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EU ADVANCED COURSE IN COMPUTATIONAL NEUROSCIENCE

An IBRO Neuroscience School

(30 July - 24 August 2001)

"Coupled Oscillators and Integrate-and-Fire Networks"

presented by:

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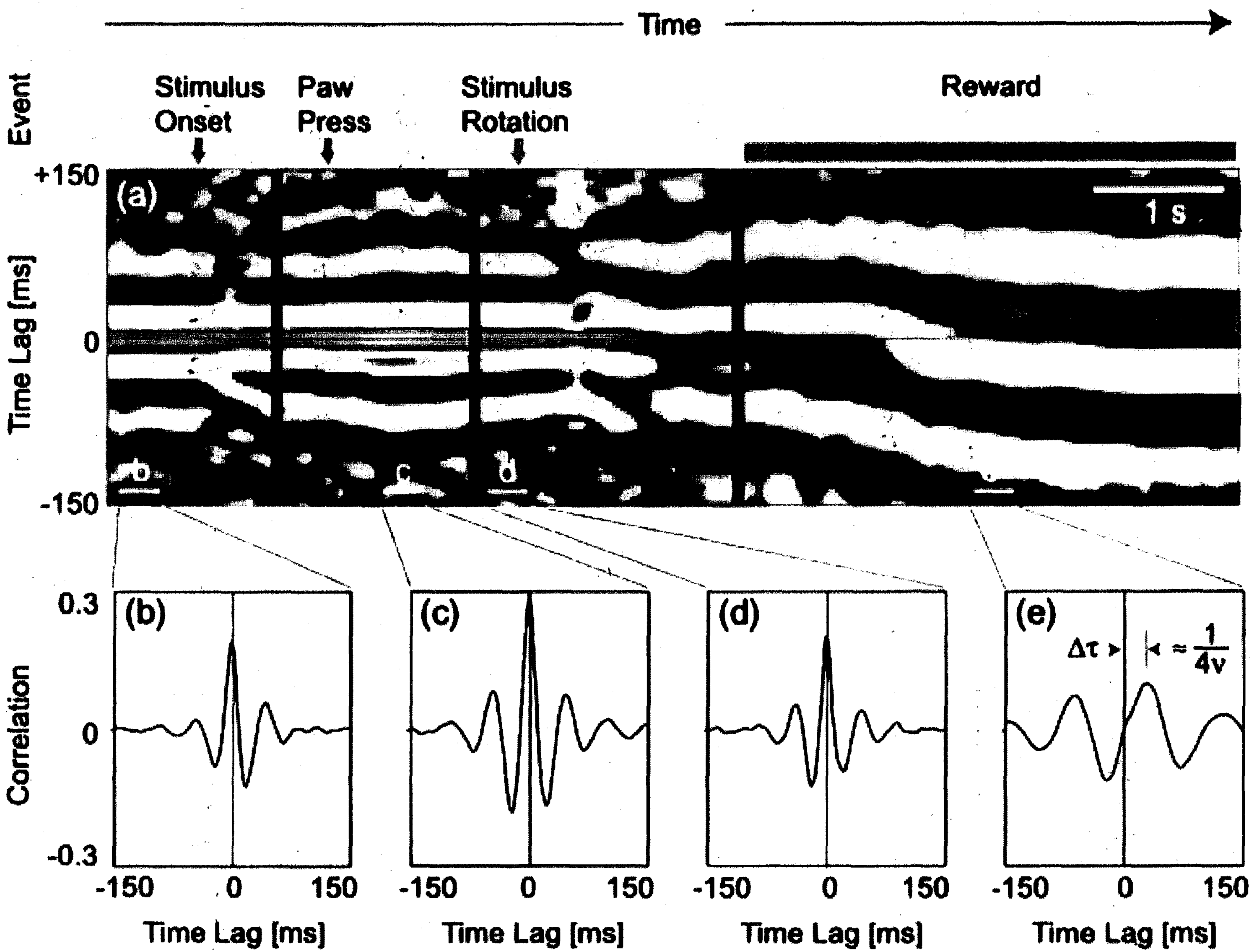
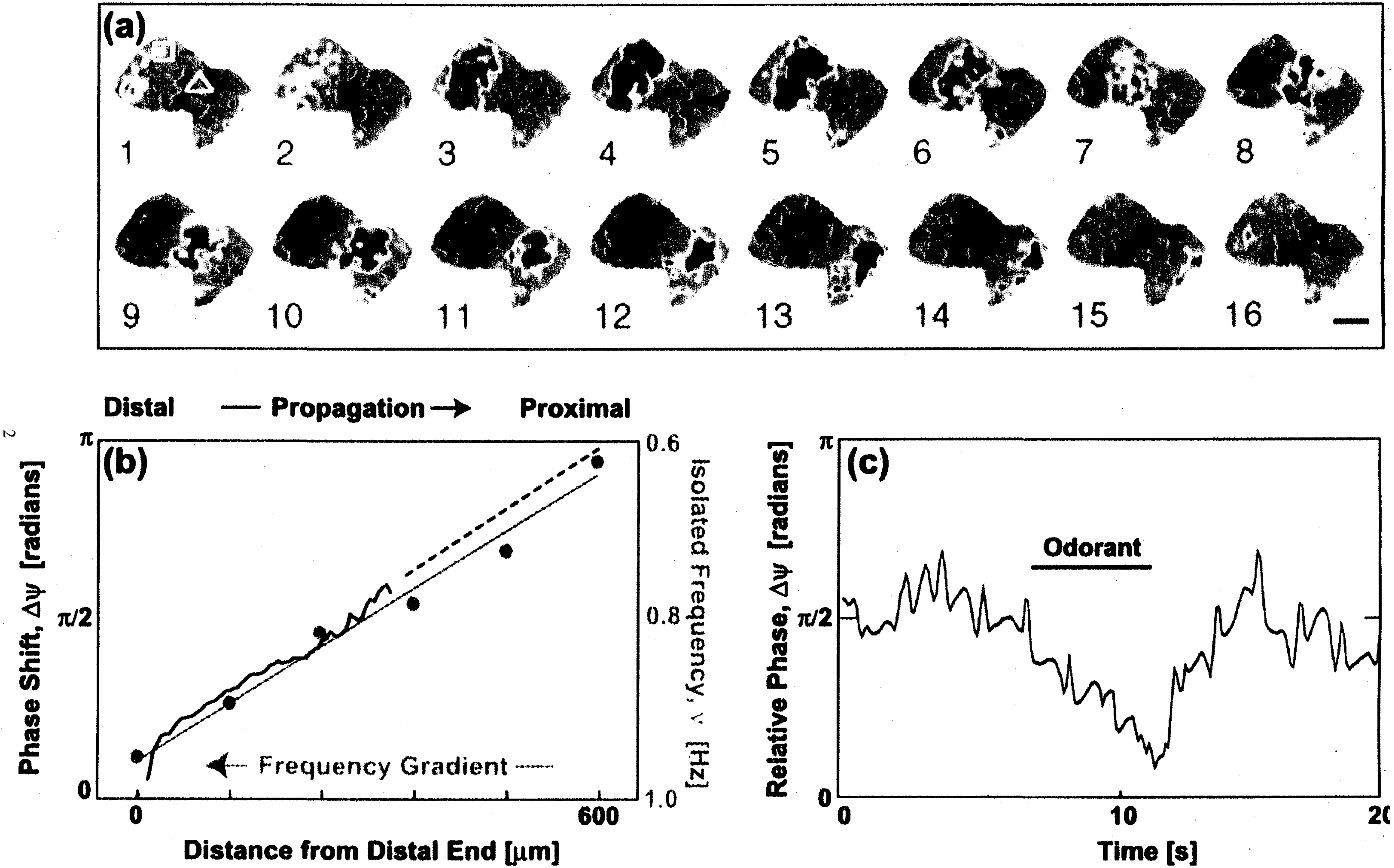
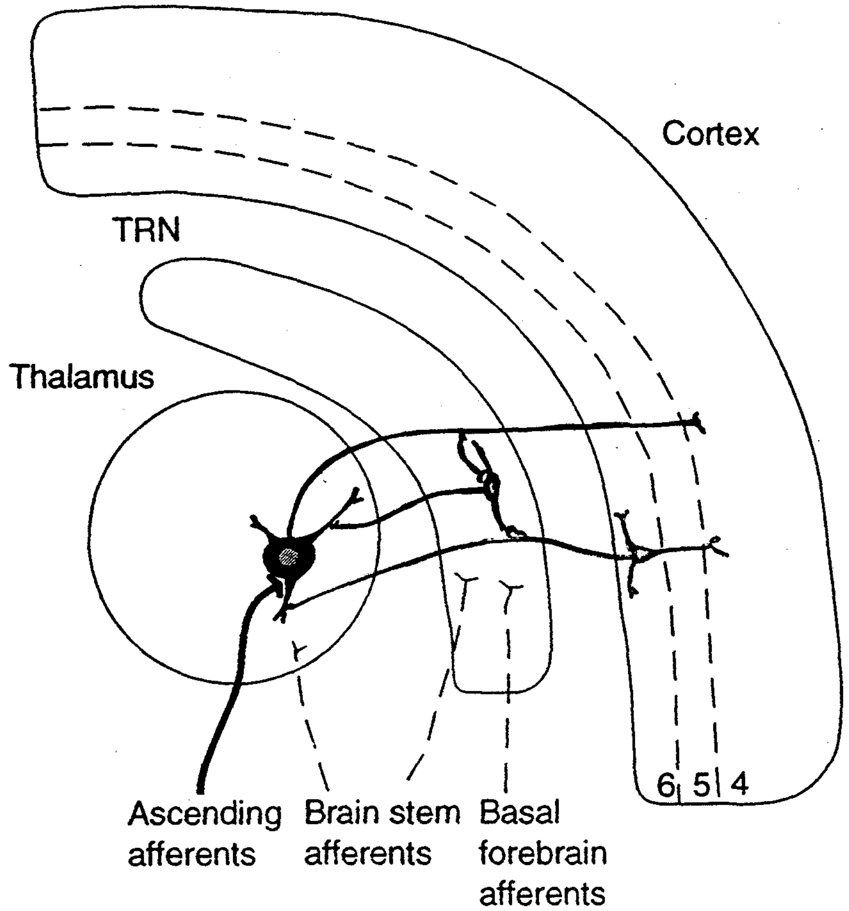
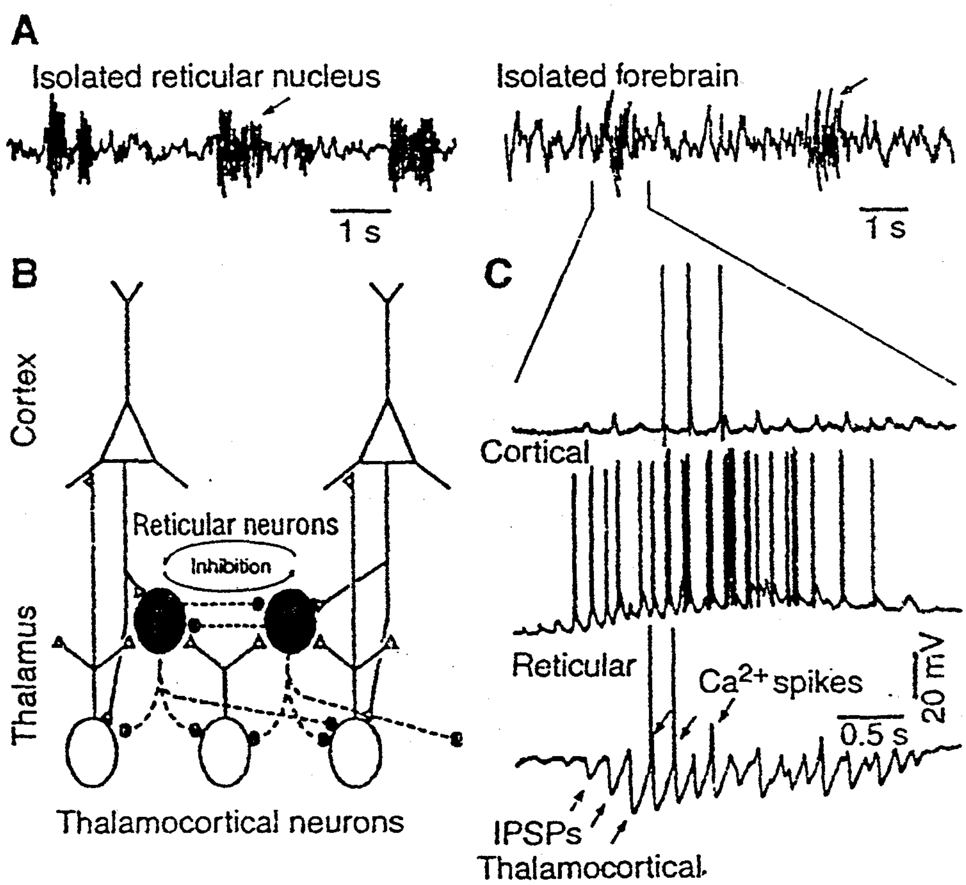
These are preliminary lecture notes, intended only for distribution to participants.

