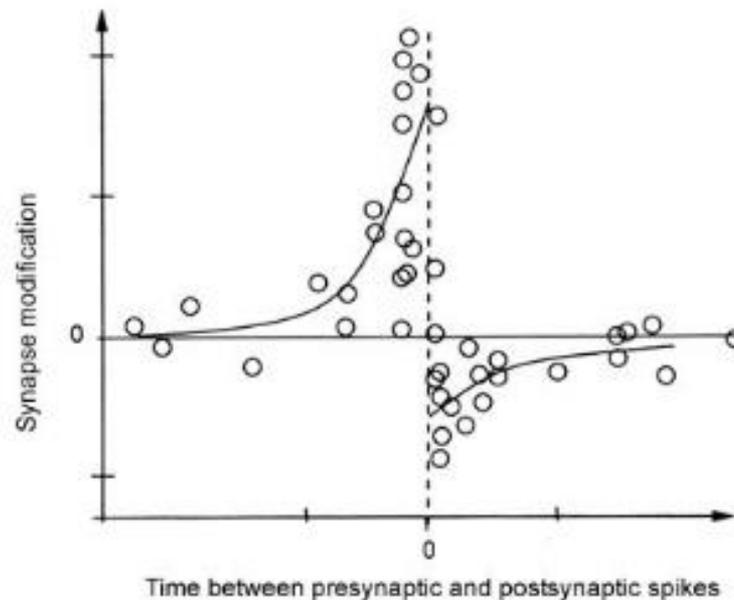
In reality ‘just before’

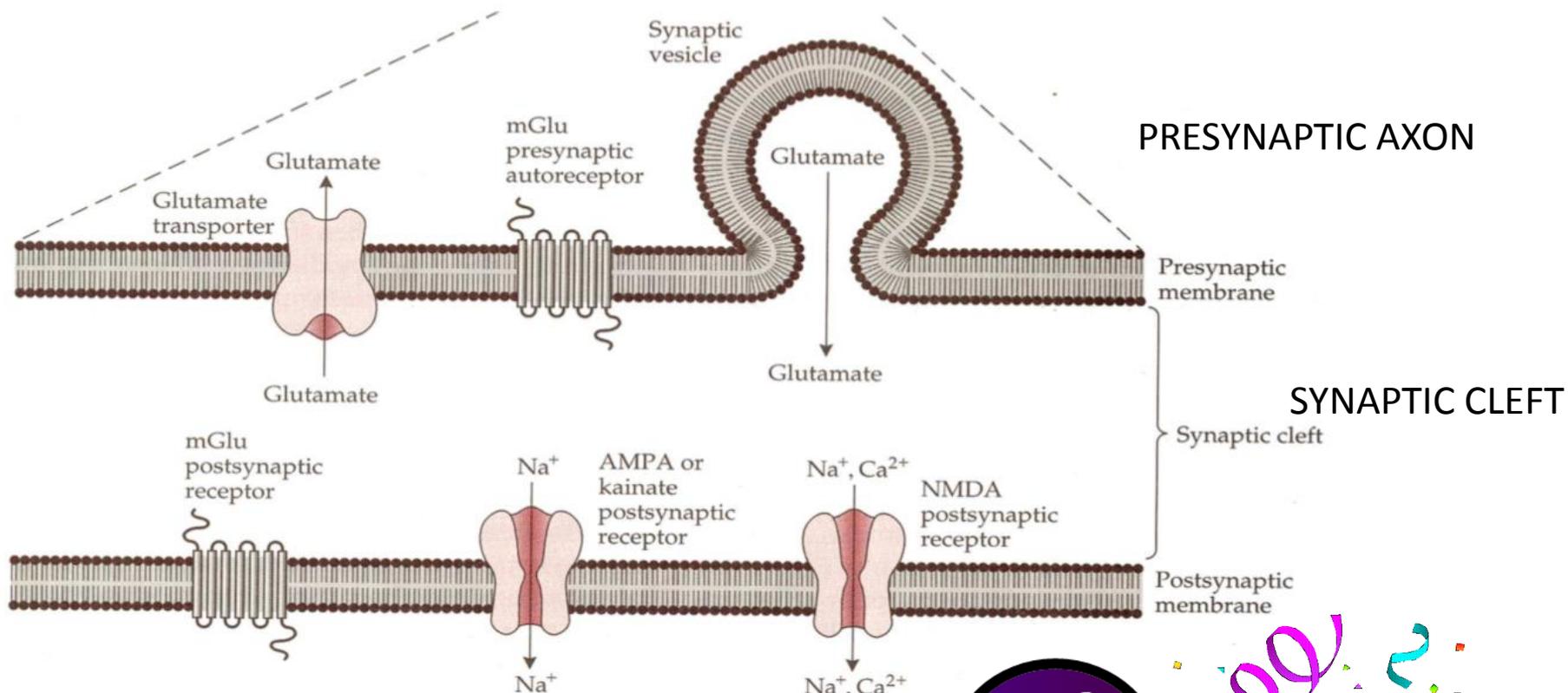
Adaptation during learning



Spike-timing-dependent plasticity (STDP)

