Synchrony, Pattern Formation, and the Adiabatic Principle: How Neuronal and Synaptic Dynamics Cooperate on Different Time

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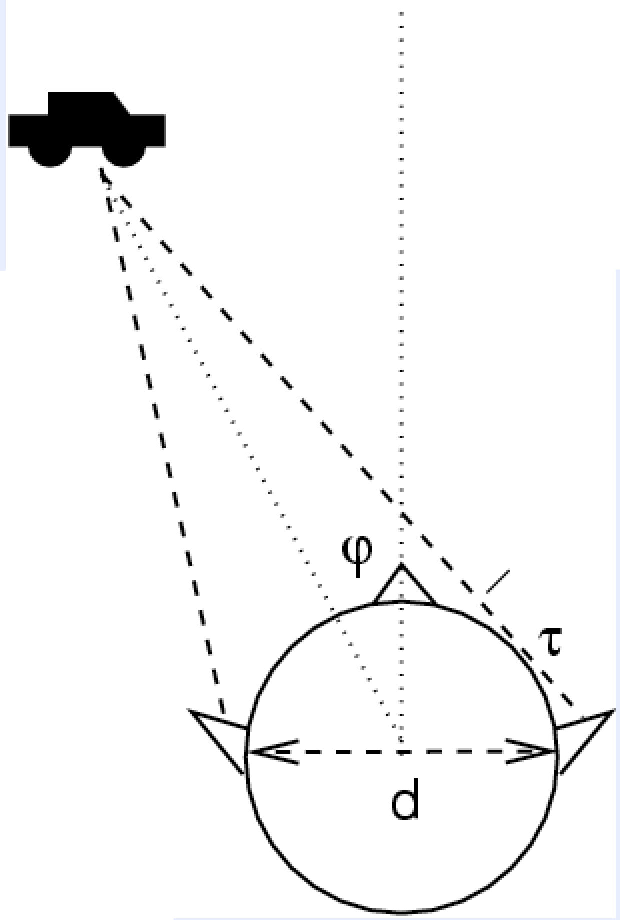
Lit.:

W. Gerstner, R. Kempter, JLvH & H. Wagner, A neuronal learning rule for sub-m temporal coding. Nature (1996) **383**:76-81

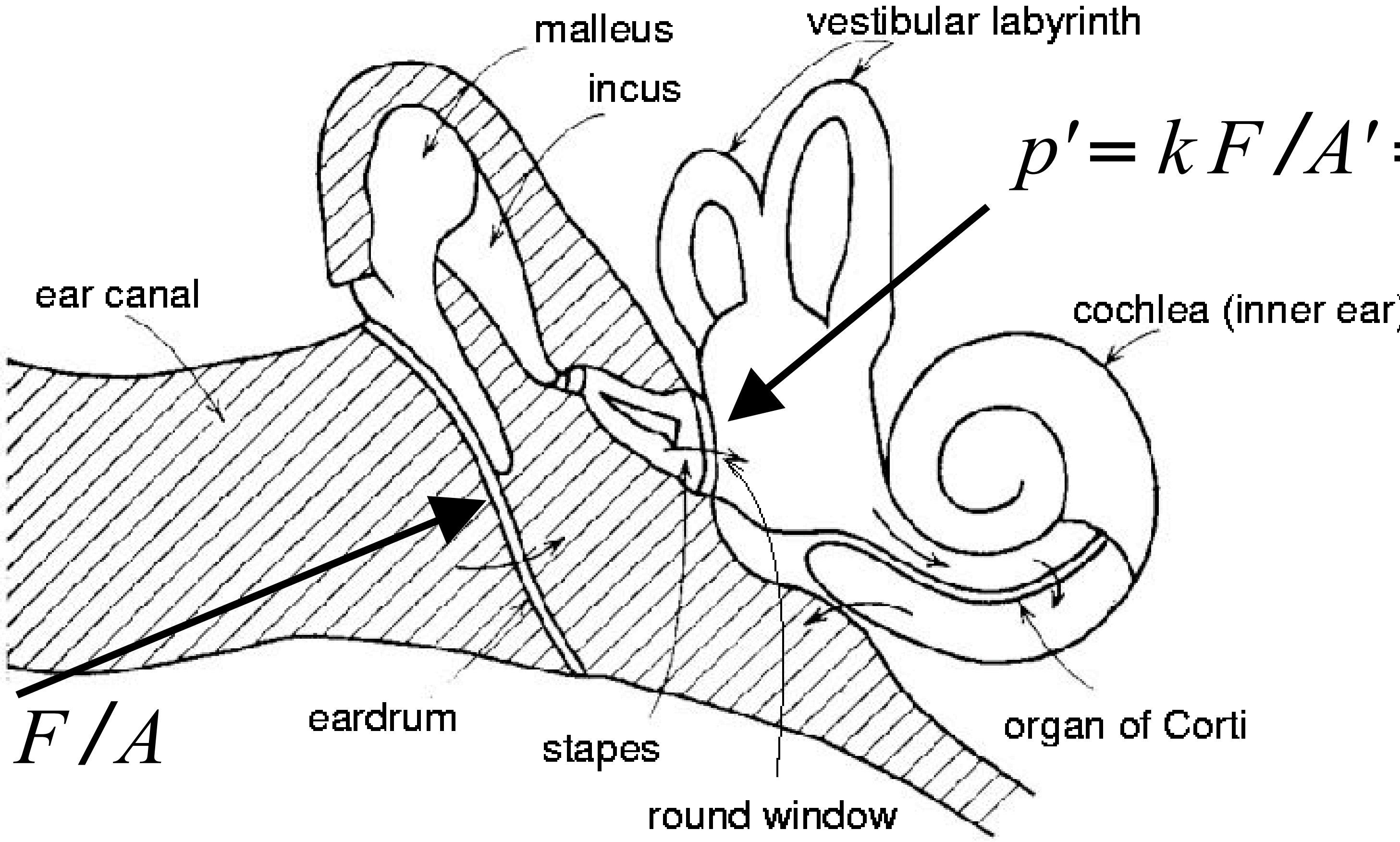
R. Kempter, W. Gerstner & JLvH, Phys. Rev. E (1999) **59**(4):4498–4514
R. Kempter, W. Gerstner & JLvH, Neural Computation (2001) **13**:2709–2741
C. Leibold, R. Kempter & JLvH, Phys. Rev. Lett. (2001) **87**(24):248101
C. Leibold, R. Kempter & JLvH, Phys. Rev. E (2002) **65**:051915
C. Leibold & JLvH, Biol. Cybern. (2002) **87**:428–439