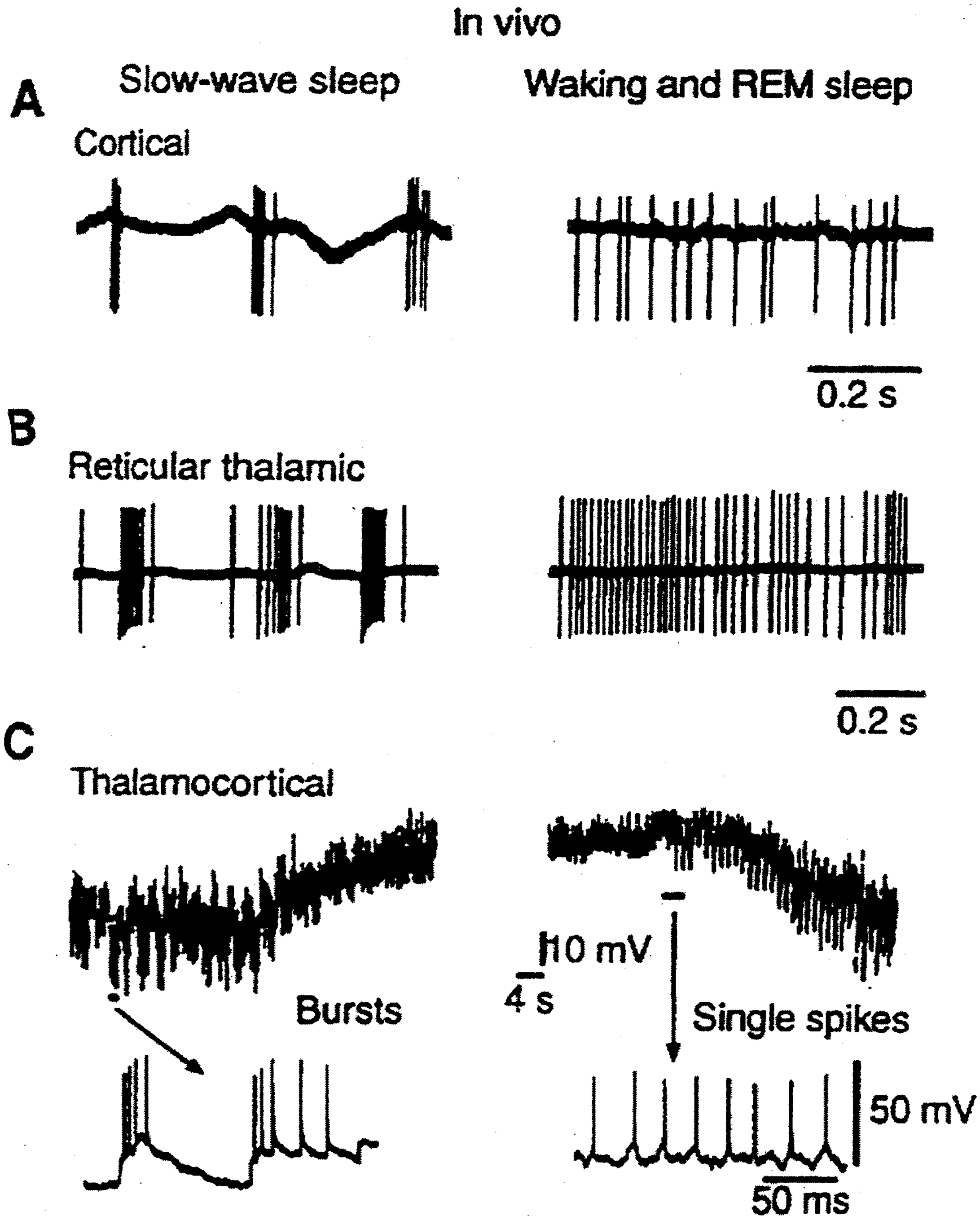

Time
Event
Stimulus Onset
Paw Press
Stimulus Rotation
Reward
(a)
1 s
+150
0
-150
Time Lag [ms]
b
c
d
0.3
0
-0.3
Correlation
(b)
(c)
(d)
(e)
Δτ
≈ 1/4ν
-150
0
150
Time Lag [ms]

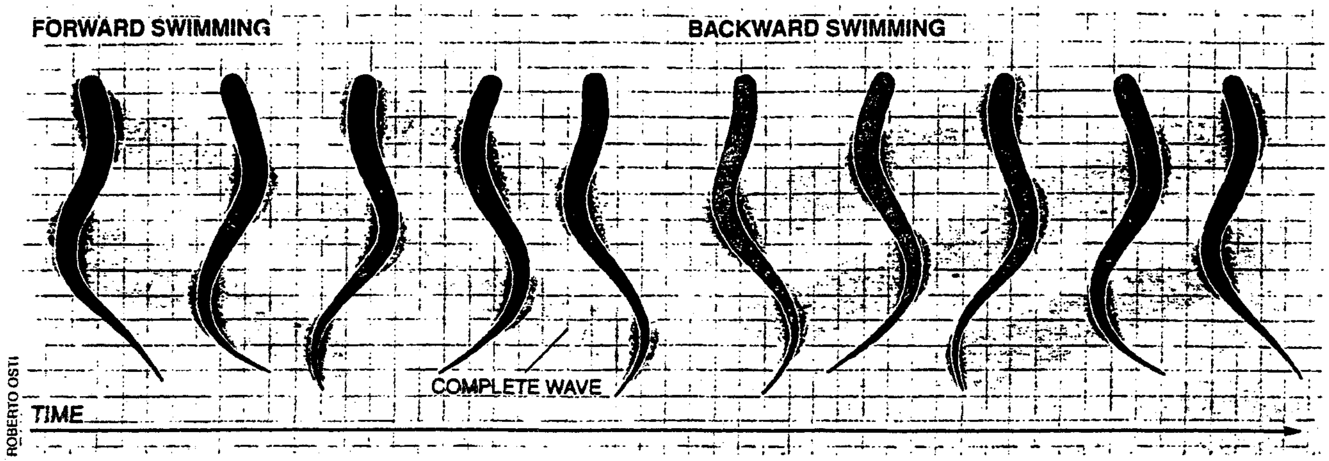

(a)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Distal
Propagation
Proximal
(b)
Phase Shift, Δψ [radians]
π
π/2
0
0.6
0.8
1.0
Isolated Frequency, ν [Hz]
Frequency Gradient
0
600
Distance from Distal End [μm]
(c)
Relative Phase, Δψ [radians]
π
π/2
0
Odorant
0
10
Time [s]





Steriade, McCormick + Sejnowski (Science 1993)


In vivo
A
Slow-wave sleep
Waking and REM sleep
Cortical
0.2 s
B
Reticular thalamic
0.2 s
C
Thalamocortical
10 mV
4 s
Bursts
Single spikes
50 mV
50 ms



UNDULATORY SWIMMING in the eellike lamprey constitutes a relatively simple form of vertebrate locomotion that neuroscientists can examine effectively. In response to signals emitted by the brain, wave after wave of muscle contraction (*red*) and extension (*green*) pass from head to tail down the body of a fish, propelling it forward through the water (*left*). Similar waves traveling from tail to head can drive the creature backward (*right*).

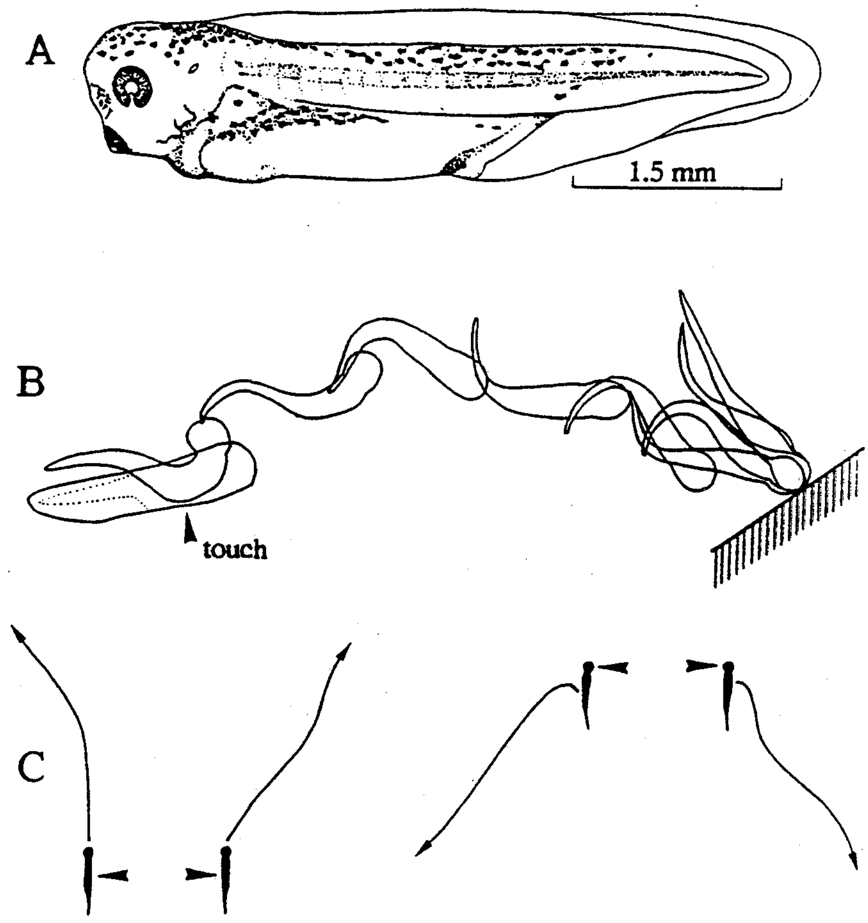
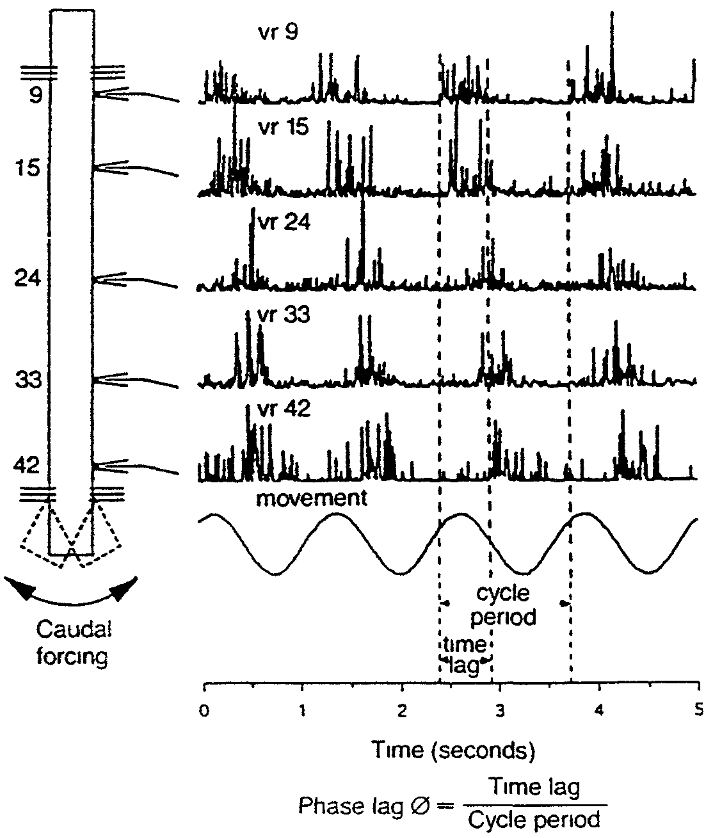
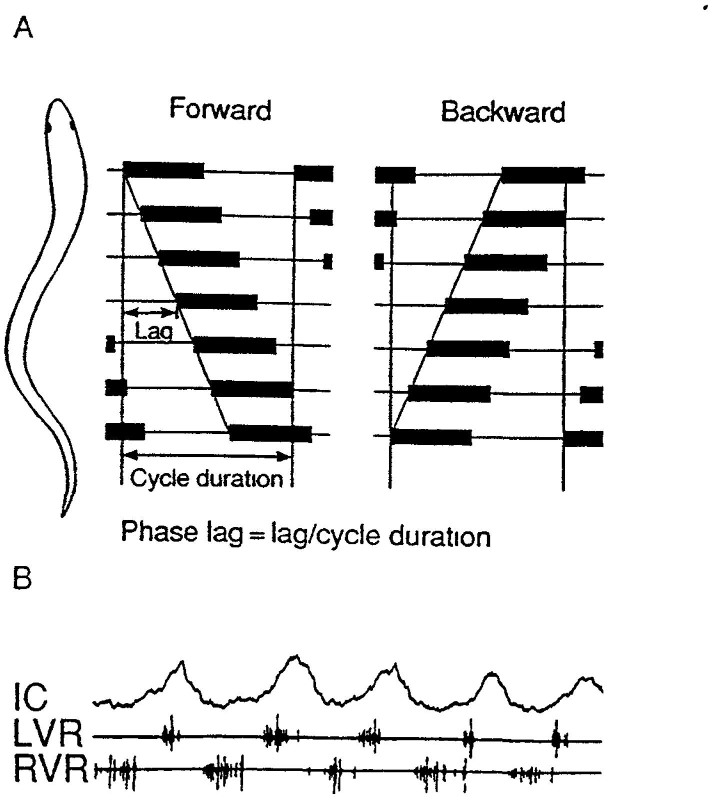


Fig. 1. The tadpole (A) and its responses to touch (B,C). (B) Tracings from high-speed video show that when touched on the flank (arrowhead), the tadpole flexes to the opposite side, swims off and stops when it contacts the side of the dish (hatched). (C) When touched on the flank, it swims forwards and to the opposite side. When touched on the head, it first flexes away, and then swims off. ((B) and (C) based on videos made by K. Boothby and P. Stonehewer.)


vr 9
vr 15
vr 24
vr 33
vr 42
movement
9
15
24
33
42
Caudal forcing
cycle period
time lag
0
1
2
3
4
5
Time (seconds)
Phase lag Ø = Time lag / Cycle period


A
Forward
Backward
Lag
Cycle duration
Phase lag = lag/cycle duration
B
IC
LVR
RVR

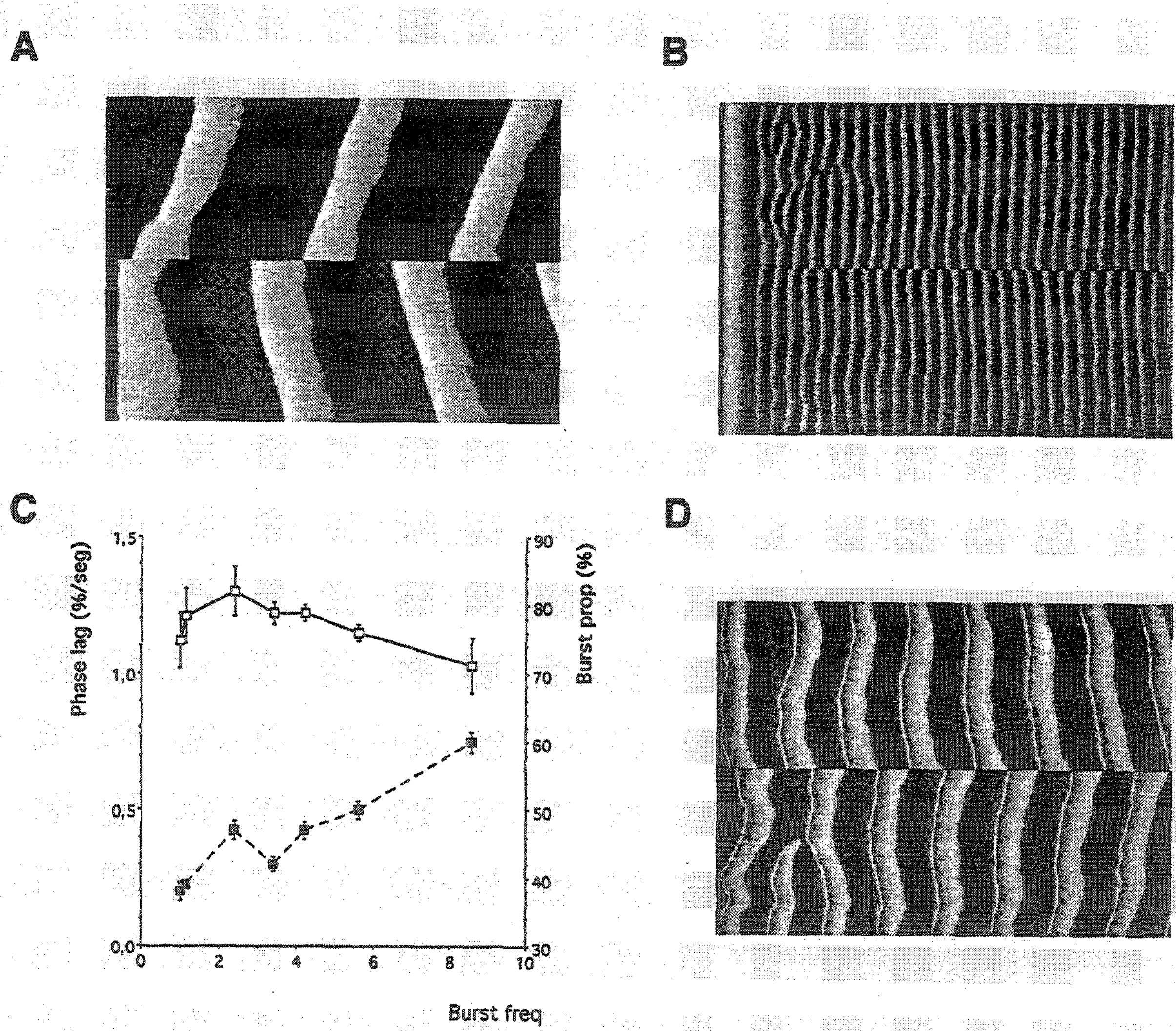
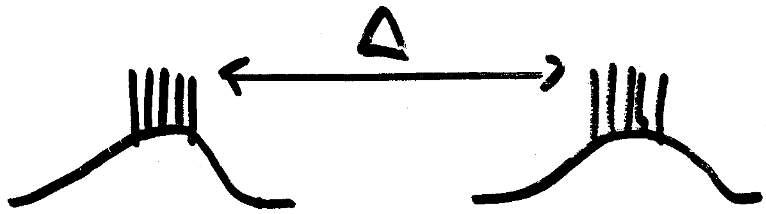


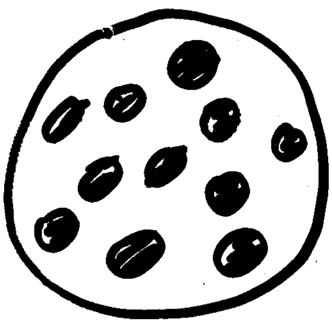
Figure 15.2
(A) Slow swimming. (B) Fast swimming. (C) Phase lag (upper curve) and burst proportion (lower curve) versus bursting frequency. (D) Backward swimming. In A, B, and D, activation at different levels of the spinal cord as a function of time is shown. White corresponds to maximum activity and black to maximum inhibition. Time is indicated along the horizontal dimension. Activity on the right and left side is show the upper and lower half, respectively. The rostral end is at the cer with progressively more caudal parts toward the top and bot respectively.