Important synapses are strengthened, *vice versa*



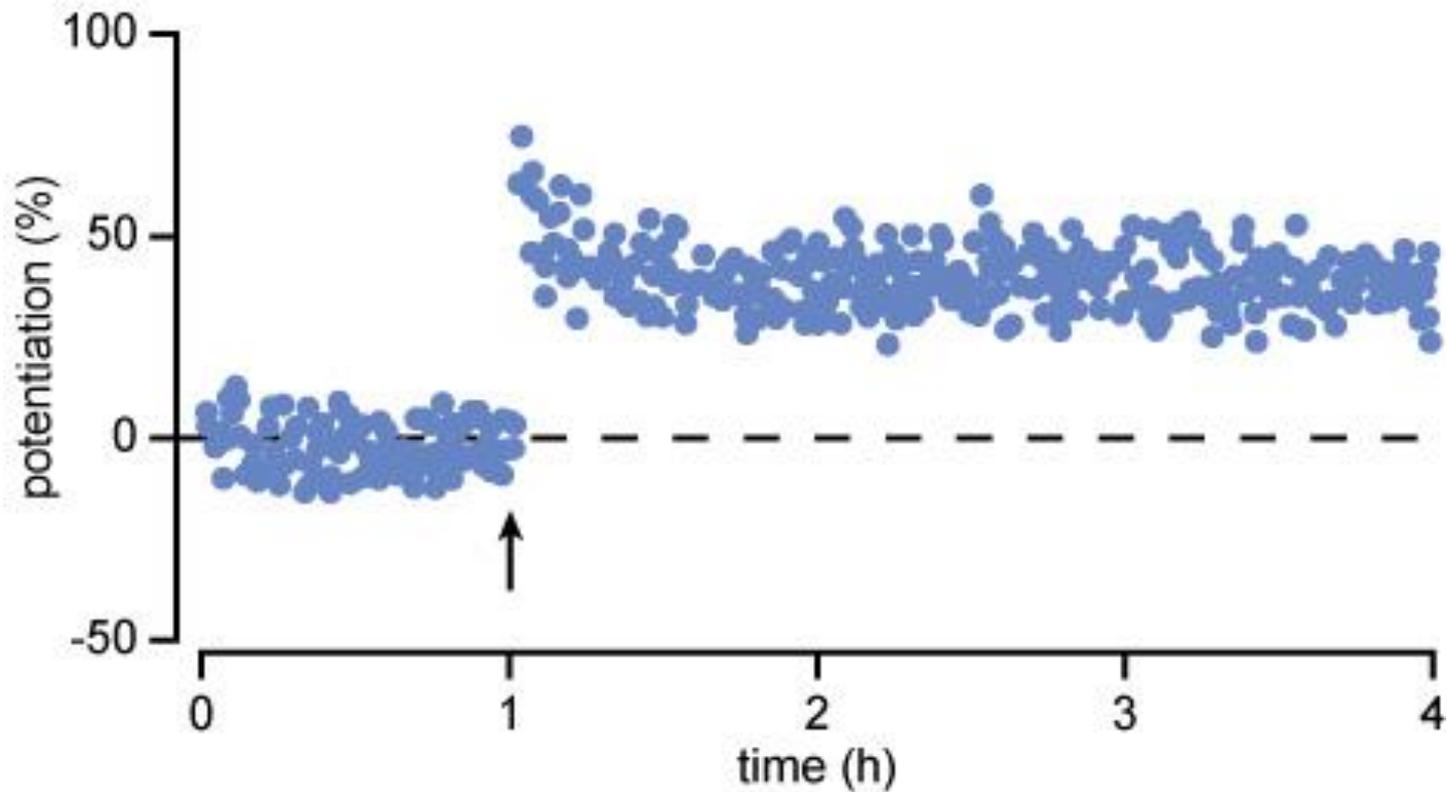


POSTSYNAPTIC DENDRITE