Interaural
Time Differences



$$\tau(\varphi) = \frac{d}{2c}(\varphi + \sin\varphi)$$

Auditory Periphery

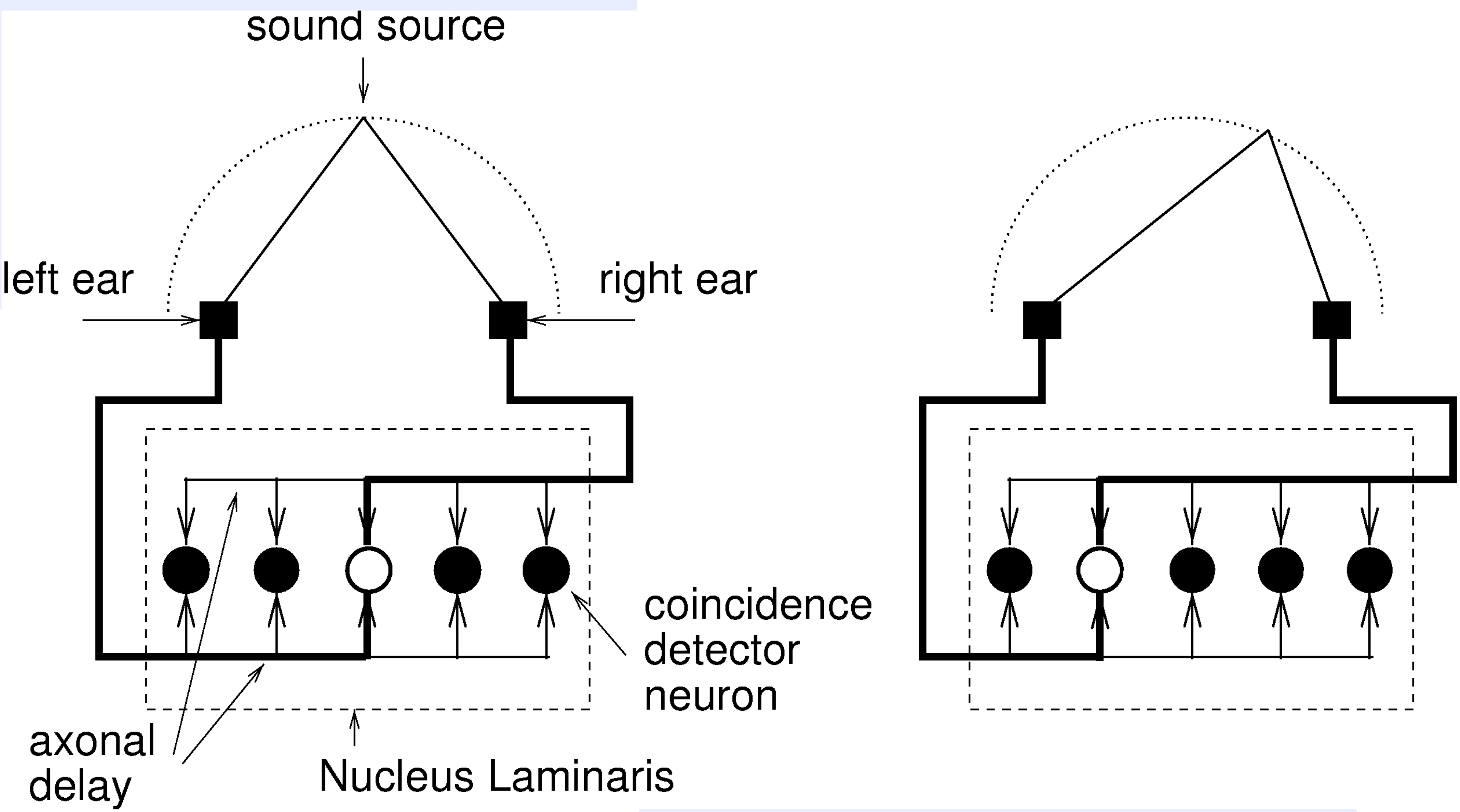


$$p' = kF/A' = k$$

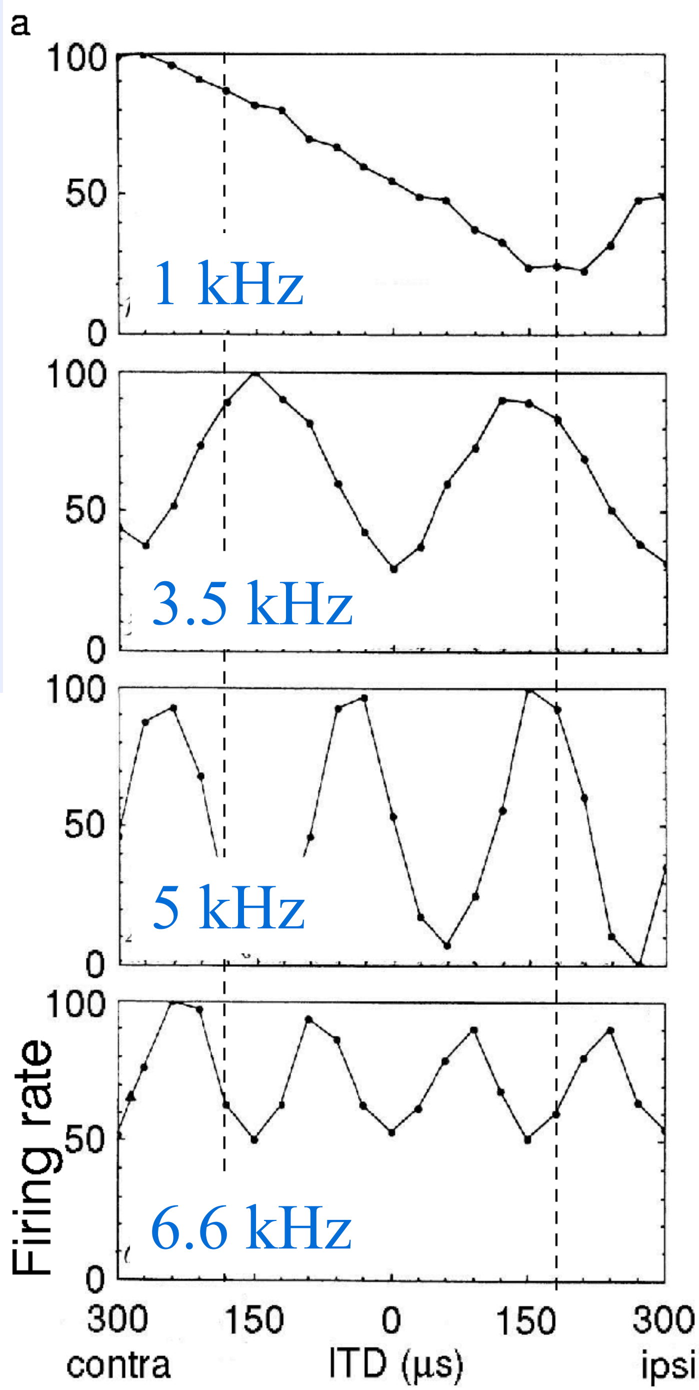
$$p = F/A$$

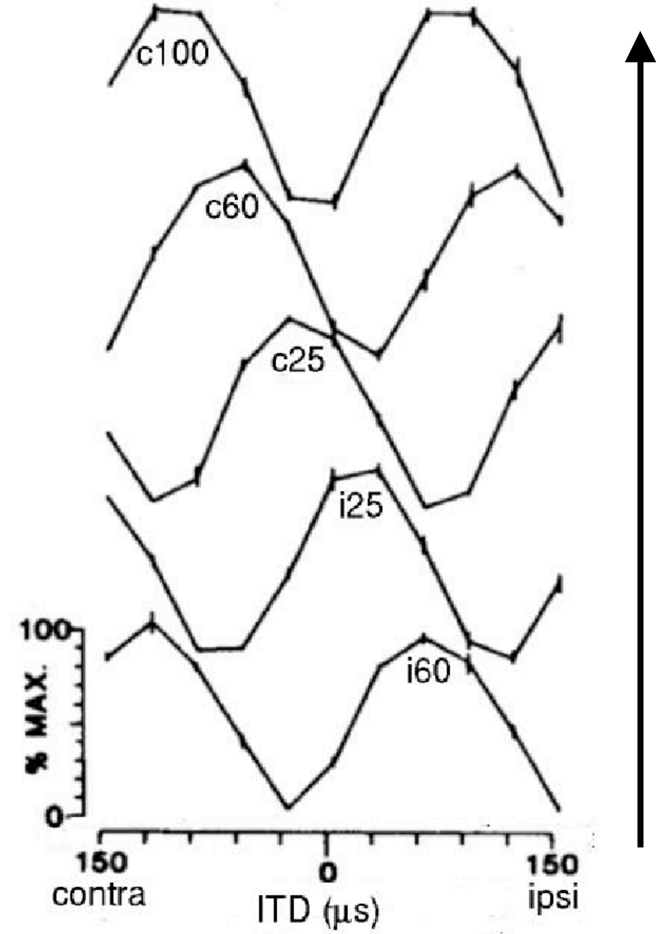
The classical model of ITD coding

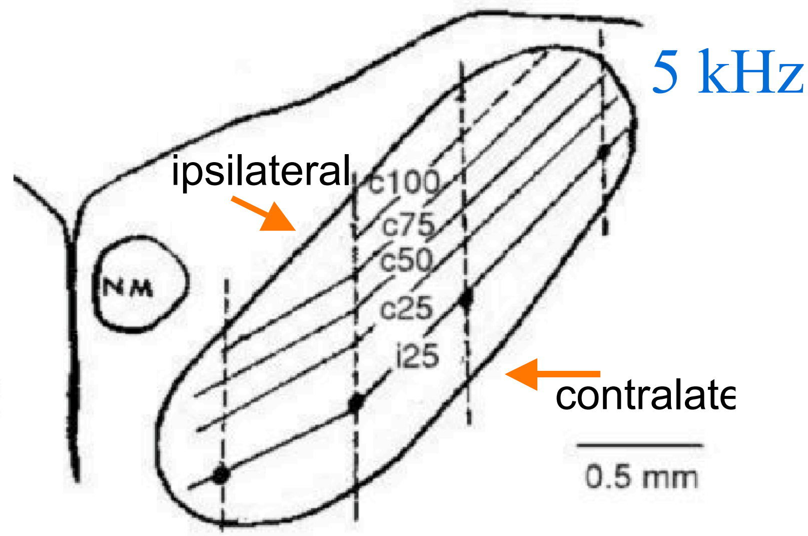
Jeffress Model (1948)