What is oscillating?

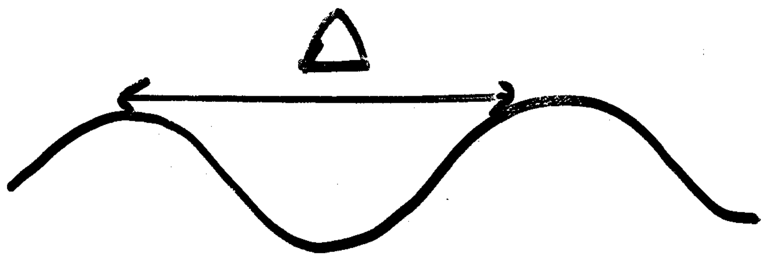
Single spikes



Bursting



Pool of neurons



Population Activity rate

Integrate-and-fire networks

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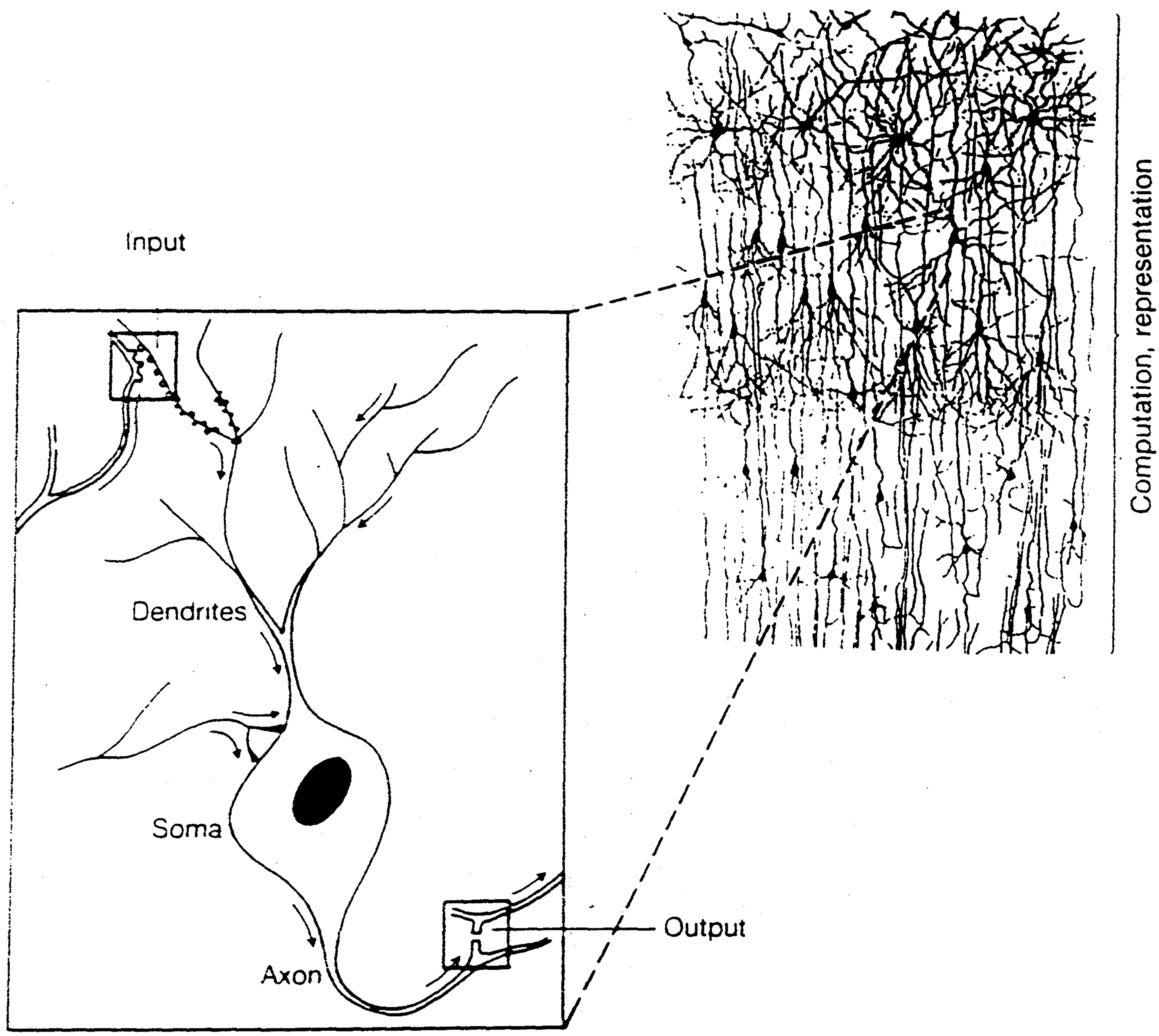
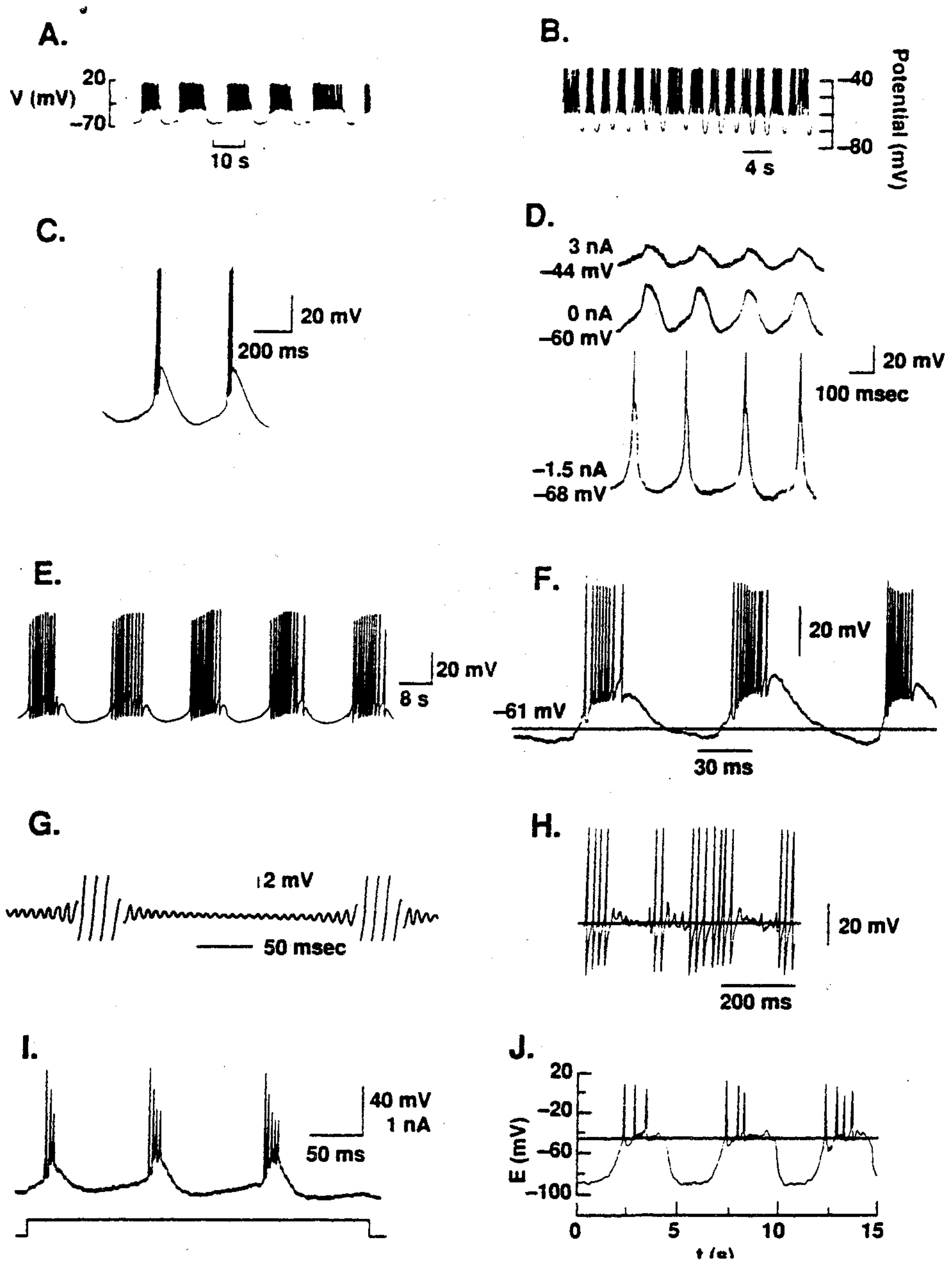


Figure 2.15 (Upper right) Network of pyramidal neurons in mouse cortex, stained by the Golgi method, which stains only about 10% of the population. (Lower left) Schematic of a generalized neuron showing one of its inputs to a dendrite, one to the cell body, and one of its[1] axonal contacts.

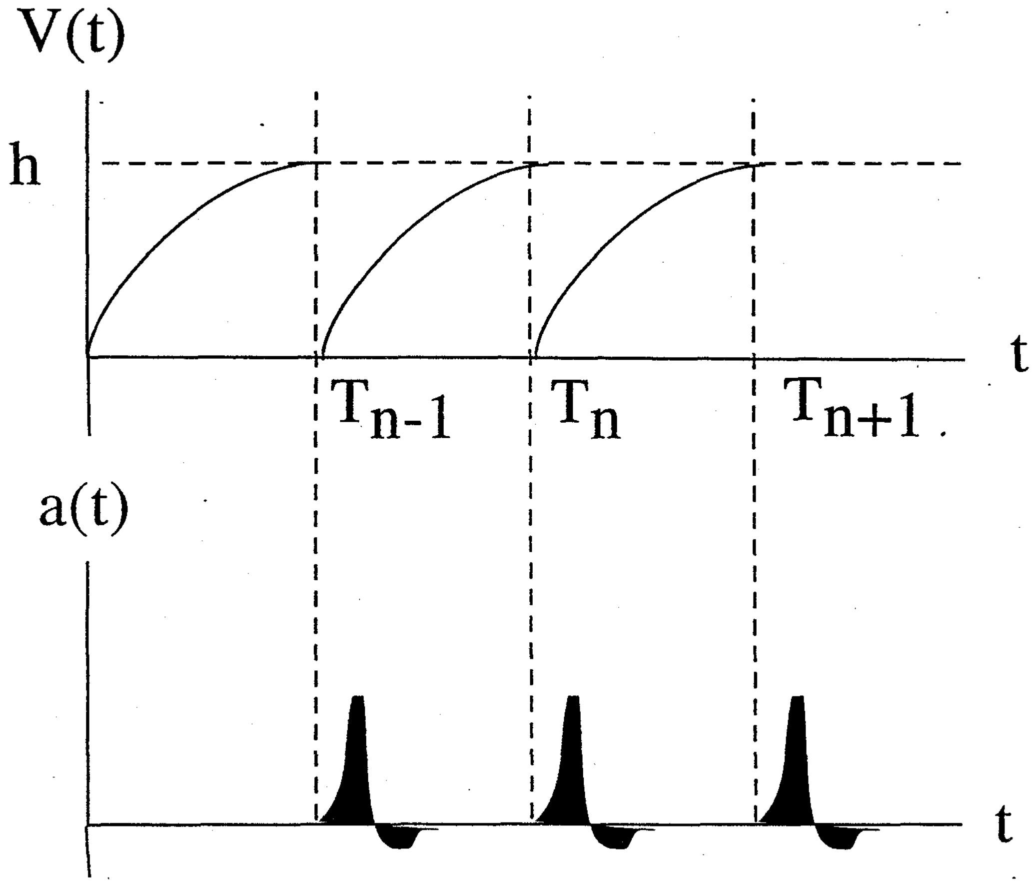

A.
20
V (mV)
−70
10 s
B.
−40
−80
Potential (mV)
4 s
C.
20 mV
200 ms
D.
3 nA
−44 mV
0 nA
−60 mV
20 mV
100 msec
−1.5 nA
−68 mV
E.
20 mV
8 s
F.
20 mV
−61 mV
30 ms
G.
2 mV
50 msec
H.
20 mV
200 ms
I.
40 mV
1 nA
50 ms
J.
20
−20
−60
−100
E (mV)
0
5
10
15

SPIKES

I. Integrate-and-fire neuron

$$\boxed{\frac{dV(t)}{dt} = I(t) - \frac{V(t)}{\tau}}$$

$$V(T^m) = h, \quad \lim_{\delta \to 0} V(T^m + \delta) = 0$$



Constant input $I(t) = I_0$

$$\frac{dV}{dt} + \frac{V}{\tau} = I_0$$

$$\frac{d}{dt}\left[e^{t/\tau} V\right] = e^{t/\tau} I_0$$

$$\int_{T^n}^{T^{n+1}} \frac{d}{dt}\left[e^{t/\tau} V\right] dt = \int_{T^n}^{T^{n+1}} e^{t/\tau} I_0 \, dt$$

$$e^{T^{n+1}/\tau} V(T^{n+1}) - e^{T^n/\tau} V(T^n)$$

$$= \tau I_0 \left[e^{T^{n+1}/\tau} - e^{T^n/\tau}\right]$$

$$V(T^n) = 0, \quad V(T^{n+1}) = h$$

$$\therefore \quad h = \tau I_0 \left[1 - e^{-(T^{n+1} - T^n)/\tau}\right]$$

$$\boxed{\therefore \quad T^{n+1} - T^n = \Delta_0 = \tau \log\left[\frac{\tau I_0}{\tau I_0 - h}\right]}$$

OSCILLATOR !