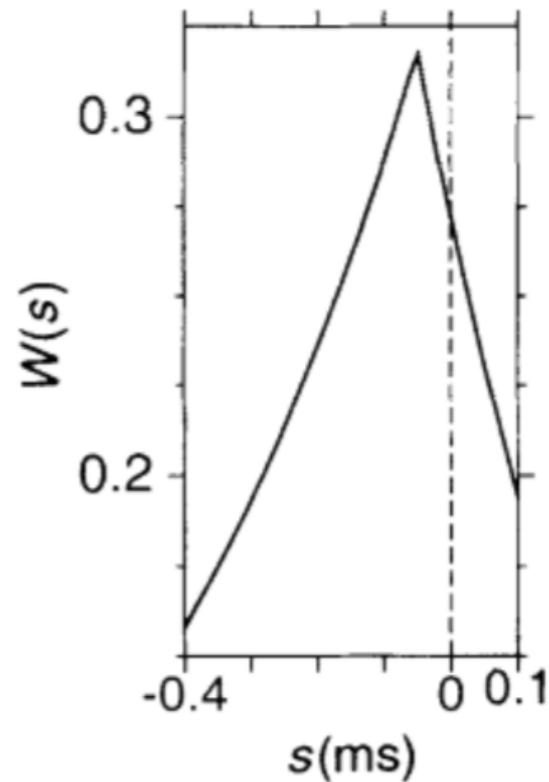
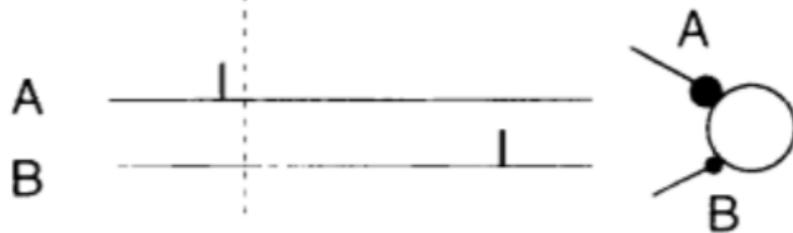
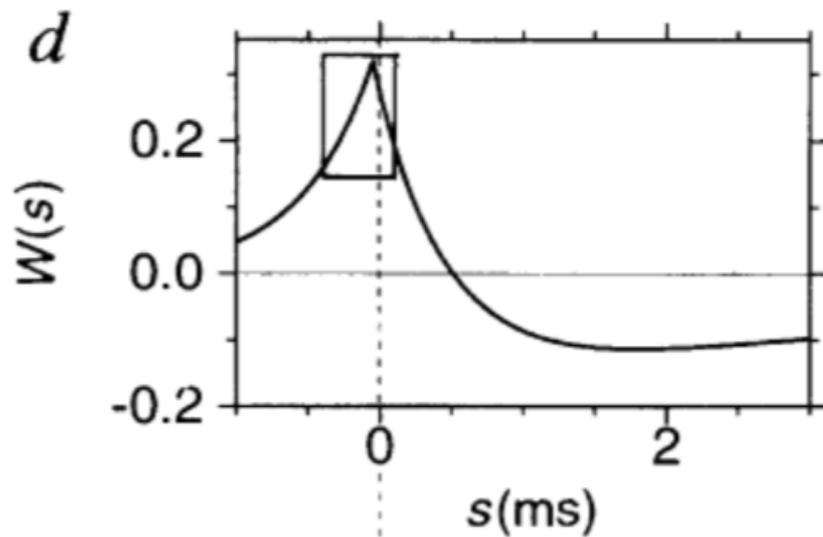
Long-term potentiation