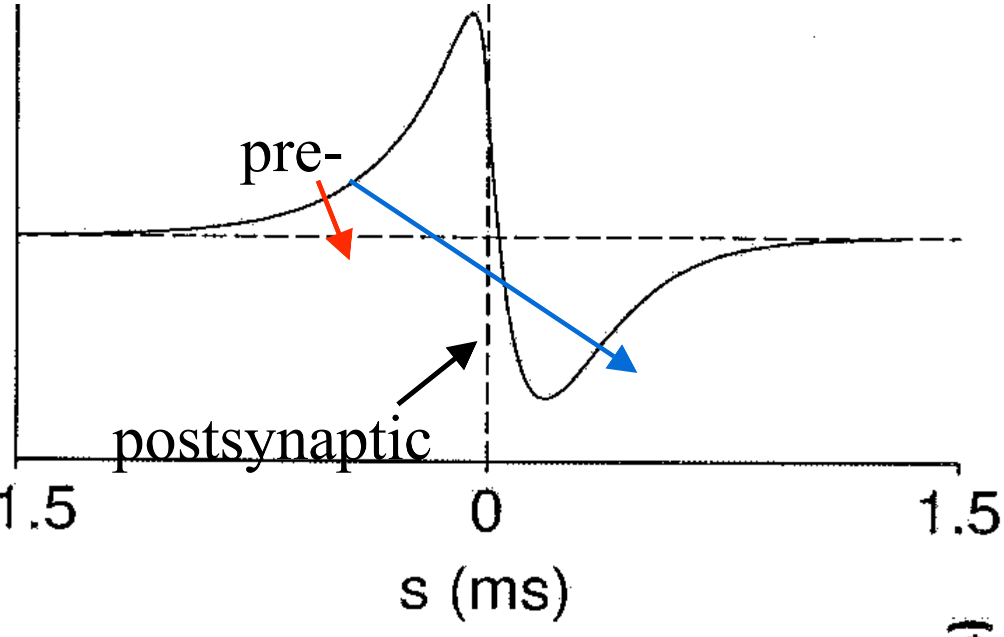
Experimental evidence







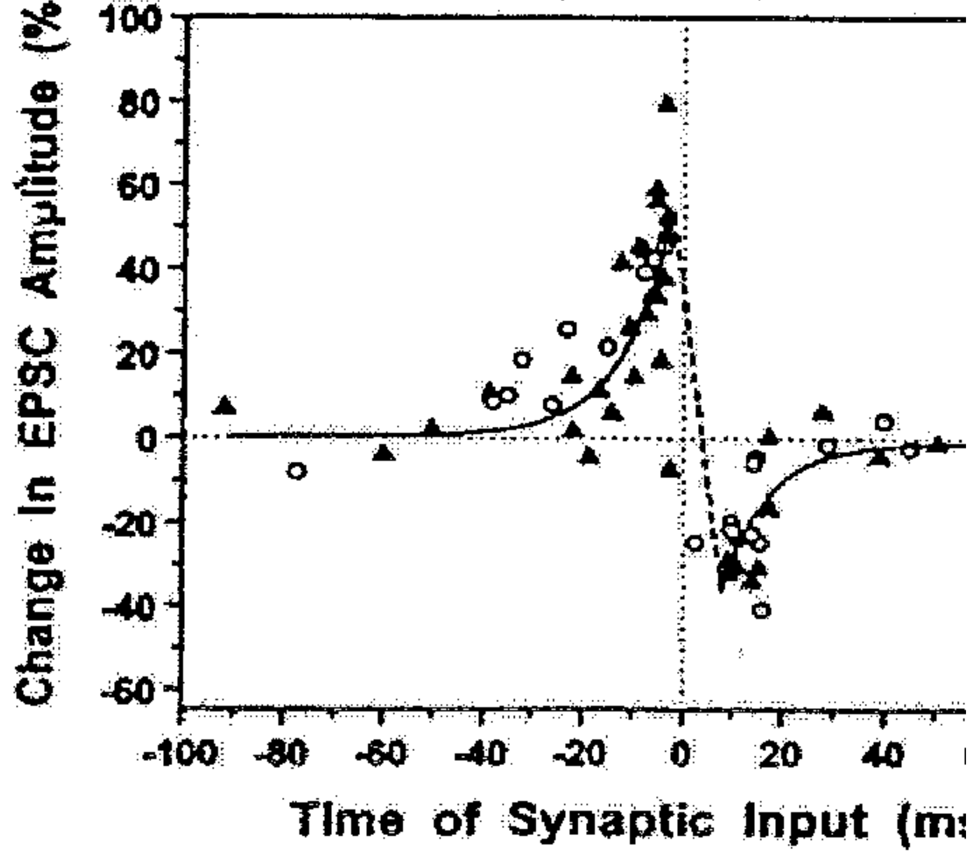
arr and Konishi 1990 J. Neurosci.
ullivan and Konishi 1986 PNAS



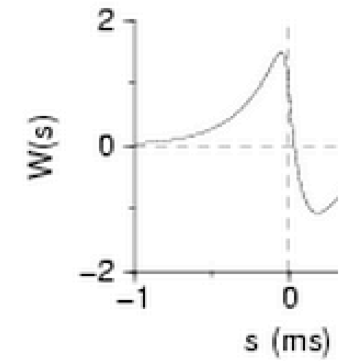
Kempter et al. (2001) PNAS

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

Zhang et al. (1998) Nature



Stochastic Synaptic Dynamics



Learning =
Activity-dependent modification of synaptic weights J_n.

$$\begin{aligned}\Delta J_n(t) &= J_n(t) - J_n(t-\mathcal{T}) \\ &= \eta \left[\sum_{t-\mathcal{T} \le t_n^{(f)} < t} w^{\text{in}} + \sum_{t-\mathcal{T} \le t^{(f)} < t} w^{\text{out}} + \sum_{t-\mathcal{T} \le t_n^{(f)}, t^{(f)} < t} W(t_n^{(f)} - t \right.\end{aligned}$$

can be written as a temporal average $\left[\overline{f(t)} = \frac{1}{\mathcal{T}} \int_{t-\mathcal{T}}^{t} \mathrm{d}t' \, f(t')\right]$ for input spike trains $S_n(t) = \sum_{\{t_n^{(f)}\}} \delta(t - t_n^{(f)})$:

$$\frac{\Delta J_n(t)}{\mathcal{T}} = \eta \left[w^{\text{in}} \, \overline{S_n(t-\Delta_n)} + w^{\text{out}} \, \overline{S(t)} + \int_{-\mathcal{W}}^{\mathcal{W}} \mathrm{d}s \, W(s) \, \overline{S(t) \, S_n(t+s-\Delta \right.}$$

Temporal Averaging

small

$$\frac{\mathrm{d}}{\mathrm{d}t}\mathbf{x} = \eta F(\mathbf{x}, t)$$

$$F(\mathbf{x}, t + T) = F(\mathbf{x}, t)$$

$$\bar{F}(\mathbf{x}) := \frac{1}{T}\int_{t-T}^{t} \mathrm{d}t' \, F(\mathbf{x}, t') \quad \Rightarrow \quad \frac{\mathrm{d}}{\mathrm{d}t}\mathbf{x} =$$

The Learning Equation

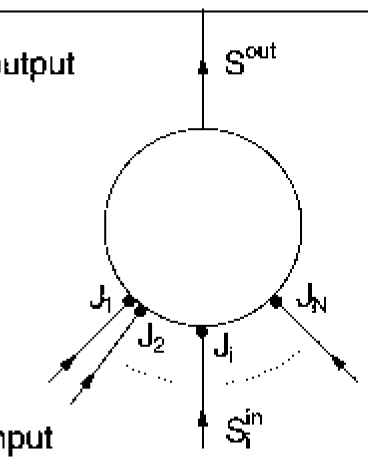
$\eta \ll 1 \Rightarrow J_n$ changes *slowly* in $[t - \mathcal{T}, t)$ and $\mathcal{T}$ can be taken large so that the dy
self-averaging with respect to the input process, e.g., inhomogenious Poisson.