Sinusoidal input

$$\frac{dV}{dt} + \frac{V}{\tau} = I_o + \epsilon \sin \omega t$$

Integrate from T^n to T^{n+1} :

$$e^{T^{n+1}/\tau} = \int_{T^n}^{T^{n+1}} [I_o + \epsilon \cos \omega t] e^{t/\tau} dt$$

which can be written in the form

$$\boxed{F(T^{n+1}) = F(T^n) + e^{T^n/\tau}}$$

where

$$F(T) = (I_o \tau - 1) e^{T/\tau} + \epsilon e^{T/\tau} \left[\frac{\omega \sin \omega T + \tau^{-1} \cos \omega T}{\omega^2 + \tau^{-2}} \right]$$

$(h = 1)$

Mode-locking

• Periodic input $I(t) = I_0 + \varepsilon \sin(\omega t)$

$$\boxed{F(T^{m+1}) = F(T^m) + e^{T^m/\tau}}$$

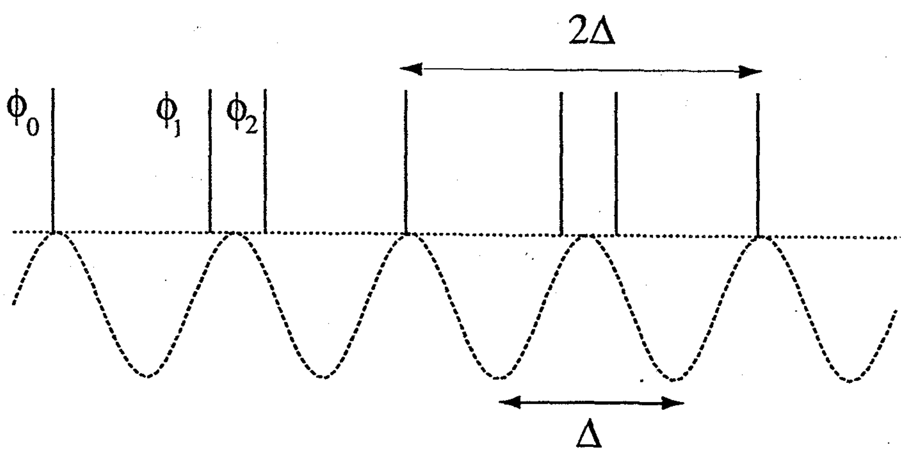
$$F(t) = e^{t/\tau}(A + B\sin[\omega t + \vartheta])$$

• Let $\Delta = 2\pi/\omega$ and define a p:q mode-locked state by

$$T^{m+q} = T^m + p\Delta$$

• Distinguish 3 types of mode-locked solution:

(i) *simple bursting*: p = 1, q > 1
(ii) *skipping*: p > 1, q = 1
(iii) *mixed state*: p,q > 1



• Parameter space over which a given mode-locked state exists and is stable defines an Arnold tongue.

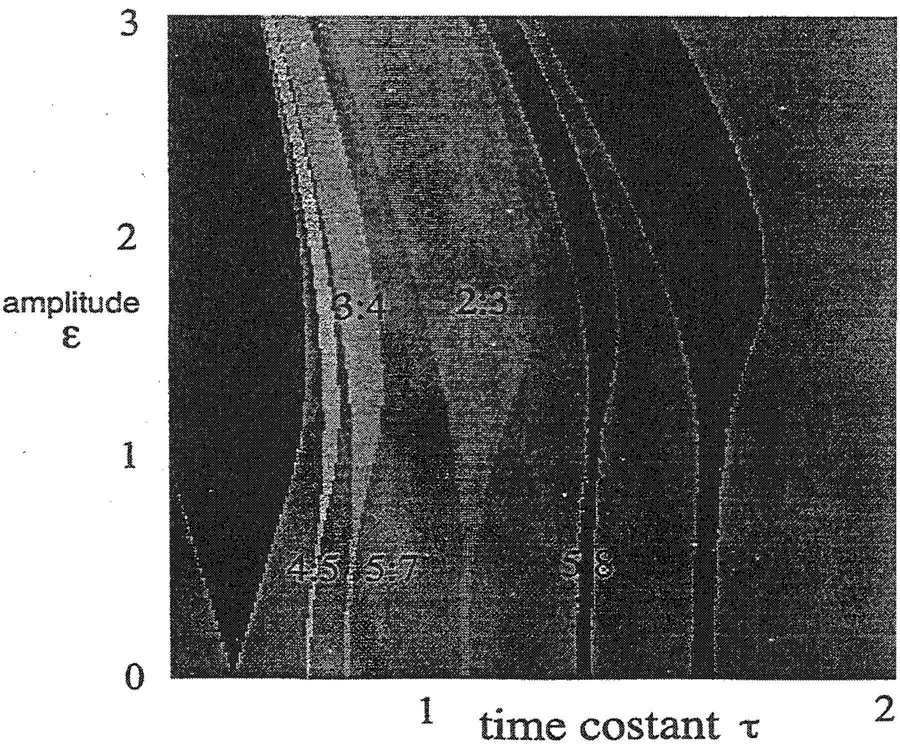
• For small coupling the Arnold tongues are non-overlapping such that the given mode-locked state is a global attractor of the system.

• Define mean ISI

$$\boxed{\langle \Delta \rangle = \lim_{N \to \infty} \frac{1}{N} \sum_{n=0}^{N} (T^{n+1} - T^{n})}$$

such that within Arnold tongue

$$\langle \Delta \rangle = \frac{q}{p} \Delta$$

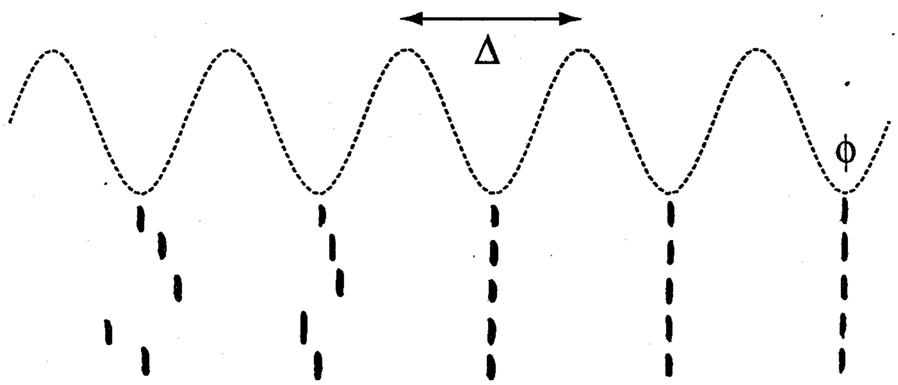


Reliability

Mode-locking provides a mechanism for spike time reliability.

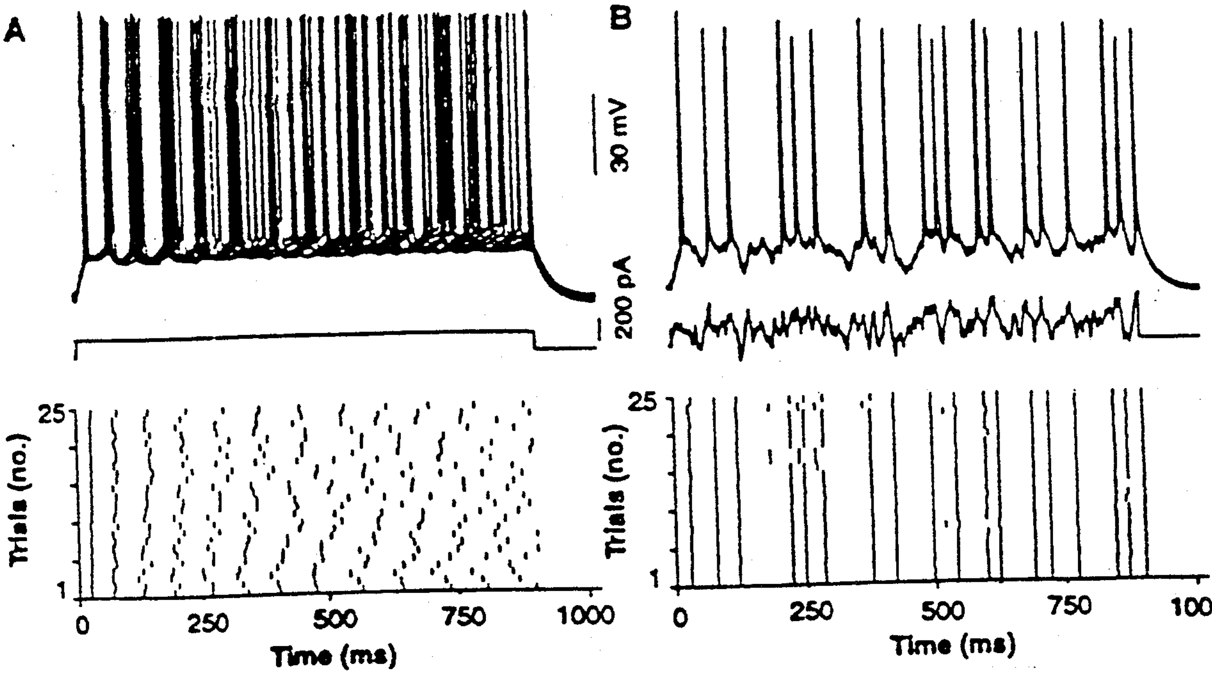
Consider 1:1 mode-locking: For almost all initial conditions firing times converge to the solution $T^n = (n - \phi)\Delta$ with

$$\boxed{\varepsilon \sin(2\pi\phi + \varphi_0) = \left[\frac{1}{e^{\Delta_0/\tau} - 1} - \frac{1}{e^{\Delta/\tau} - 1}\right]\sqrt{\frac{1}{\tau^2} + \left(\frac{2\pi}{\Delta}\right)^2}}$$

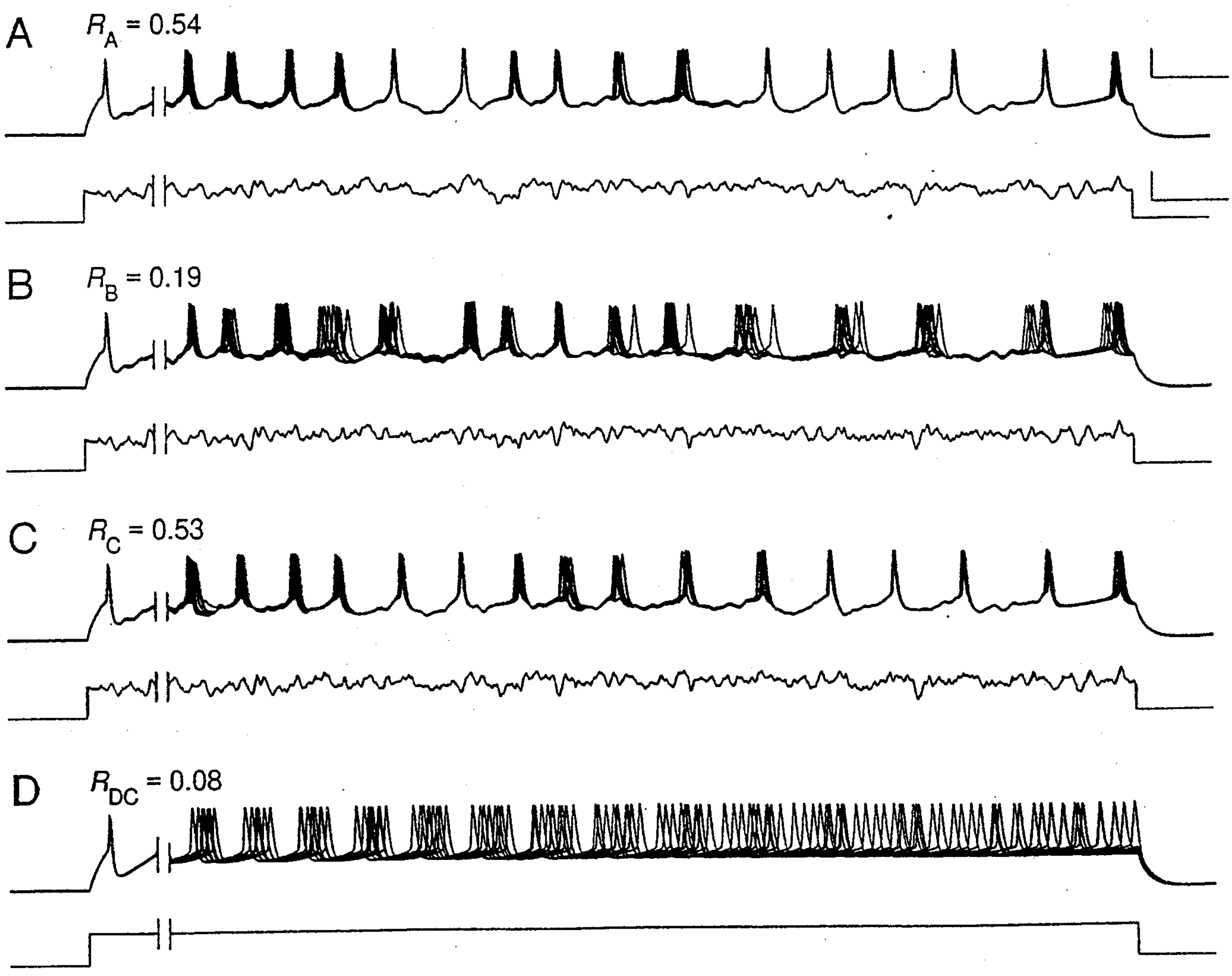


•Reliability also occurs for weak aperiodic signals

• Intrinsic noise can lead to a loss of precision and reliability



Cortical neuron (Mainen + Sejnowsky, Science 1995)



Aplysia neuron (Hunter et al, J. Neurophys. 1998)

Phase model: single IF neuron

Suppose $I(t) = I_0 + \varepsilon X(t)$ for small ε and periodic input $X(\omega t)$ of frequency ω. Perform change of variables

$$\boxed{\theta(t) = \frac{2\pi}{T_0}\int_0^{V(t)} \frac{dU}{I_0 - U}}$$

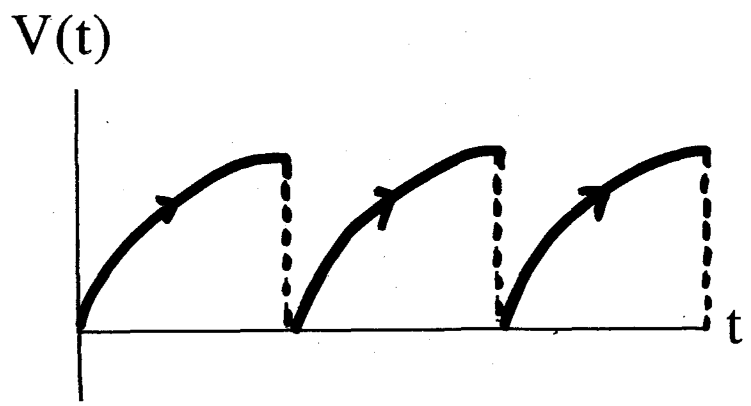
The phase variable satisfies the equation