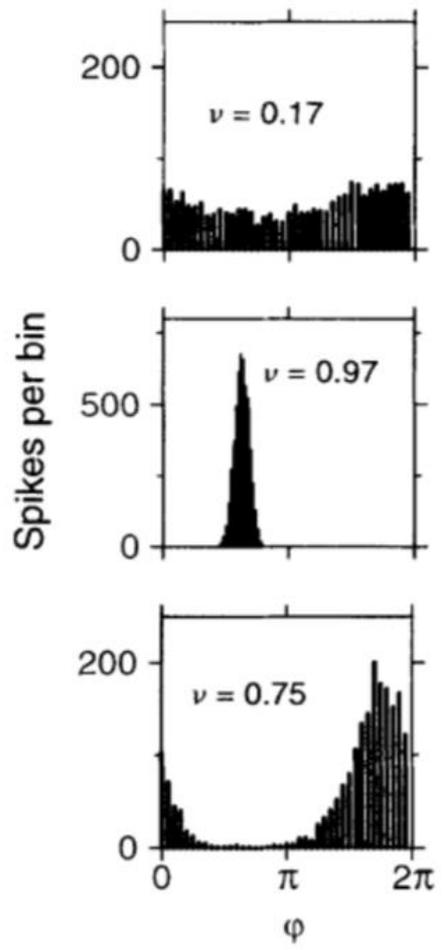
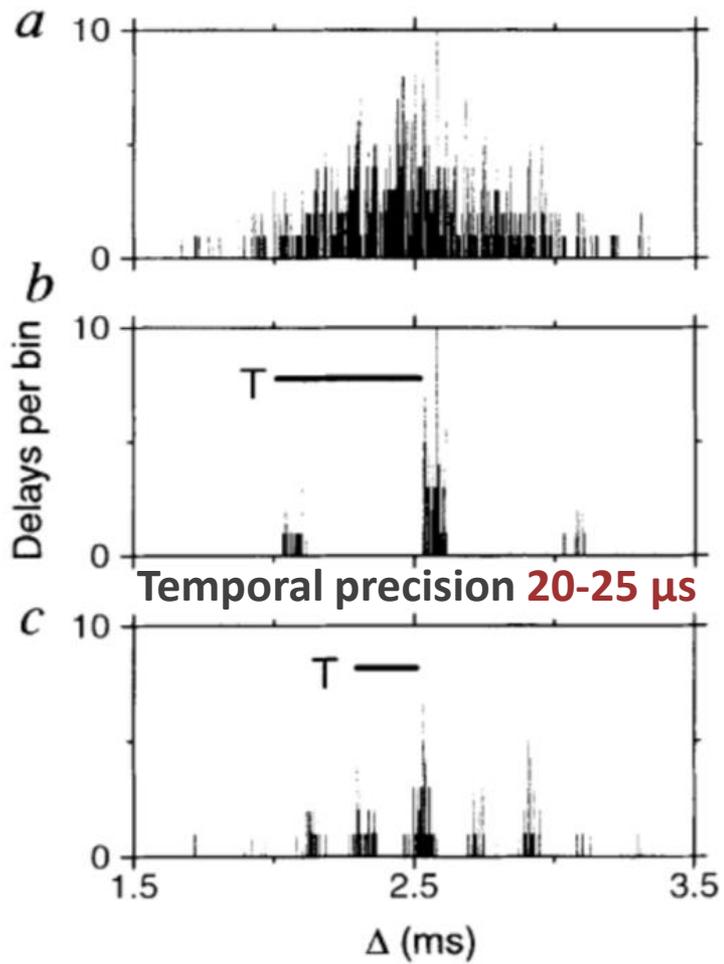