Hence the Strong Law of Large Numbers leads to an ensemble- and time-average
equation [Kempter et al., Phys Rev E **59** (1999) 4498],

$$\frac{\Delta J_n}{\mathcal{T}} \approx \frac{\langle \Delta J_n \rangle}{\mathcal{T}} = \eta \left[w^{\mathrm{in}} \, \overline{\langle S_n(t) \rangle} + w^{\mathrm{out}} \, \overline{\langle S(t) \rangle} + \int_{-\infty}^{\infty} ds \, W(s; J_1, \ldots) \, \overline{\langle S(t) \, S_n(t + \right.$$

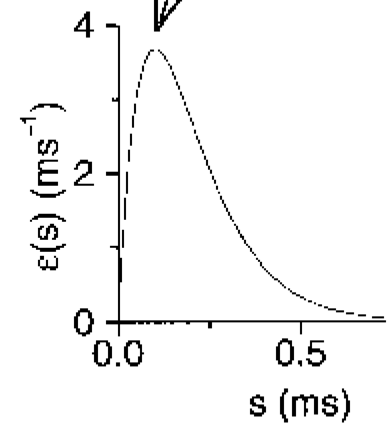
and $\frac{\overline{\langle \Delta J_n \rangle}}{\mathcal{T}} \mapsto \frac{\mathrm{d}}{\mathrm{d}t} J_n$, a consequence of the separation of time scales.

The Poisson Neuron



membrane potential = linear superposition of weighted l

$$v(t) = \sum_{n,\{t_n^{(f)}\}} J_n\,\epsilon(t - t_n^{(f)} - \Delta_n) = \sum_n J_n \int \mathrm{d}s\,\epsilon(s)\,S_n(t\cdot$$



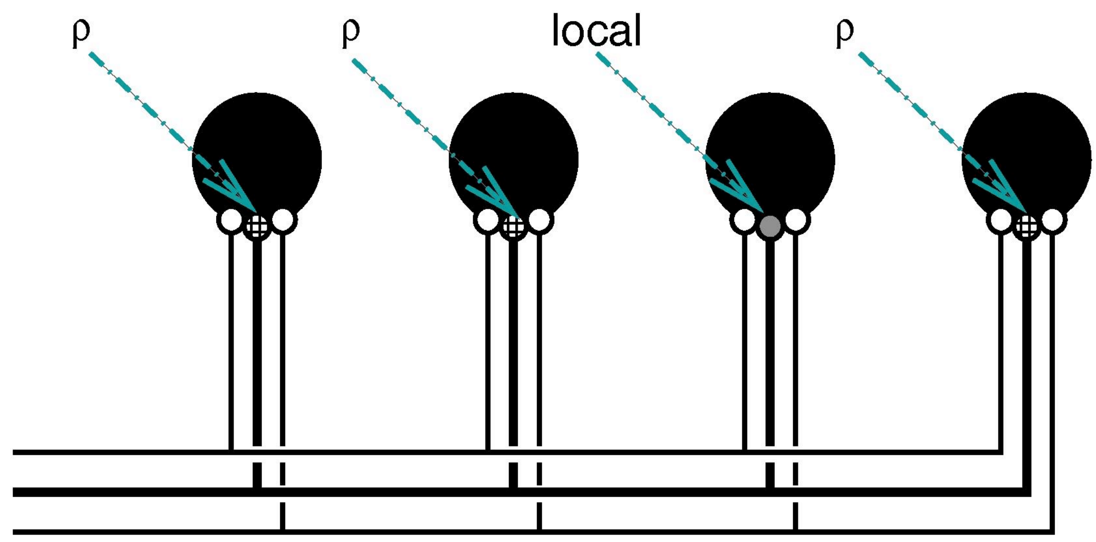
vhere $S_n(t) = \sum_{\{t_n^{(f)}\}} \delta(t - t_n^{(f)})$ is called spike train.

Poisson process:

1. $\mathrm{Prob}\{\text{cell fires in } [t, t+\delta t)\} = [\nu_0 + v(t)]\,\delta t$
2. $\mathrm{Prob}\{\text{cell fires more than once in } [t, t+\delta t)\} = o(\delta t)$
3. spike events in disjoint time intervals are independent

⇒ postsynaptic spike train $S(t) = \sum_{\{t^{(f)}\}} \delta(t - t^{(f)})$.

Axon-mediated synaptic learning (AMSL)

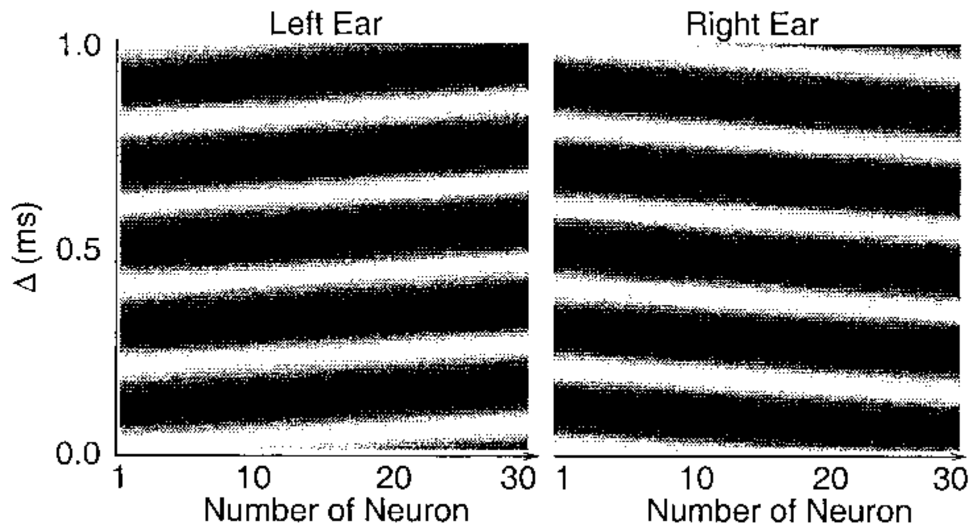


$$\frac{d}{dt}J_{mn} = \left[\frac{d}{dt}J_{mn}\right]_{local}^{STDP} + \varepsilon \sum_{m' \in axon\ n} \left[\frac{d}{dt}J_{m'n}\right]_{local}^{STDP}$$