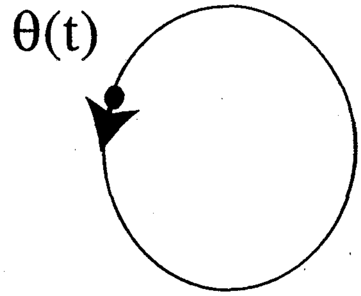
$$\boxed{\frac{d\theta}{dt} = \omega_0 + \varepsilon X(\omega t) R(\theta)}$$

where $\omega_0 = 2\pi/T_0$

$$\boxed{R(\theta) = \exp\left([\theta]T_0/2\pi\right)}$$

$[\theta] = \theta \bmod 2\pi$





•Rewrite phase equation as

$$\begin{cases} \dfrac{d\theta}{dt} = \omega_0 + \varepsilon X(\Theta)R(\theta) \\[2em] \dfrac{d\Theta}{dt} = \omega \end{cases}$$

Suppose that $\Delta\omega = \omega_0 - \omega = O(\varepsilon)$ and let $\psi = \theta - \Theta$. Since $d\psi/dt$ is small we can use *averaging theory*:

$$\boxed{\frac{d\psi}{dt} = \Delta\omega + \varepsilon H(\psi)}$$

where $H(\psi)$ is the *phase interaction function*

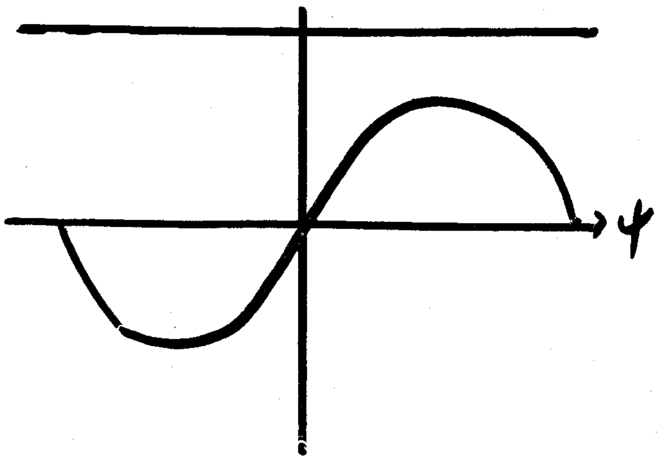
$$\boxed{H(\psi) = \frac{1}{2\pi}\int_0^{2\pi} R(\theta)X(\theta-\psi)d\theta}$$

•Phase-locking condition

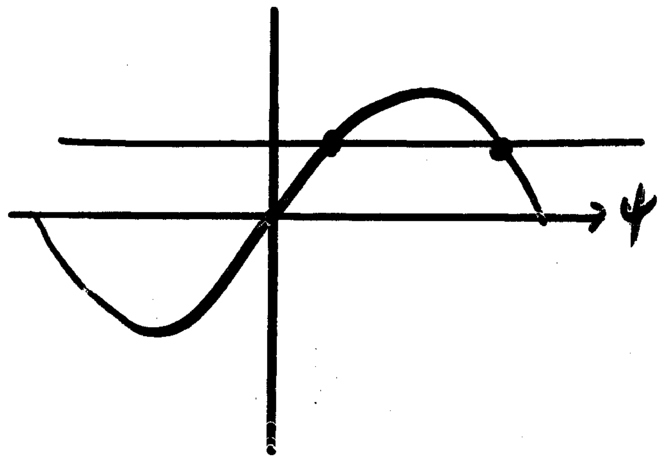
$$\boxed{\Delta\omega + \varepsilon H(\psi) = 0}$$

<u>Example</u> : $H(\psi) = -\sin\psi$

$$\Delta\omega = \epsilon \sin\psi$$

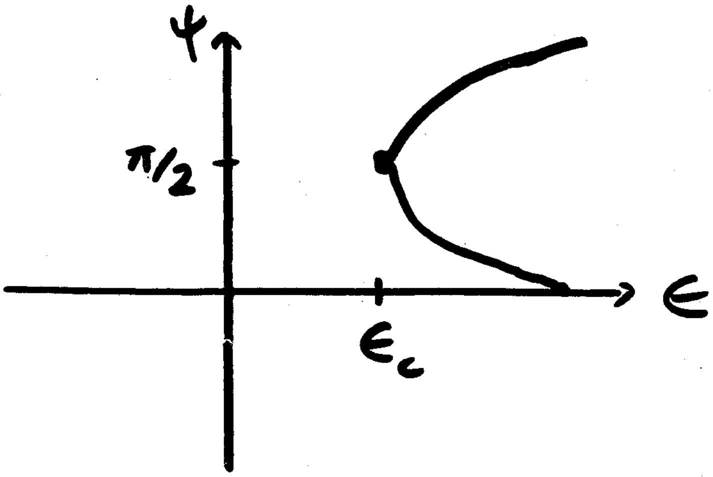


$\Delta\omega > \epsilon$

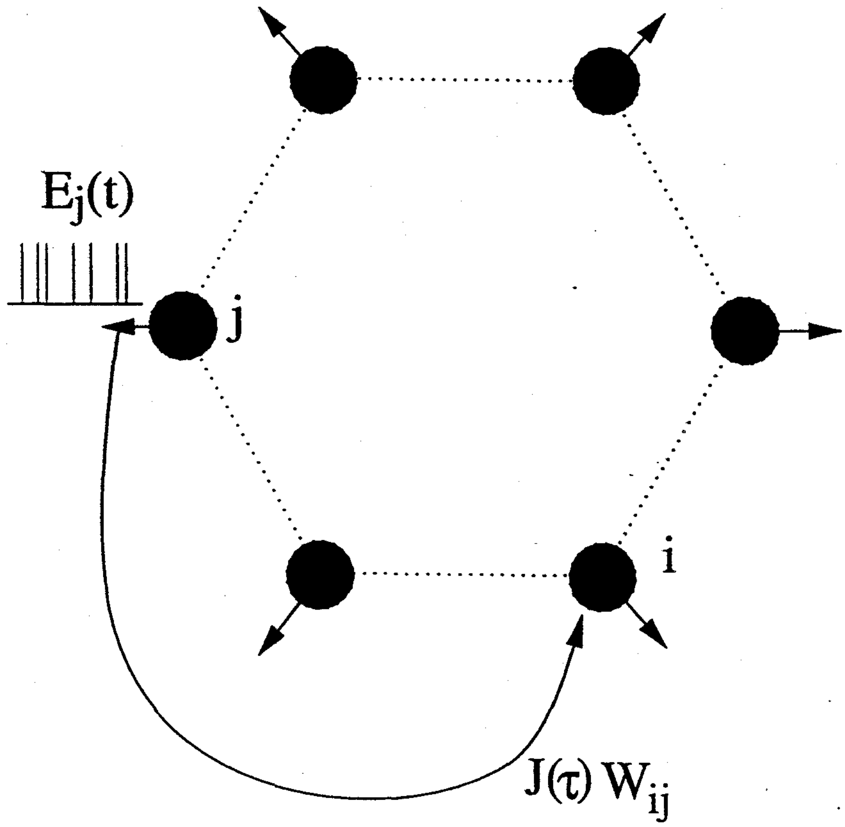


$0 < \Delta\omega < \epsilon$

- Saddle-node bifurcation



II. Network of IF neurons



$$\boxed{\frac{dV_i}{dt} = I - V_i + \varepsilon X_i(t)[V_s - V_i(t)]}$$

Synaptic input:

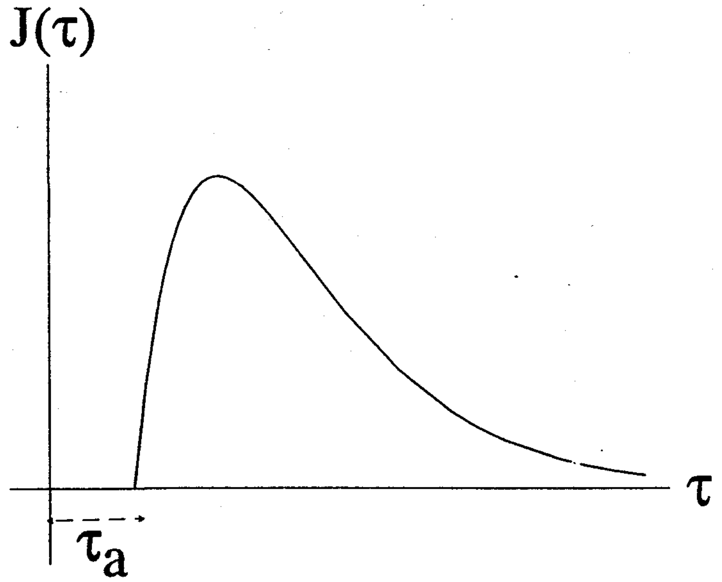
$$\boxed{X_i(t) = \sum_{j=1}^{N} W_{ij} \sum_{n} J(t - T_j^n)}$$

Threshold condition:

$$\boxed{V_j(T_j^n) = h}$$

T_j^n is the n[th] firing time of the j[th] neuron

• J(t) represents synaptic and axonal delays



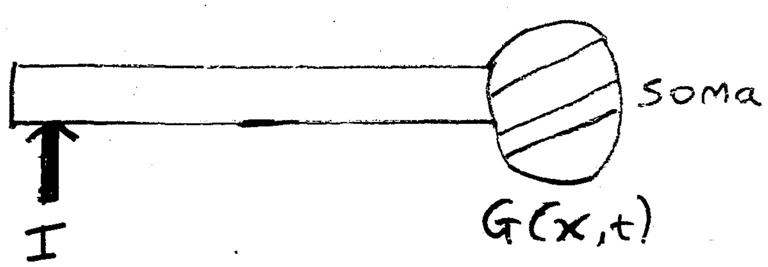
•Example:

$$J(t) = 0 \qquad for \qquad t < \tau_a$$

$$J(t) = \alpha^2 (t - \tau_a) e^{-\alpha(t-\tau_a)} \qquad for \qquad t > \tau_a$$

Large α (small α) corresponds to fast (slow) synapses, and τ_a is the axonal delay

•For simplicity assume that $V_s >> V_i(t)$



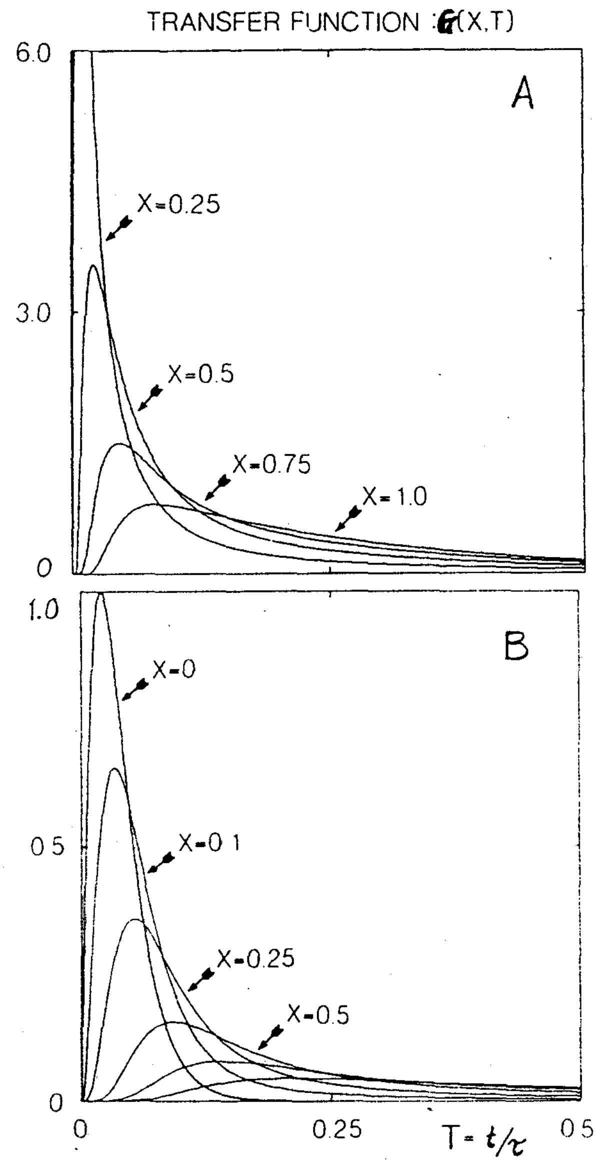
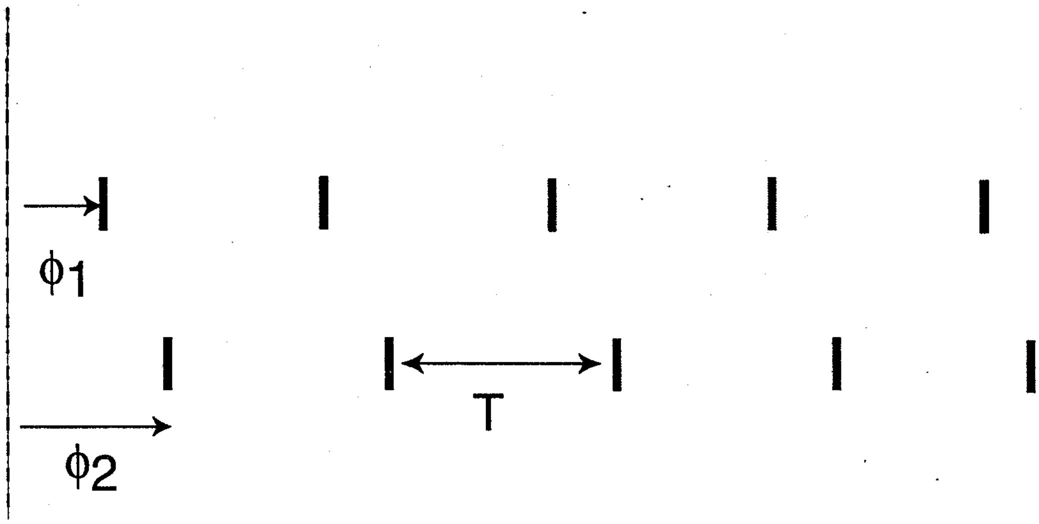


Figure 2.13
Transfer function (in A) and its convolution (in B) for voltage clamping at the soma of a passive soma-dendritic model with $L = 1.5$. Curves have two interpretations: (1) as the voltage transient, $V(X, T)$, at point X, in response to a voltage transient, $V(0, T)$, imposed by the voltage clamp at the soma, and (2) as the current transient, $I(0, T)$, detected by the voltage clamp at $X = 0$, for a synaptic current, $I_i(X, T)$, imposed at point X. In B, the imposed transient is the one labeled $X = 0$. In A, the imposed transient corresponds to a Dirac delta function. Details of equations and interpretations can be found in the original publication (Rall and Segev 1985).

Phase-locking.

• All neurons have same inter-spike interval T but the spike trains are shifted by a phase ϕ_j

$$\boxed{T_j^n = (n - \phi_j)T}$$



• In terms of the phase description

$$\boxed{\theta_j(t) = \omega t + 2\pi\phi_j}$$

• Each neuron receives a periodic input

$$\boxed{X_i(t) = \sum_{j=1}^{N} W_{ij} P(\theta_j(t))}$$

where

$$\boxed{P(\theta) = \sum_{m=-\infty}^{\infty} J(mT + \theta[T/2\pi])}$$

• Phase equation is

$$\frac{d\theta_i}{dt} = \omega_0 + \varepsilon\left[\sum_j W_{ij} P(\theta_j)\right] R(\theta_i)$$

for all j = 1,…,N.