Learning interval $W(s)$

s – difference between presynaptic input and postsynaptic firing





Structured distribution

Delay period T

Not tuned previously

Different between inputs

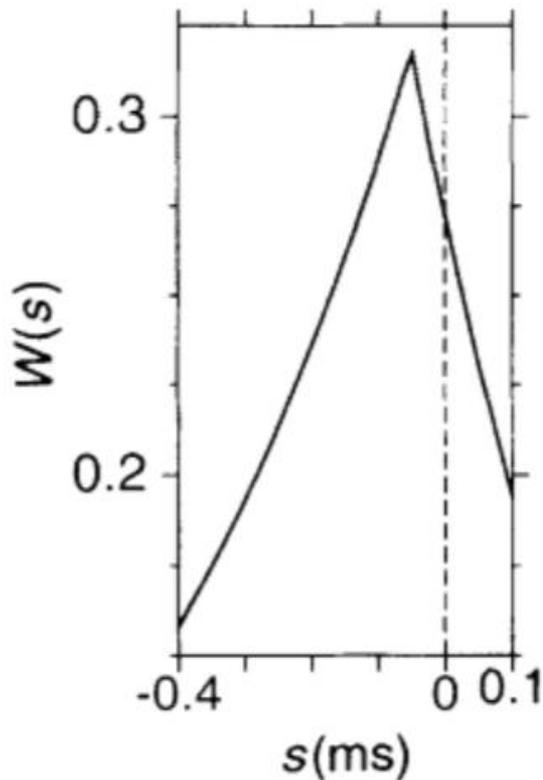


Efficacy does not depend on $W(s)$

$$\max(W(s)) = W(-\tau_s/2)$$

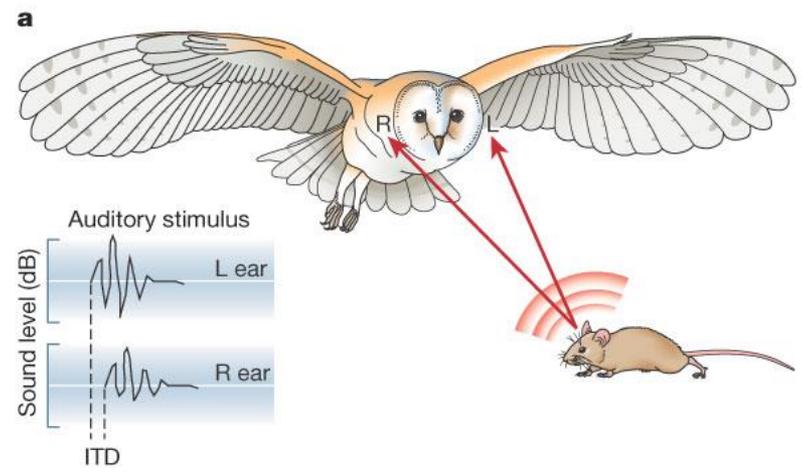
where τ_s is rise time of p.s.p.

I.e. coherently arriving input trigger p.s. spike with mean delay of $\tau_s/2$

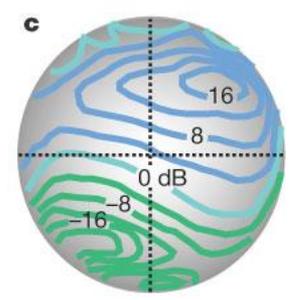
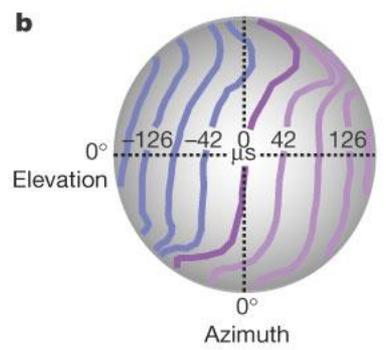
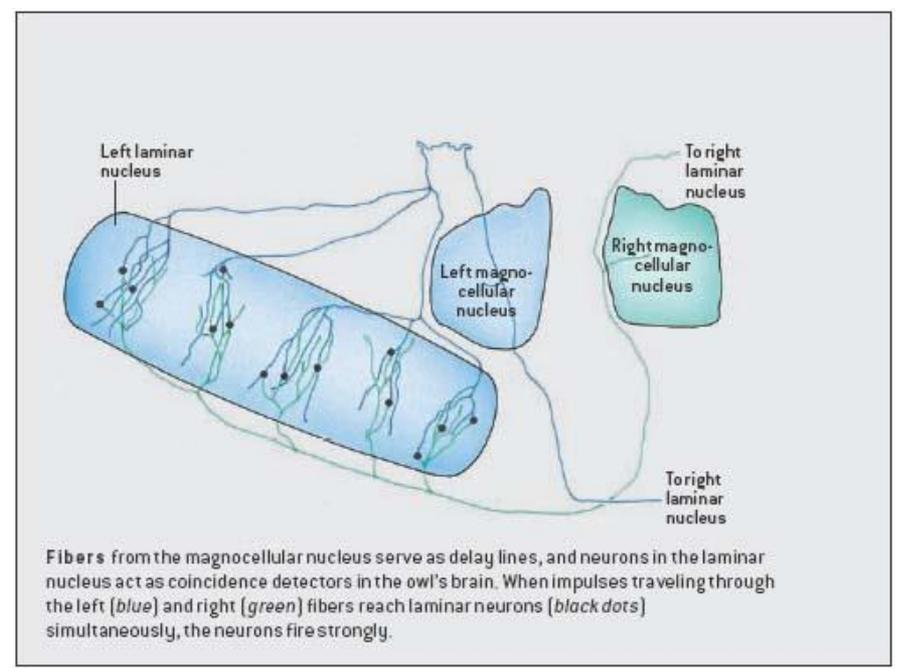




Interaural time difference (ITD)