$$\varepsilon << 1$$

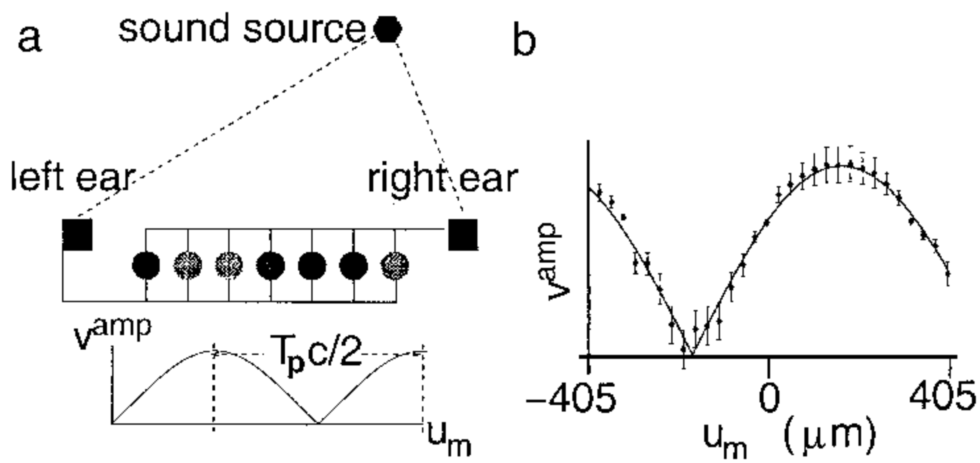
A Temporal Map

The dominating eigenvectors



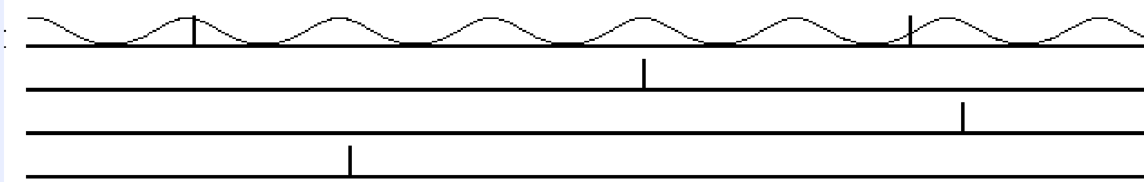
mod T_p

yield a Jeffress map



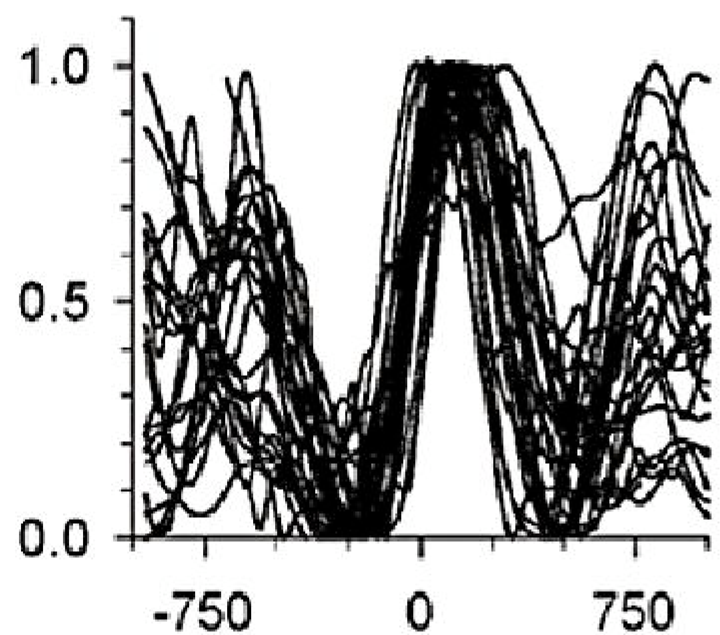
Animal with small inter-ear distance

Inter-ear distance 3.5 cm
Phase locking < 1.5 kHz

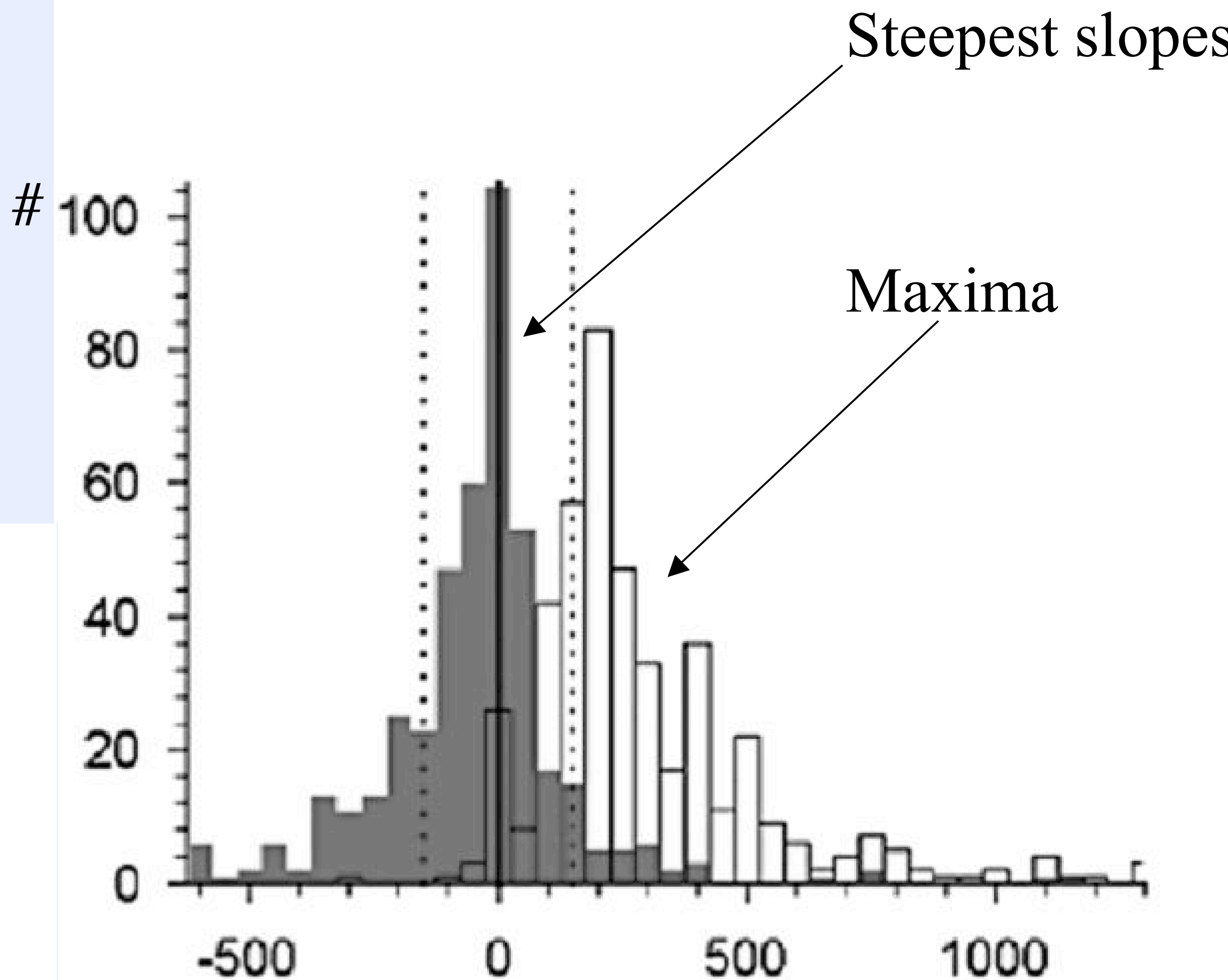


McAlpine‘s experiments

orm. Rate



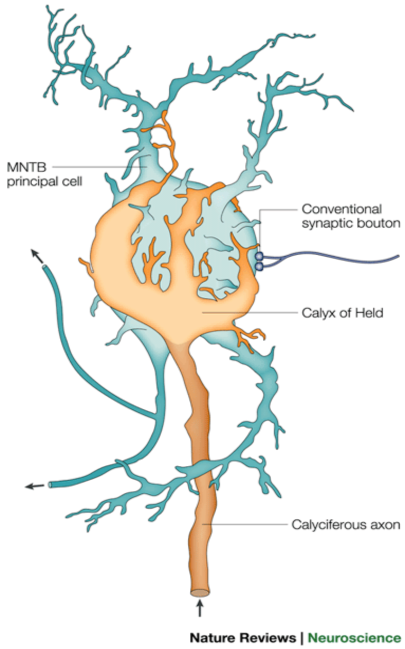
ITD (μs)

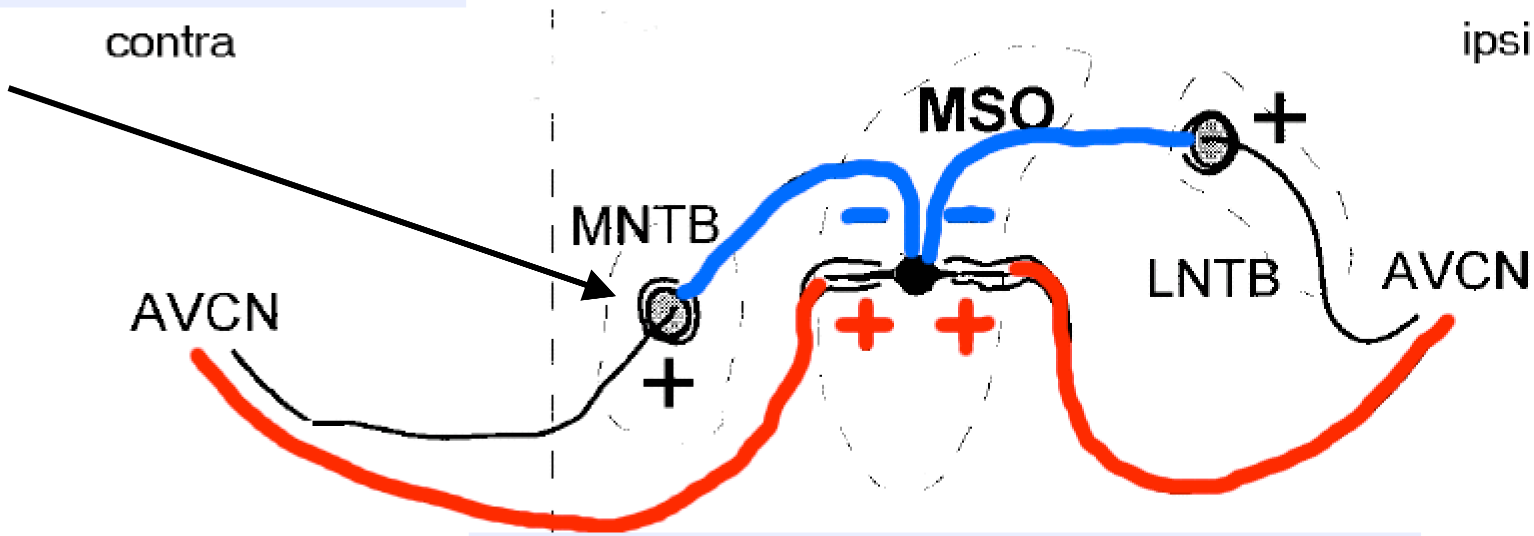


ITD (μs)