•Averaging over one period gives

$$\frac{d\theta_i}{dt} = \omega_0 + \varepsilon \sum_j W_{ij} H(\theta_j - \theta_i)$$

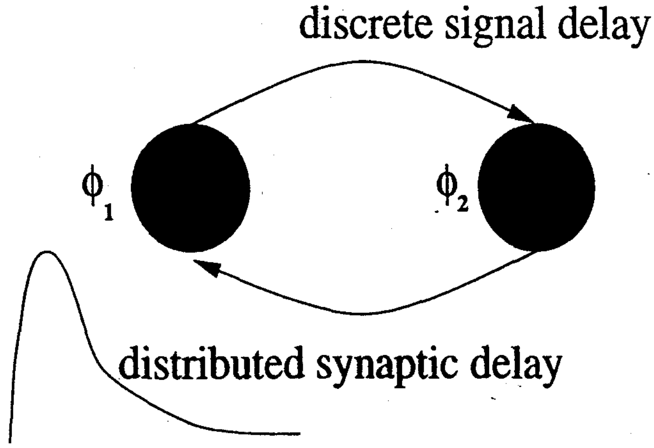
where H(θ) is the phase interaction function

$$H(\theta) = \frac{1}{2\pi}\int_0^{2\pi} R(\theta' - \theta) P(\theta') d\theta'$$

•Phase-locking equation

$$\omega = \omega_0 + \varepsilon \sum_j W_{ij} H(\phi_j - \phi_i)$$

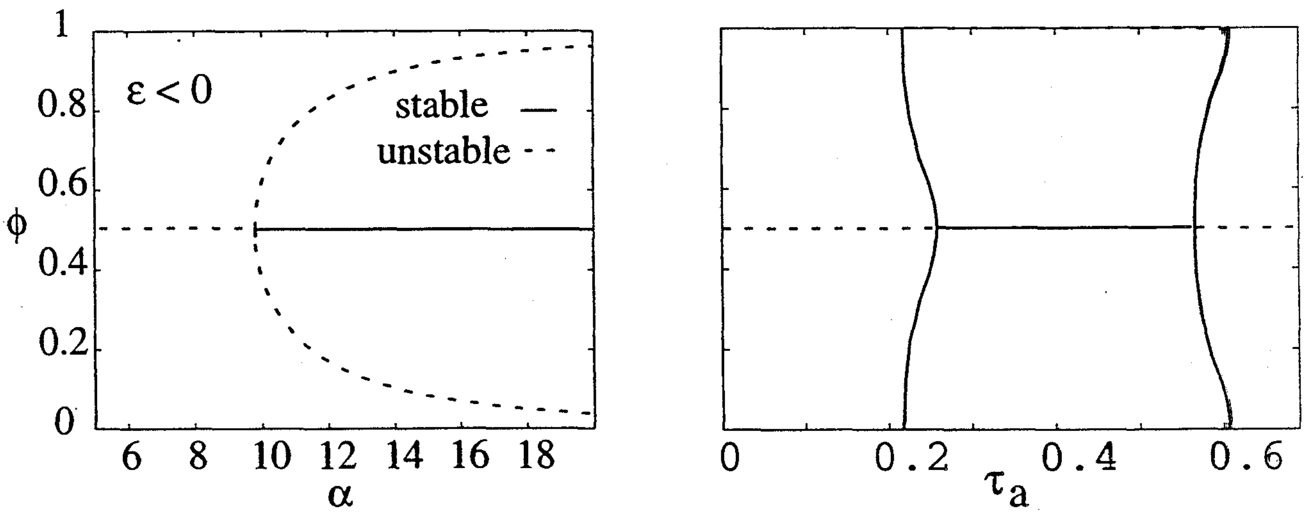
Pair of inhibitory IF neurons



$$\phi = \phi_2 - \phi_1$$

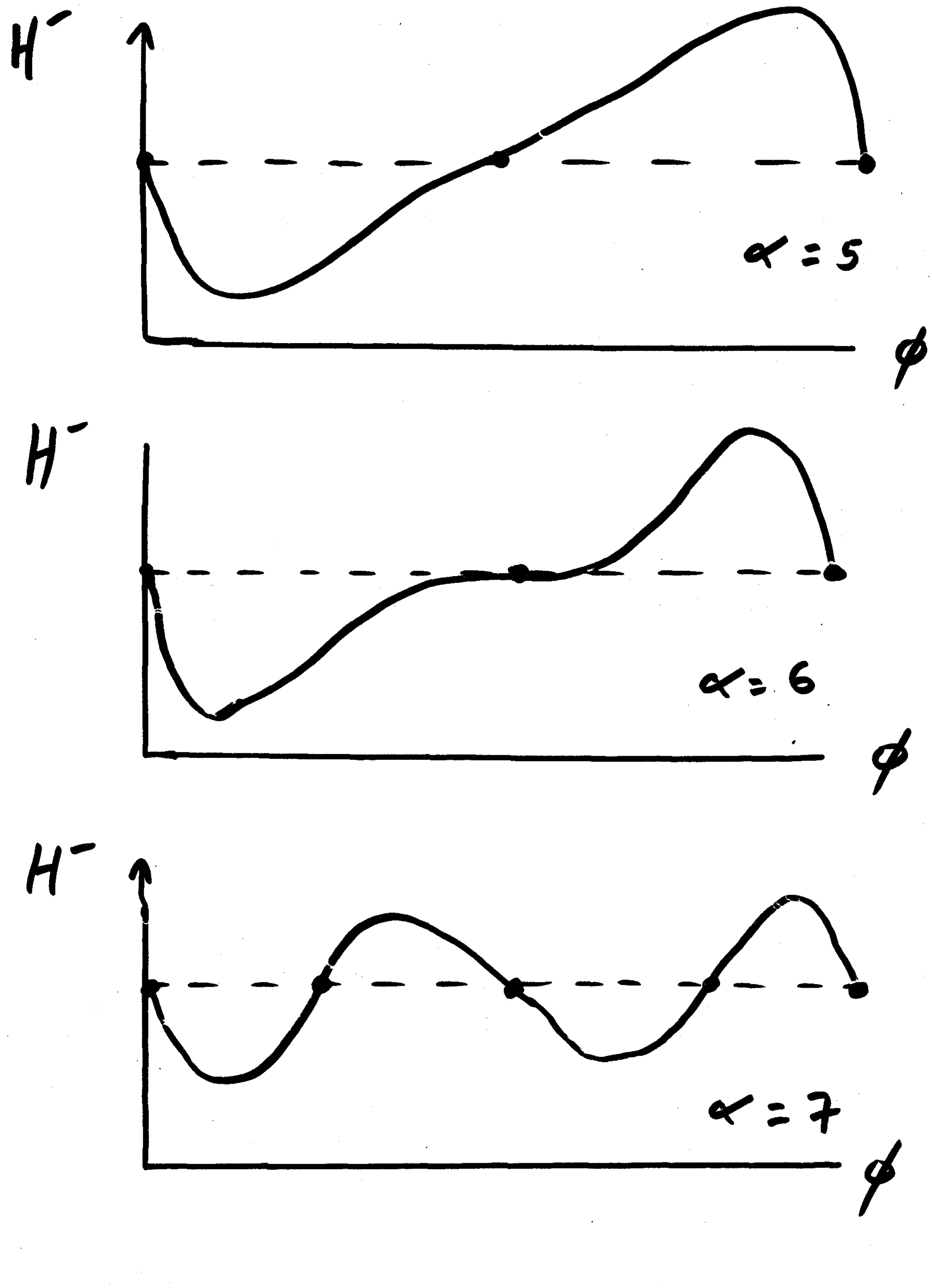
Condition for phase-locking is

$$\boxed{H^{-}(\phi) \equiv H(\phi) - H(-\phi) = 0,}$$



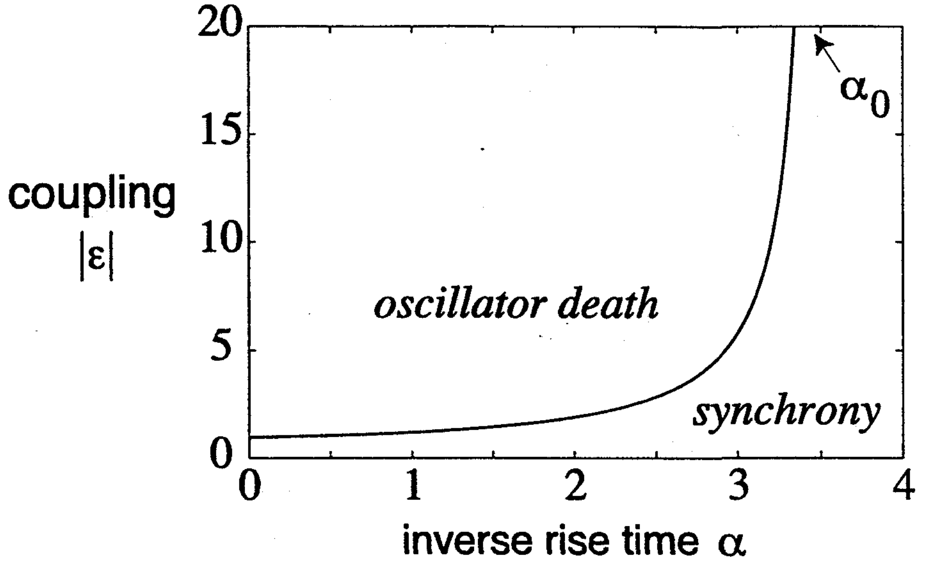
Stability condition

$$\boxed{\varepsilon \frac{dH^{-}(\phi)}{d\phi} > 0}$$



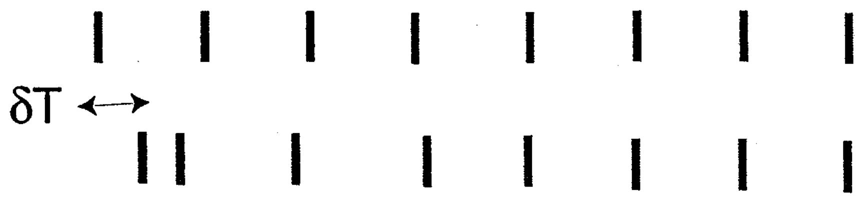
H⁻
α = 5
φ
H⁻
α = 6
φ
H⁻
α = 7
φ

•Increasing the coupling between a pair of inhibitory IF neurons leads to oscillator death – example of a **strong coupling instability**

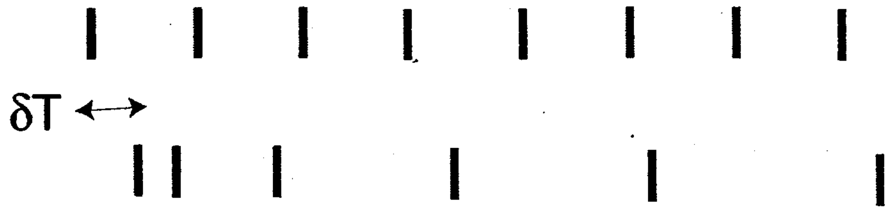


•Consider perturbations of synchronous state:

$$\boxed{T_j^n = nT + \delta T_j^n}$$



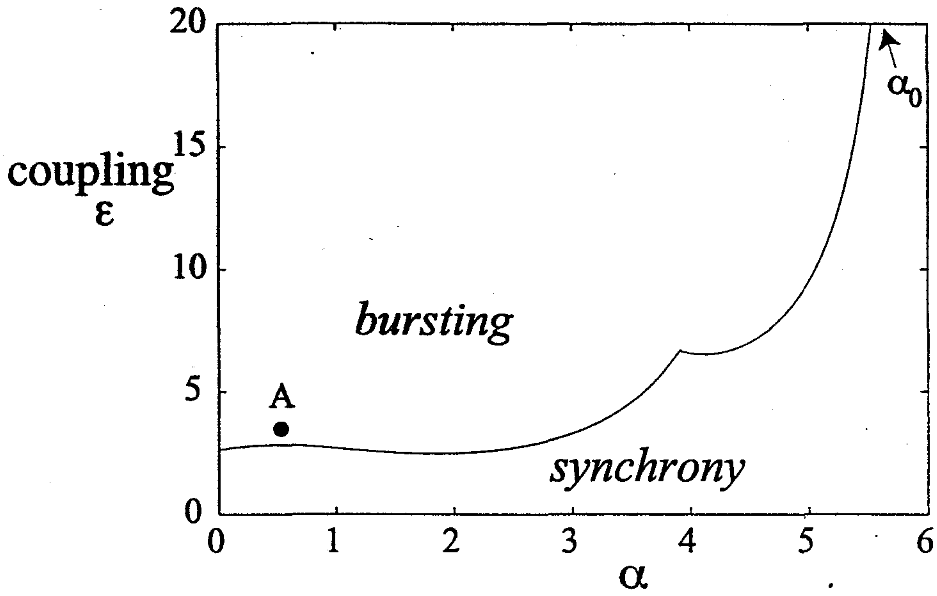
Stable solution (δT decays)



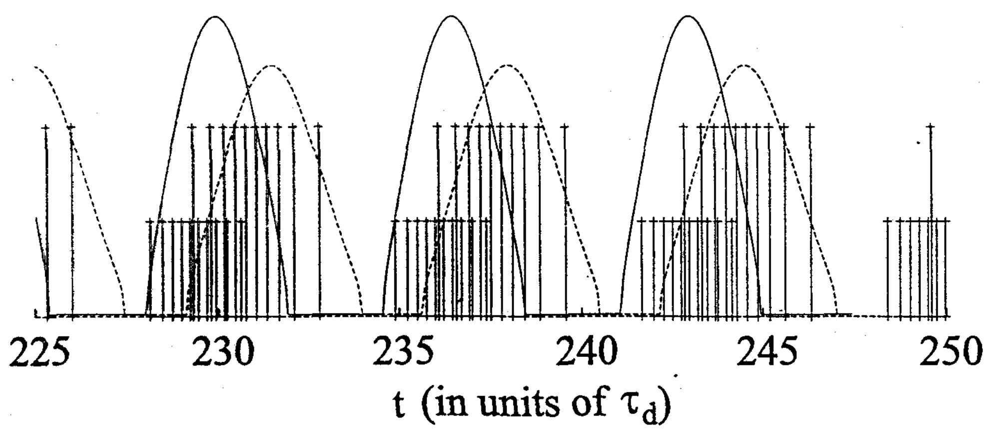
Unstable solution (δT grows)

Excitatory/inhibitory pair of IF neurons

•Increasing the coupling between an excitatory/ inhibitory pair of IF neurons leads to bursting



•Bursting state consists of a time-periodic modulation in the mean firing rate



III. Large populations of IF neurons

- Consider synaptic input

$$\boxed{X_i(t) = \sum_{j=1}^{N} W_{ij} \sum_{n} J(t - T_j^n)}$$

with $J(t) = 1$ for $0 < t < \Delta t$, and zero otherwise.