Input from two ears

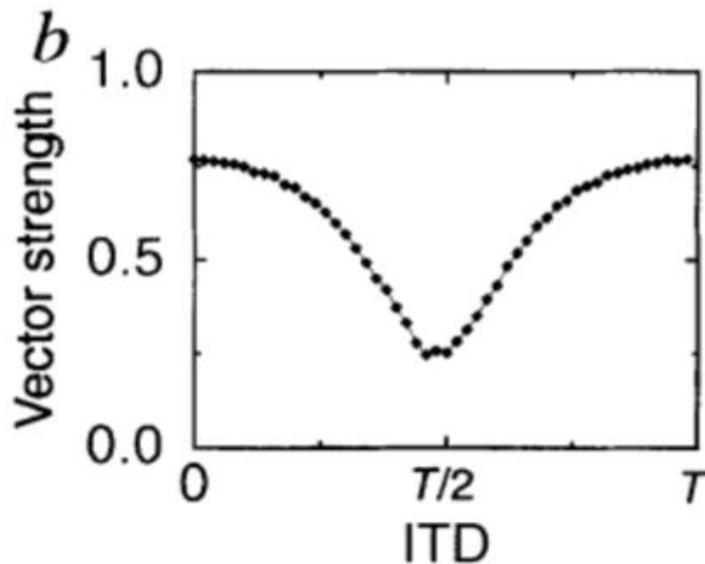
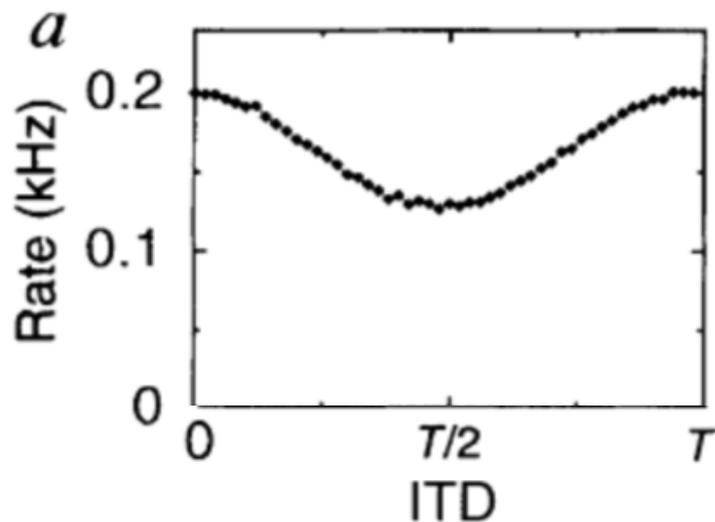




ITD tuning curve

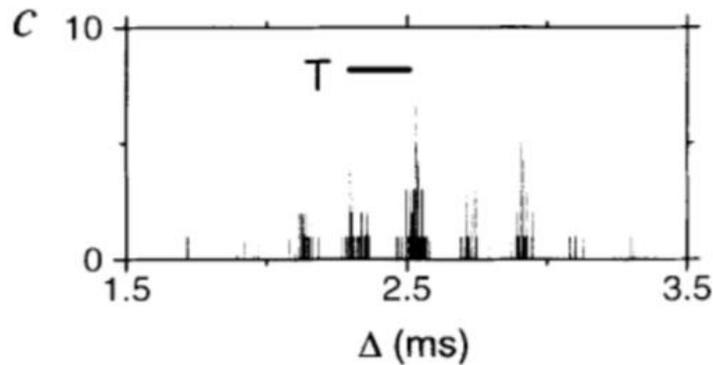
During learning, both ears are stimulated by the same signal and fixed ITD