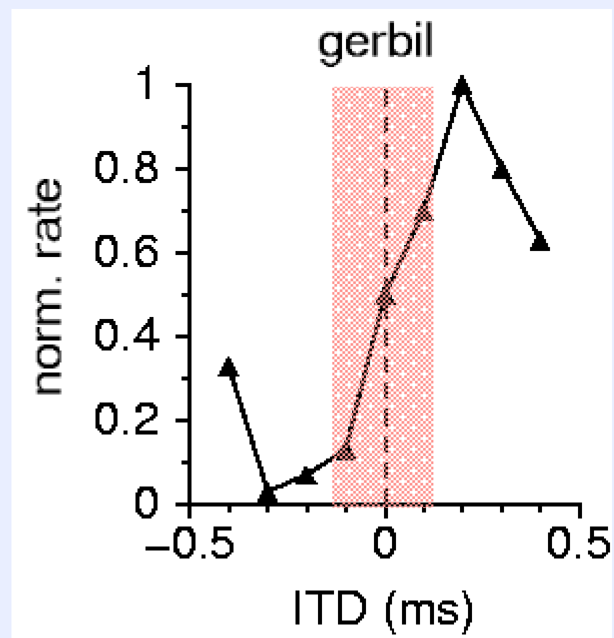
Hypothesis: Information about azimuth is encoded through slope

Circuit for Computing Time Differences

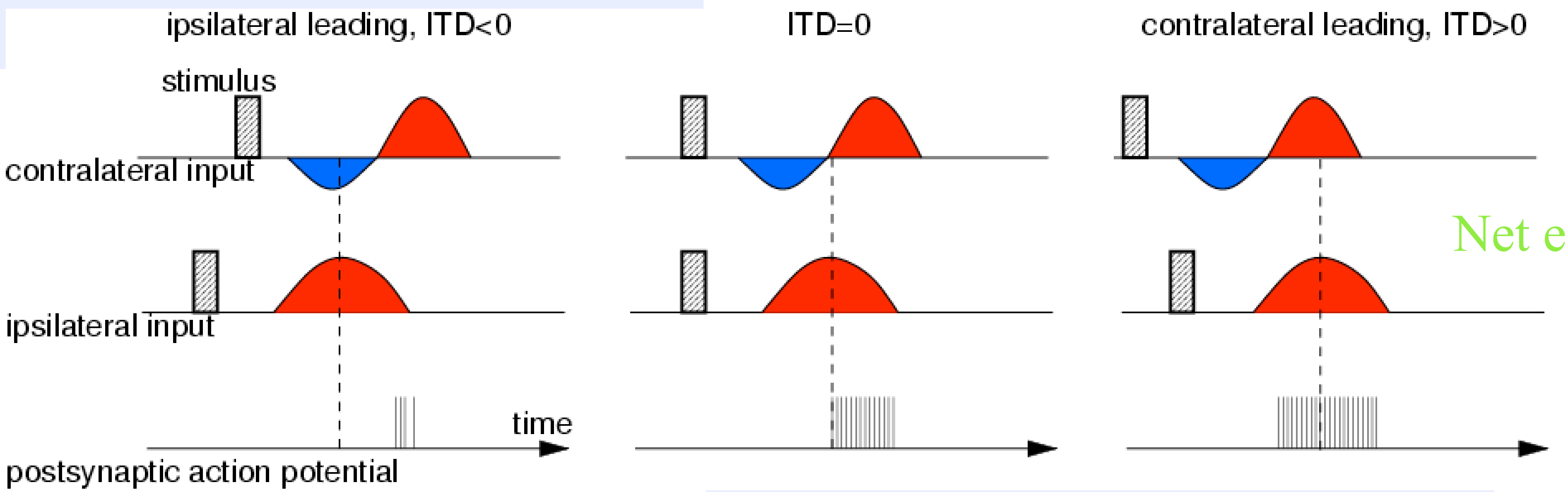




ITD tuning in gerbil MSO
(Brand et al. 2002)

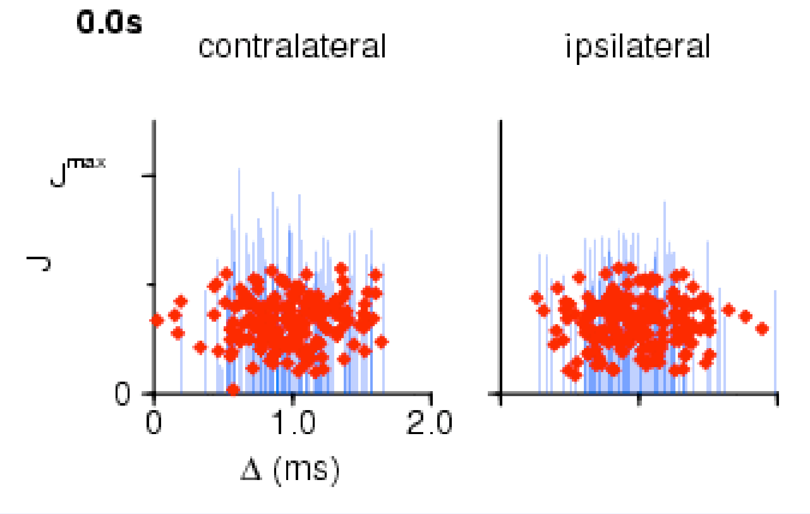


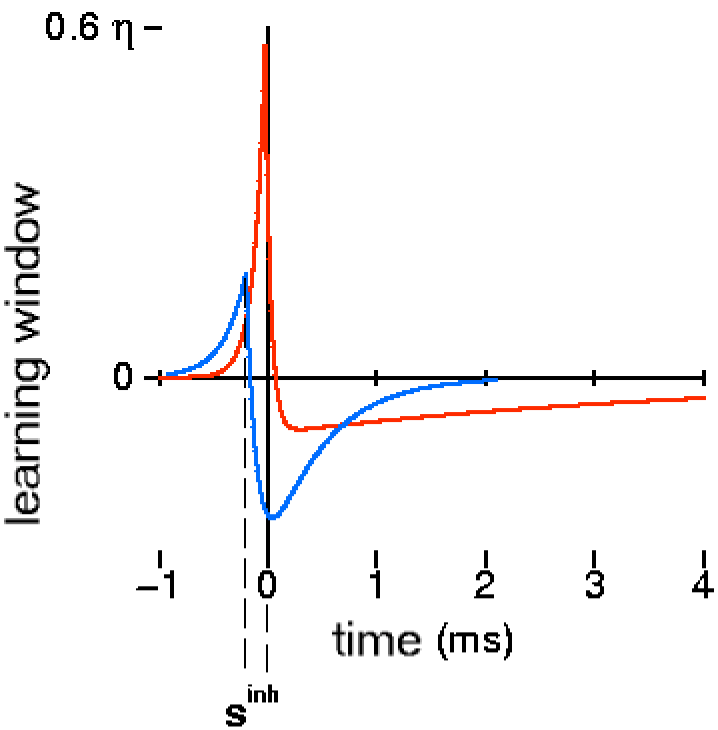
Temporal Summation Leads to Asymmetric Tuning