- Then

$$\boxed{X_i(t) = \sum_{j=1}^{N} W_{ij} N_j(t, \Delta t)}$$

where $N_j(t,\Delta t)$ is the number of spikes fired by j[th] neuron in interval $[t-\Delta t, t]$

- If $X_i(t)$ is a slowly varying function of time,

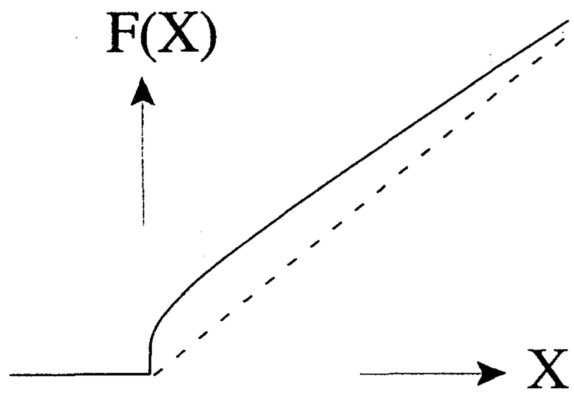
$$\boxed{\begin{aligned} X_i(t) &= \sum_{j=1}^{N} W_{ij} \int_{0}^{\Delta t} F(X_j(t - t'))dt' \\ &= \sum_{j=1}^{N} W_{ij} \int_{0}^{\infty} J(t')F(X_j(t - t'))dt' \end{aligned}}$$

where $F(X_j)$ is the firing rate for constant synaptic input X_j

• Recall that for a constant input $I_0 + \varepsilon X_j$ an IF neuron is an oscillator with constant ISI

$$\Delta T_i = \log\left[\frac{I_0 + \varepsilon X_i}{I_0 + \varepsilon X_i - 1}\right], \quad I_0 + \varepsilon X_i > 1$$

Hence, $\qquad F(X_i) = \Delta T_i^{-1}$



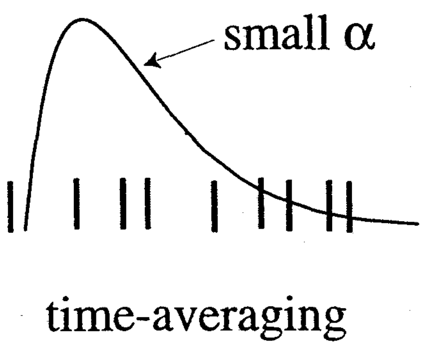
• Argument holds for more general $J(t)$. For example, if $J(t) = e^{-t}$ then

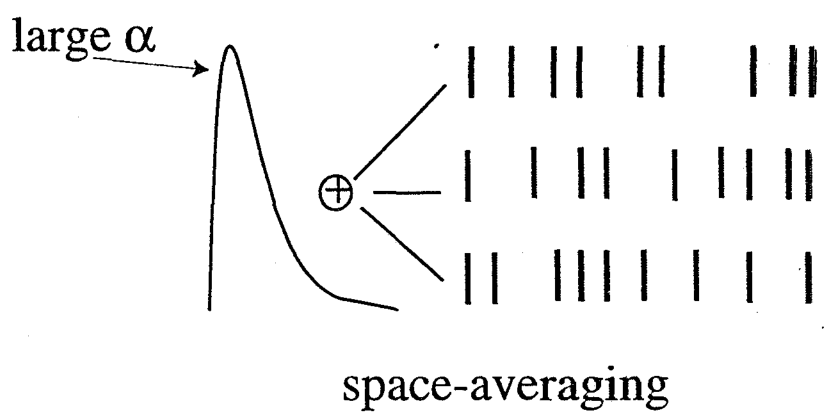
$$\boxed{\frac{dX_i}{dt} = -X_i + \sum_{j=1}^{N} W_{ij} F(X_j)}$$

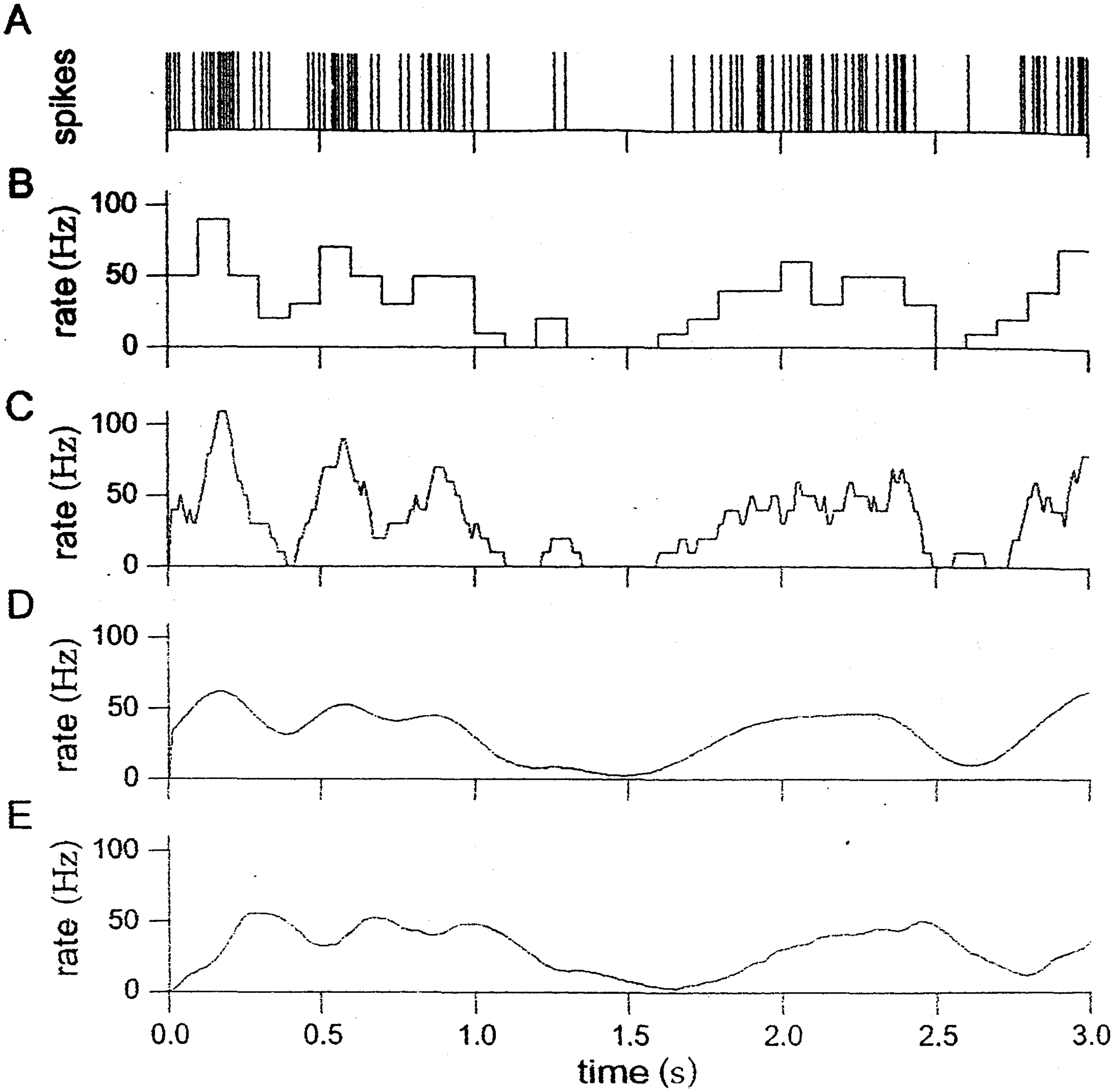
• There are two scenarios in which $X_i(t)$ is slowly varying with time t:

Slow synapses - J(t) has a broad profile (small α) so that there is time-averaging of incoming spike trains over a sliding window

Incoherent states - space-averaging of spike trains over a large population with a uniform distribution of firing times







$$r(t) = \int_0^\infty J(\tau)\, \rho(t-\tau)\, d\tau$$

$$= \sum_{i=1}^{N} J(t - T_i)$$

$$\rho(t) = \sum_{i=1}^{N} \delta(t - T_i)$$

The incoherent state

- Consider a large pool of globally coupled IF neurons, and define the population activity by

$$\boxed{A(t) = \lim_{N\to\infty} \frac{1}{N} \sum_{j=1}^{N} \sum_{n} \delta(t - T_j^n)}$$

The number of neurons that fire in interval $[t,t+\Delta t]$ is then $N(t)$ where

$$\boxed{N(t) = \int_{t}^{t+\Delta t} A(t')dt'}$$

- All neurons receive the same synaptic input

$$\boxed{X(t) = \int_0^\infty J(t')A(t-t')dt'}$$

- Incoherent state defined as $A(t) = A_0$. The value for A_0 is determined self-consistently from

$$\boxed{\frac{1}{A_0} = \log\left[\frac{I + \varepsilon A_0}{I + \varepsilon A_0 - 1}\right]}$$

• Can derive a MF equation for A(t)

$$\boxed{A(t) = \int_{-\infty}^{t} P(t \mid s)A(s)ds}$$

where $P(t|s)$ is the probability of firing at time t given a neuron last fired at time s. In the case of zero noise

$$\boxed{P(t \mid s) = \delta(t - s - T(s))}$$

where $T(s)$ is determined from integrating the IF equation between s and $s + T(s)$,

Stability

• Consider perturbations of incoherent state

$$\boxed{A(t) = A_0 + \delta A_n e^{i\lambda_n t}}$$

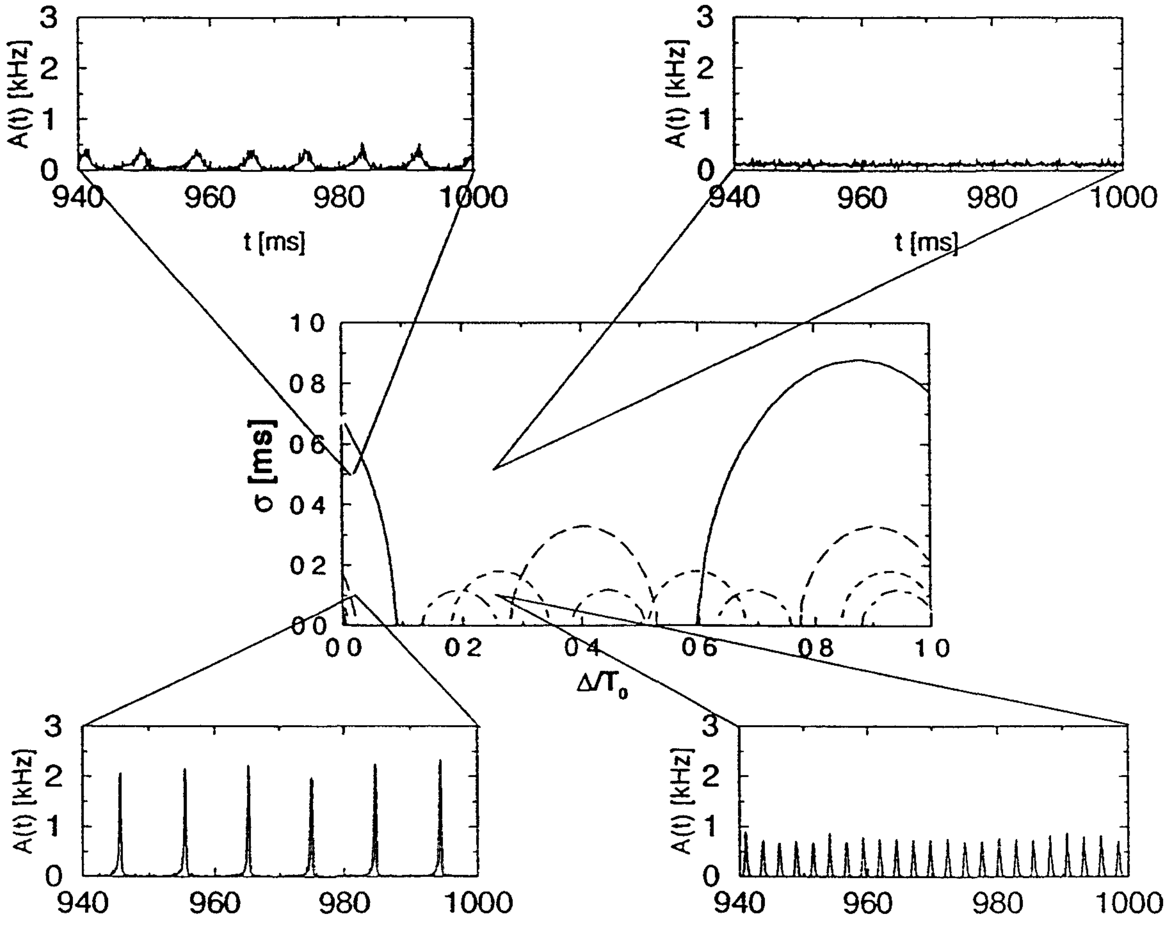
where $\lambda_n = 2\pi i n + \Lambda_n$

i) For excitatory coupling, incoherent state is stable with respect to n^{th} eigenmode provided that $\alpha < \alpha_n$ where

$$\boxed{\alpha_n = -1 + \sqrt{1 + 4\pi^2 n^2 A_0^2}}$$

ii) Inhibitory network is unstable with respect to high harmonics, that is, large *n* eigenmodes, since we now require $\alpha > \alpha_n$

iii) Axonal delays tend to have a destabilizing effect whereas noise has a stabilizing effect by suppressing higher harmonics



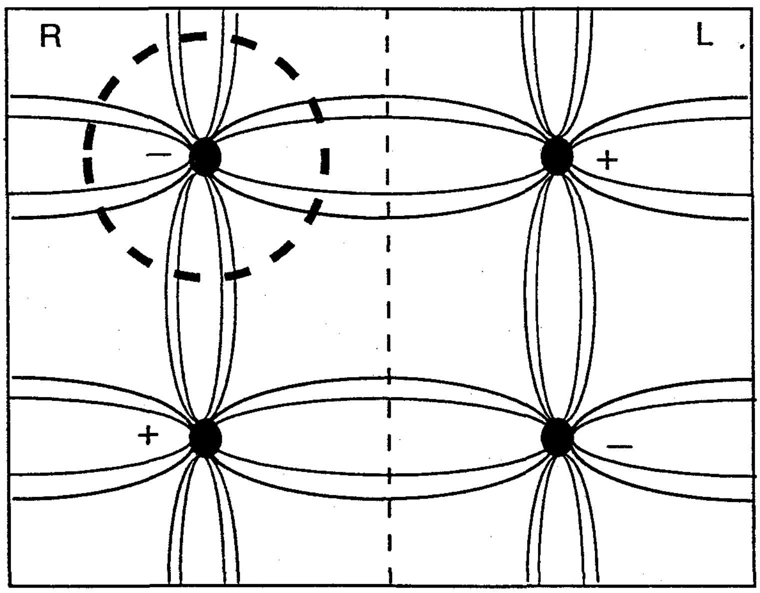
Gerstner + Van Hemmen

IV. IF model of orientation tuning

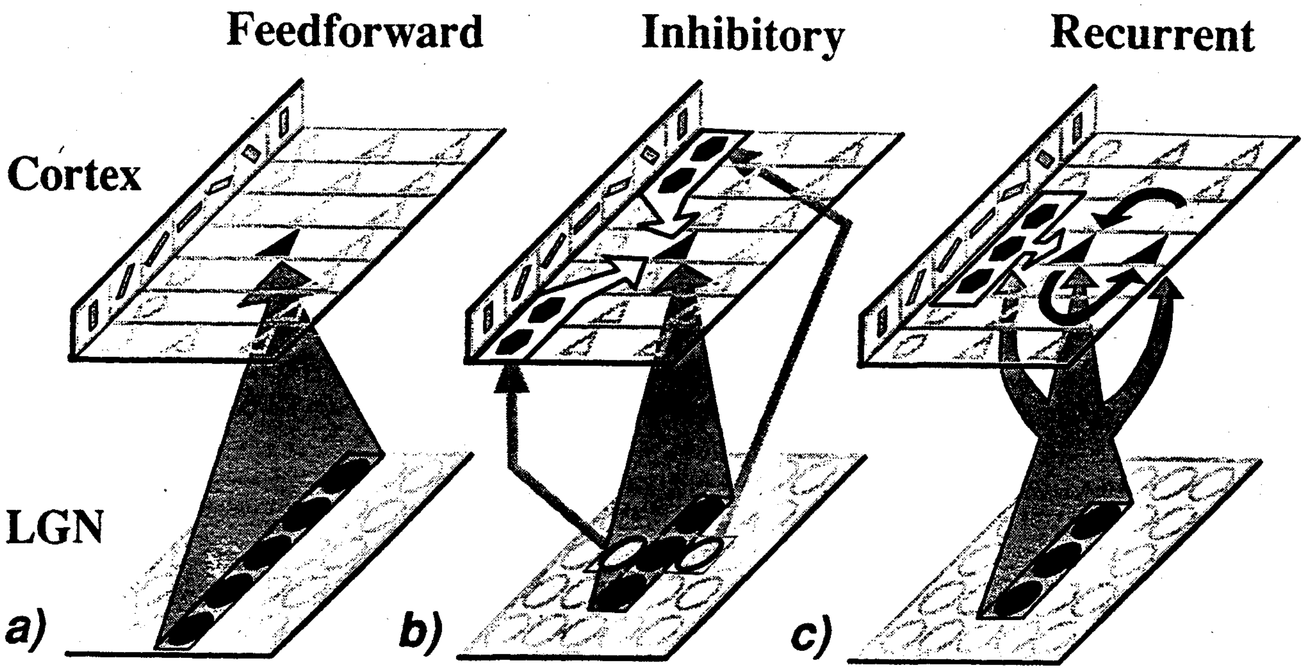
i) Orientation preference changes continuously as a function of cortical location except at pinwheels