If ITD does not match, phase locking breaks



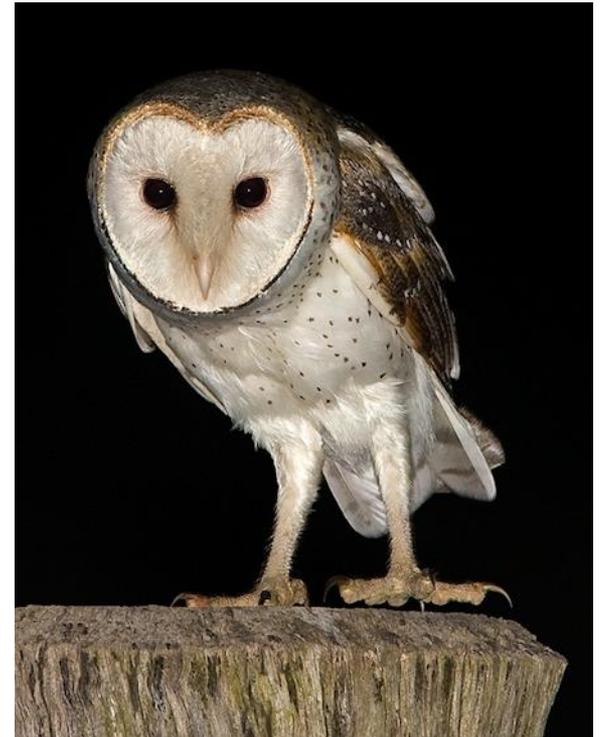


Single laminar neuron
precision is limited to 20-25 μ s



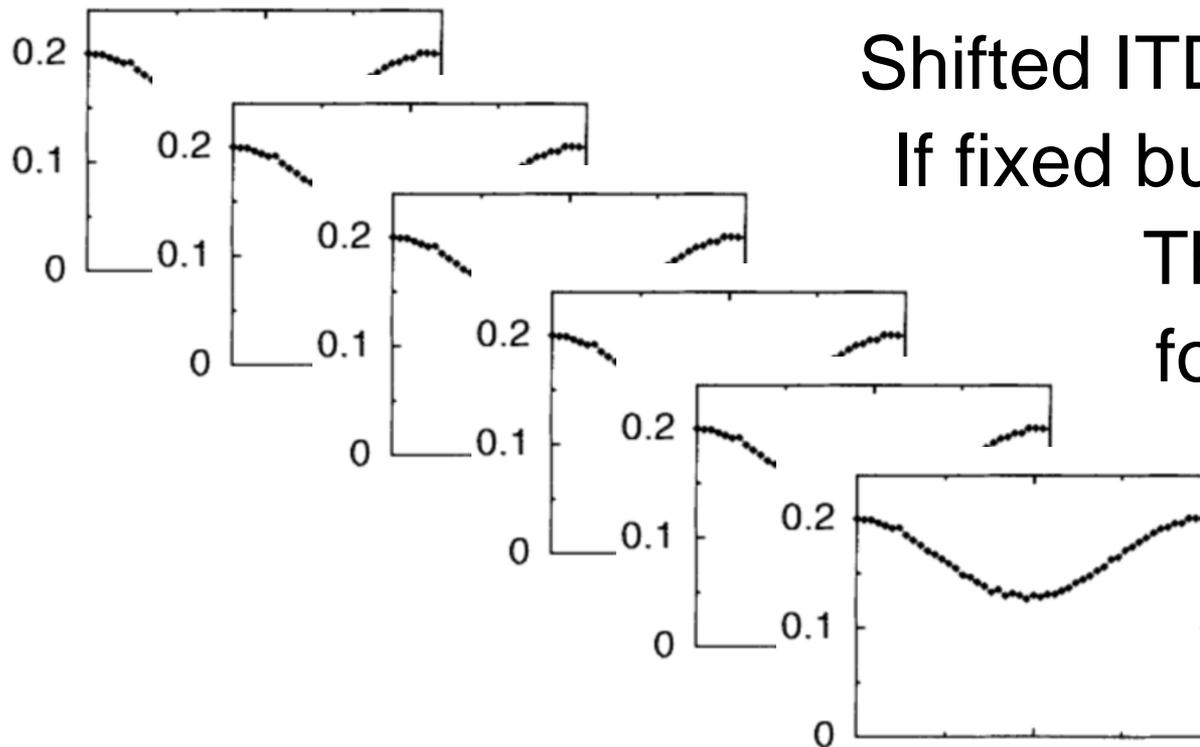
Barn owl temporal resolution
5 μ s

Ahaa! Reaction time 100 ms





Group of laminar neurons



Shifted ITD tuning curves

If fixed but unknown ITD

Then get optimal
for each neuron,

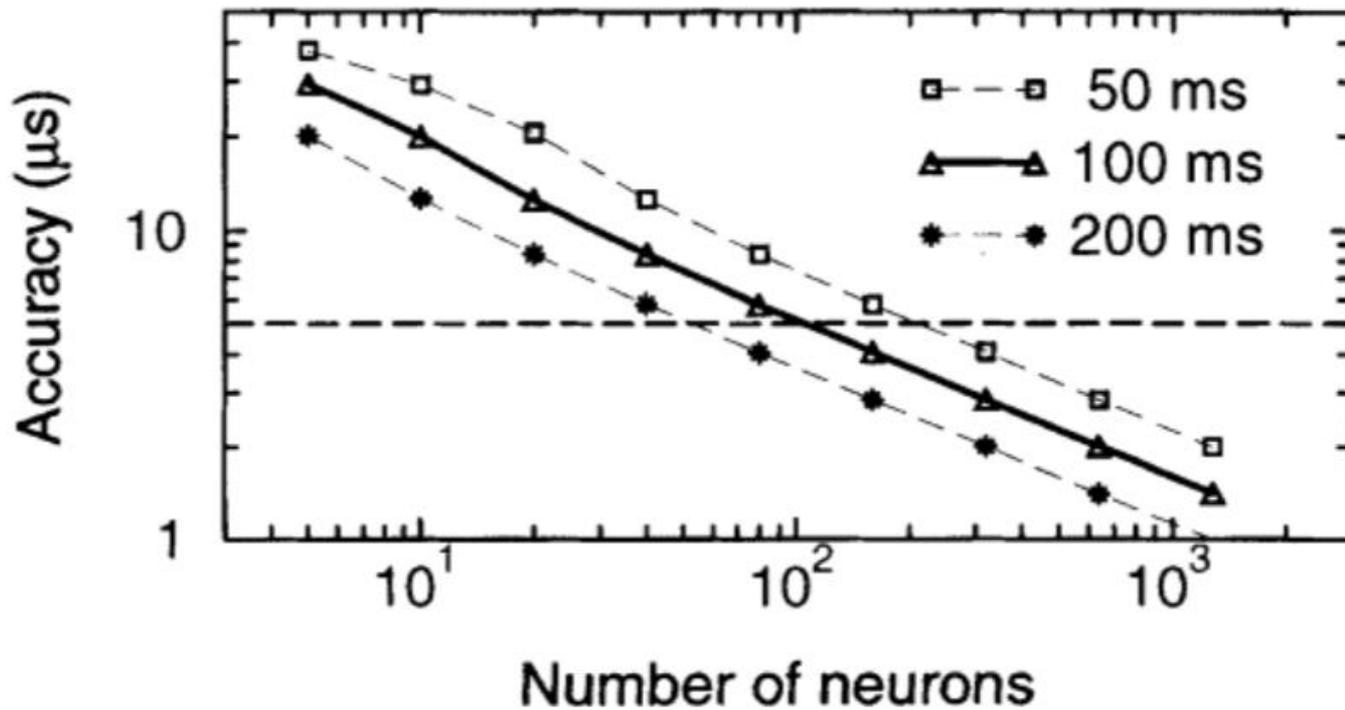
weighted by

N of spikes

per 100ms

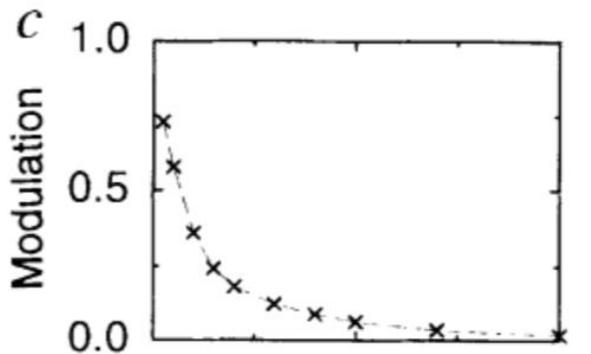


Population coding



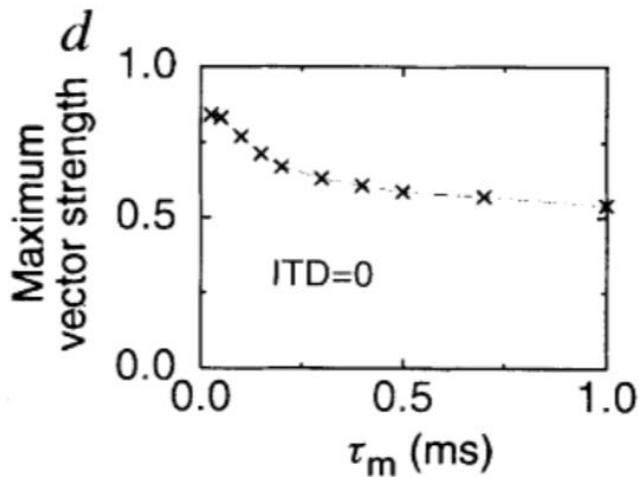


Membrane time constant



ITD tuning breaks down rapidly if τ_m exceeds 0.1 ms

Where modulation is $(f_{max} - f_{min})/f_{max}$



Temporal precision depends only weakly on τ_m



What does this tell us? (laconically)

Coherent input \rightarrow spike timing precision $\ll \tau_m$

Hebbian learning rule works

Works for two ears

Allows generalization: τ_m 10-20 ms, accuracy 1-3 ms



Reading

Gerstner, W., Kempter, R., van Hemmen, J. L., & Wagner, H. (1996). *Nature*, 383, 76-78

Carr, C. E. (1993). *Annual review of neuroscience*, 16(1), 223-243