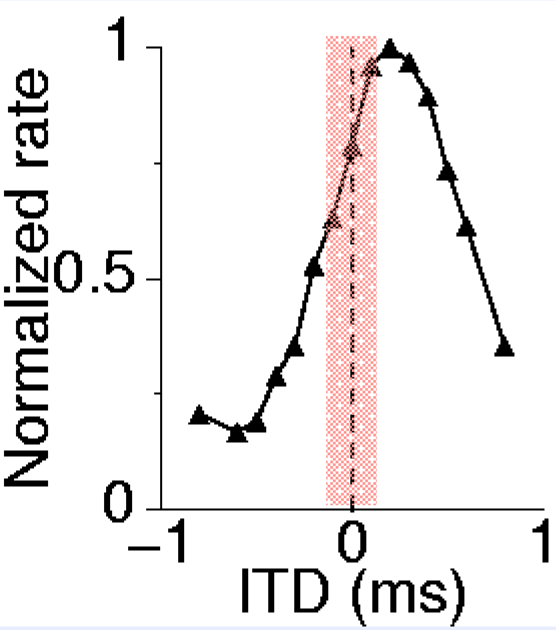


Net effect

Asymmetry Induced by Synaptic Learning





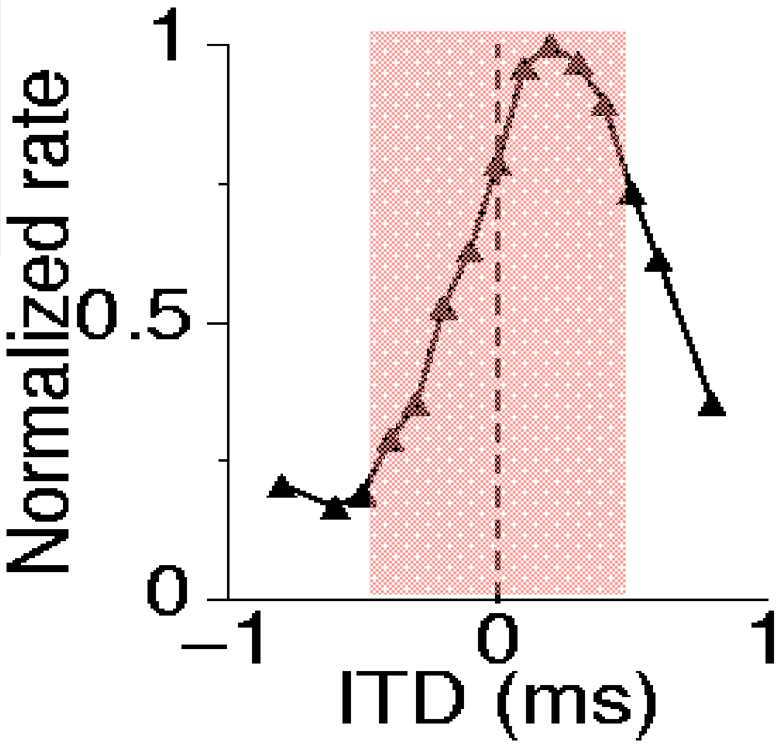


Gerstner et al. (1996) Nature **383**
Kempter et al. (2001) PNAS **98**

The work presented in this talk

Do barn owls and gerbils provide special singular solutions, or is there a generalization?

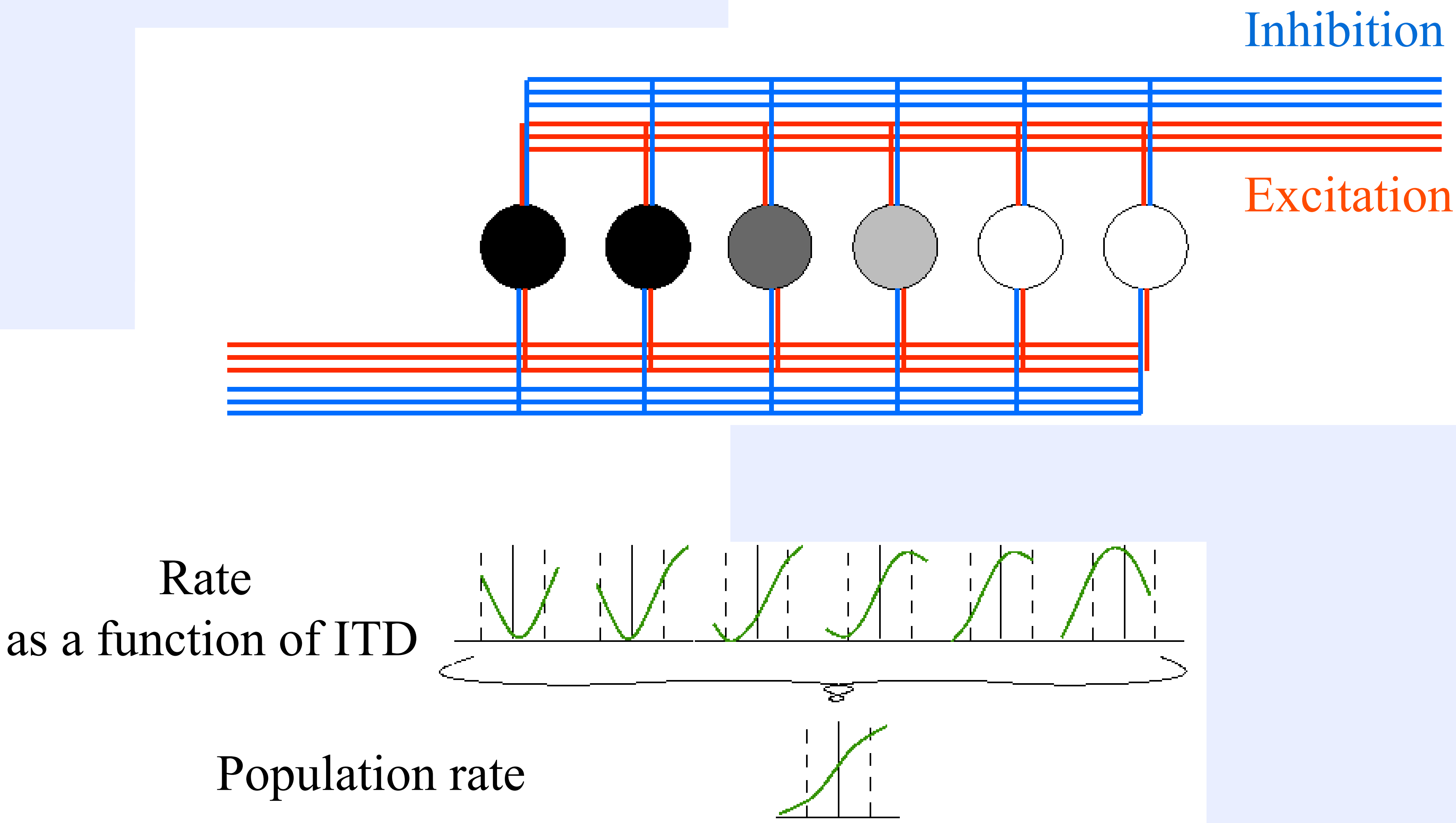
Ambiguities induced by increasing inter-ear distance or frequency



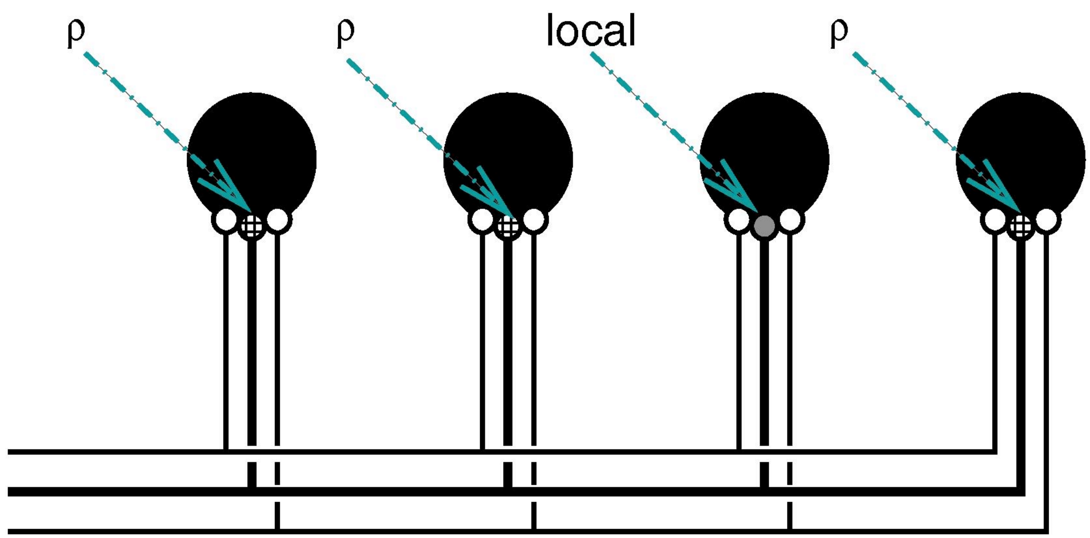
e.g.:
Humans: 200 mm /(330 m/s) = +\- 600 μs
critical frequency ~> f=800 Hz

Solution: Distribution of tuning maxima

How to produce a distribution of maxima: Neuronal implementation of a dual coding architecture



Axon-mediated synaptic learning (AMSL)

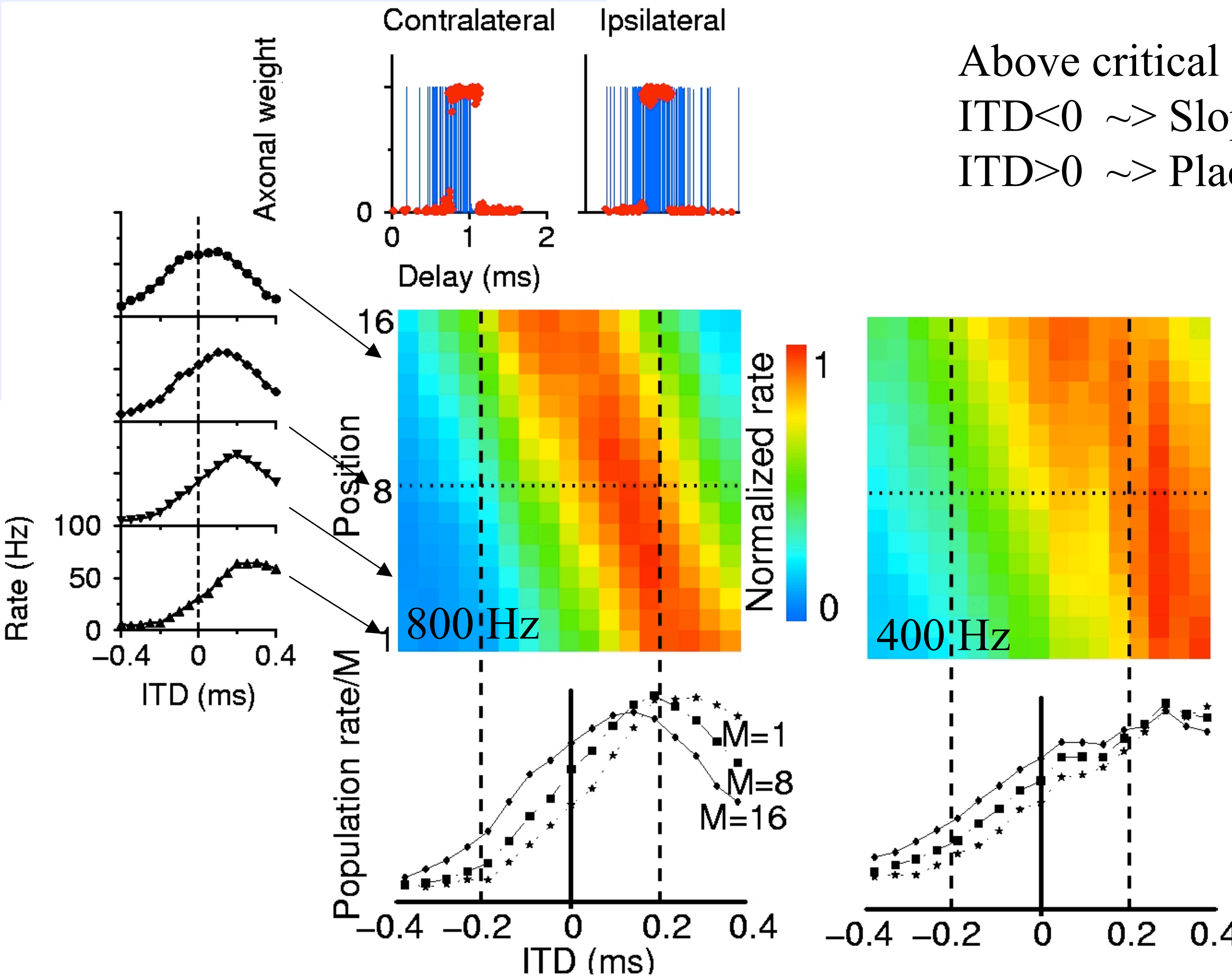


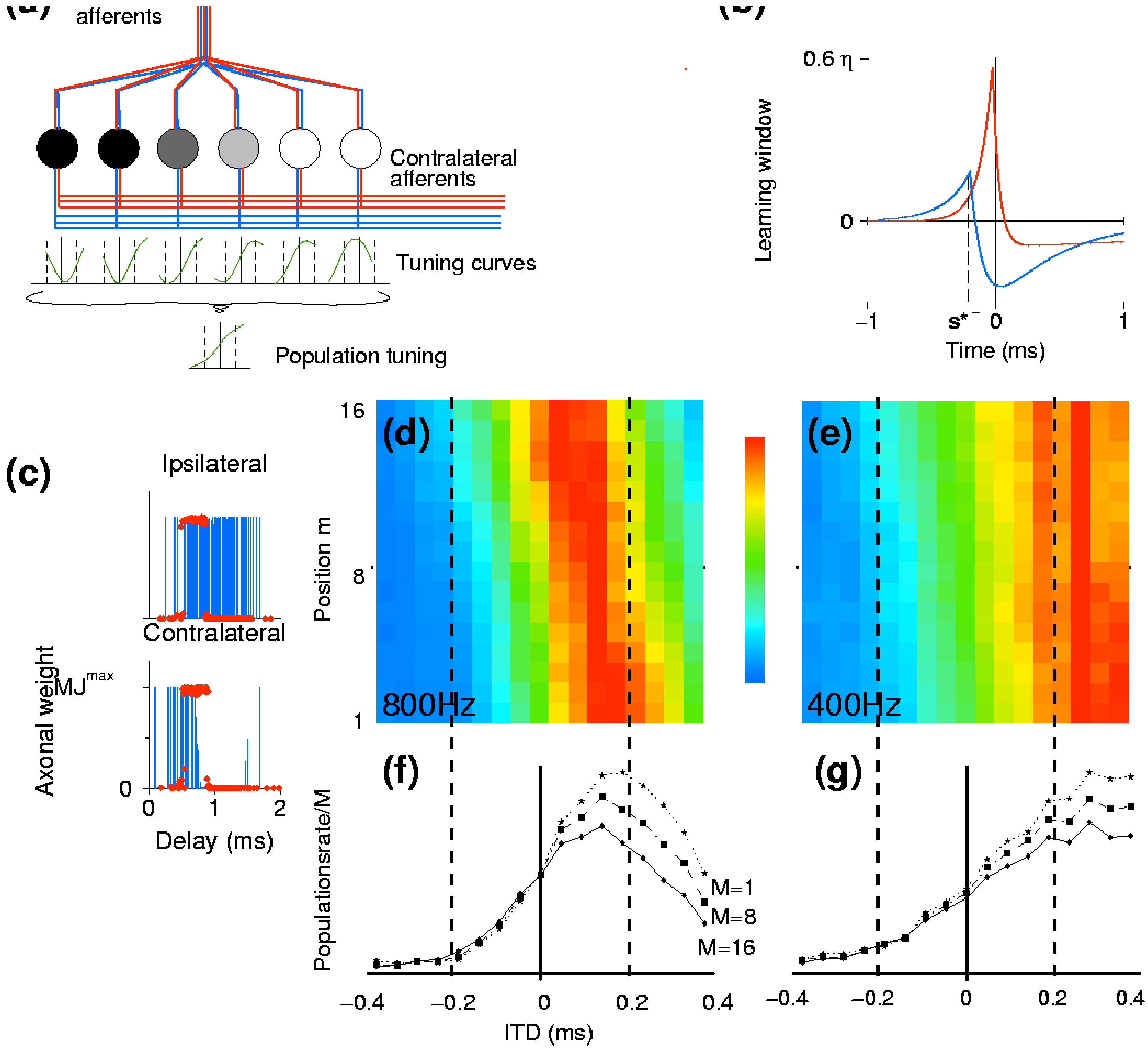
$$\frac{d}{dt}J_{mn} = \left[\frac{d}{dt}J_{mn}\right]_{local}^{STDP} + \varepsilon \sum_{m' \in axon\ n} \left[\frac{d}{dt}J_{m'n}\right]_{local}^{STDP}$$

$$\varepsilon << 1$$

Realization of the dual coding principle

Above critical frequency:
ITD<0 ~> Slope Code
ITD>0 ~> Place Code





afferents
Contralateral afferents
Tuning curves
Population tuning
0.6 η
Learning window
0
s*
Time (ms)
(c)
Ipsilateral
Contralateral
Axonal weight
MJ max
Delay (ms)
(d)
800Hz
(e)
400Hz
Position m
(f)
(g)
Populationsrate/M
M=1
M=8
M=16
ITD (ms)

Conclusion

1. STDP explains both excitatory and inhibitory synaptic setup as well as temporal accuracy of binaural ITD coding

2. Support by experimentally found inhibitory plasticity during ontogeny

3. Interpolation between place code (barn owl) and slope code (gerbil)