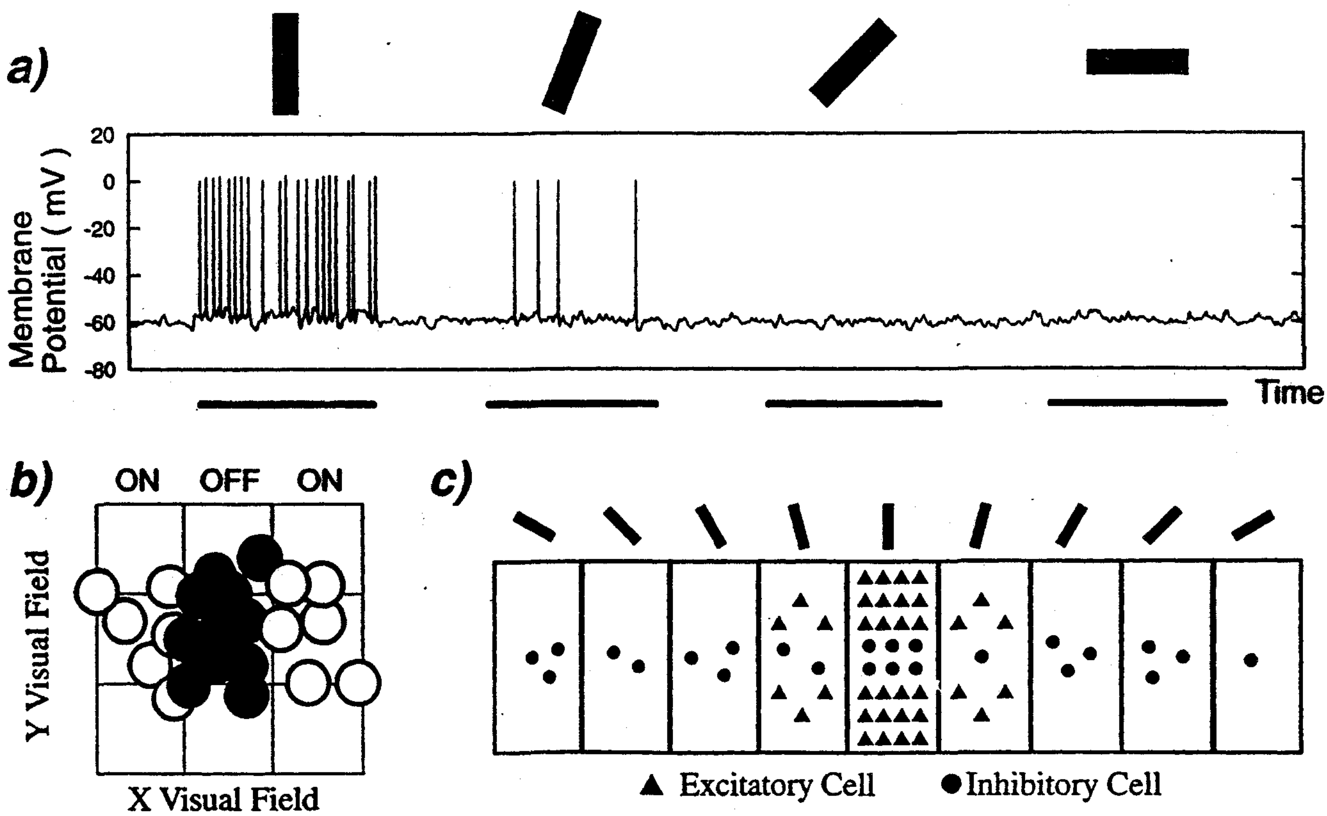
ii) There exist linear regions bounded by pinwheels within which iso-orientation domains form parallel slabs

iii) Linear regions cross OD stripes at right-angles. Pinwheels tend to align with centers of OD stripes.

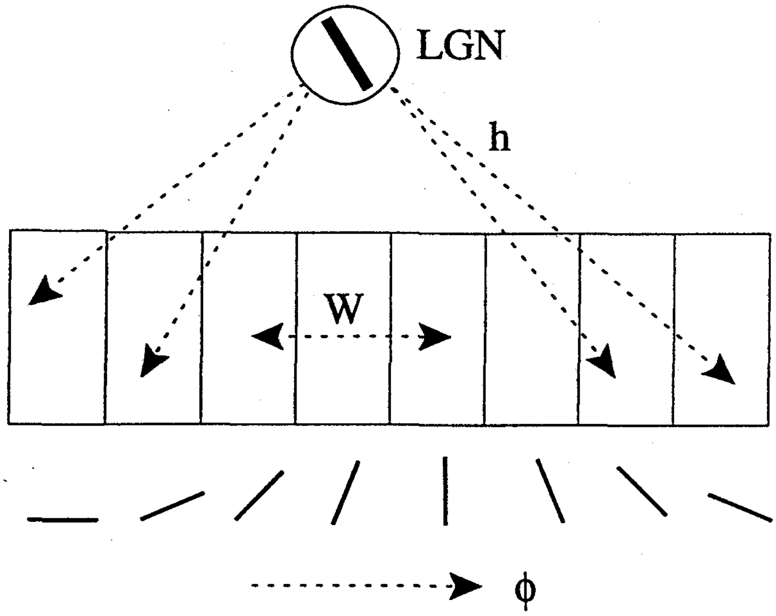


iv) Four pinwheels per hypercolumn

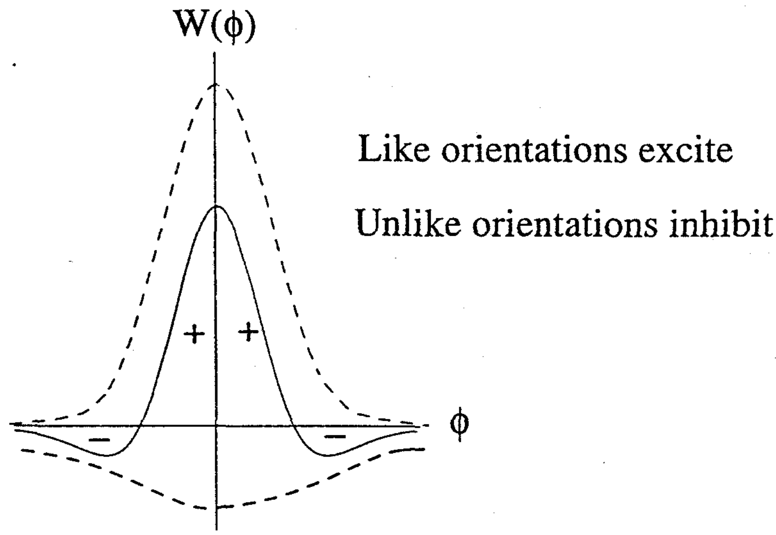

Feedforward
Inhibitory
Recurrent
Cortex
LGN
a)
b)
c)


a)
Membrane Potential (mV)
20
0
-20
-40
-60
-80
Time
b)
ON
OFF
ON
Y Visual Field
X Visual Field
c)
▲ Excitatory Cell
● Inhibitory Cell

- Ring model of orientation selectivity

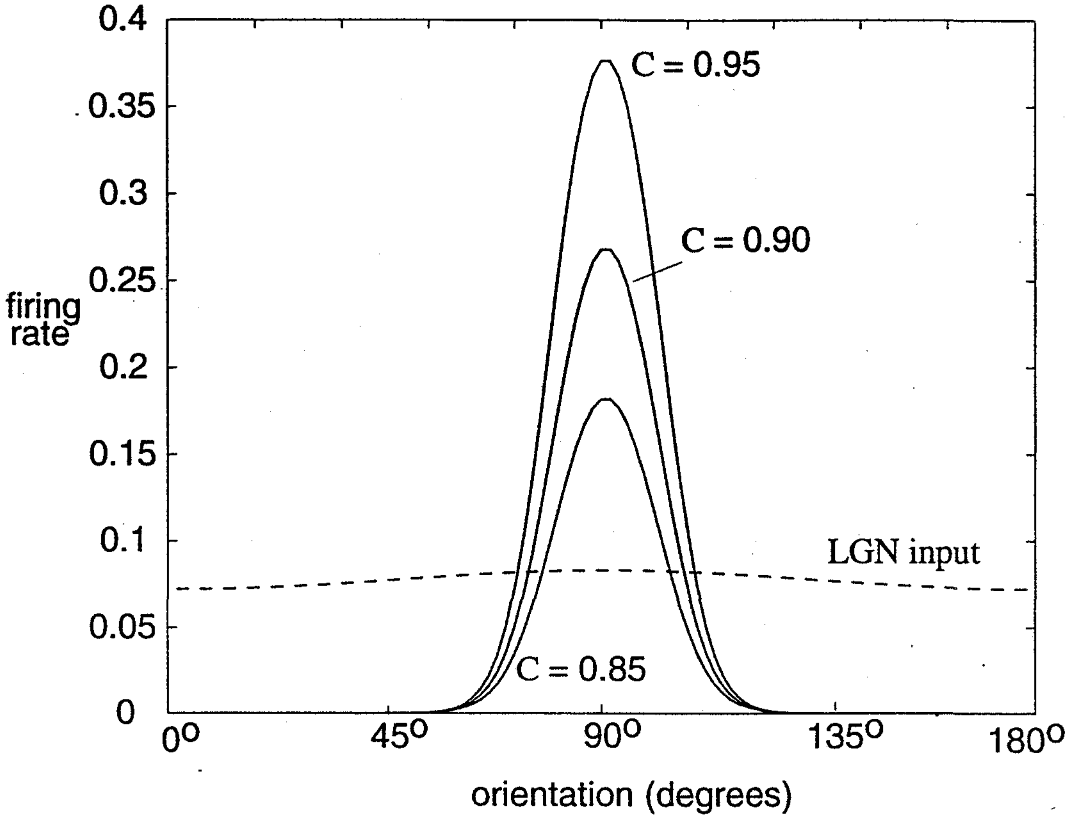


$$\frac{dV(\phi)}{dt} = I - V(\phi) + \varepsilon X(\phi, t) \quad + \quad reset$$



$$X(\phi, t) = \int_0^{\pi} W(\phi - \phi')\left[\sum_n J(t - T_n(\phi))\right] d\phi'$$

• For small coupling IF neurons are phase-locked. Increasing the coupling generates an instability leading to sharp orientation tuning.



• Mean firing rate is given by

$$\boxed{a(\phi)^{-1} = \frac{1}{M}\sum_{m=1}^{M} \Delta T_m(\phi)}$$

• Width of tuning curve is contrast invariant

- Recurrent mechanism of orientation tuning - an example of **spontaneous symmetry breaking**

- Consider the corresponding rate model

$$\frac{dX(\phi)}{dt} = -X(\phi) + \int_0^{\pi} W(\phi-\phi')F(X(\phi',t))d\phi'$$

- Suppose *F(0) = 0* so that *X = 0* is a fixed point solution of the rate equation. Linearize and set $X(\phi,t) = e^{\lambda t}u(\phi)$

$$(\lambda+1)u(\phi) = \int_0^{\pi} W(\phi-\phi')u(\phi')d\phi'$$

- Solutions of eigenvalue equation are

$$u_n(\phi) = \cos(2n(\phi-\phi_0)), \qquad \lambda_n = -1+\varepsilon W_n$$

where W_n is the n[th] Fourier component of $W(\phi)$

$$W(\phi) = W_0 + 2\sum_{n>0} W_n \cos(2n\phi)$$

- For small coupling ε, we have $\lambda_n < 0$ for all n and so fixed point is stable

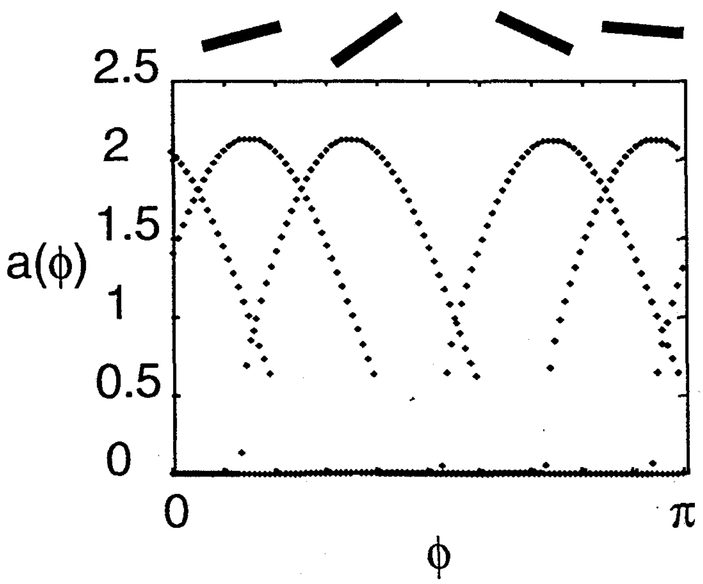
• Suppose that $W_1 > W_n$ for all $n \neq 1$. Then fixed point destablilizes at critical coupling $\varepsilon_c = 1/W_1$ due to excitation of eigenmode $u_1(\phi)$

• The growing eigenmode has a single peak at the orientation ϕ_0 and leads to the formation of a tuning curve

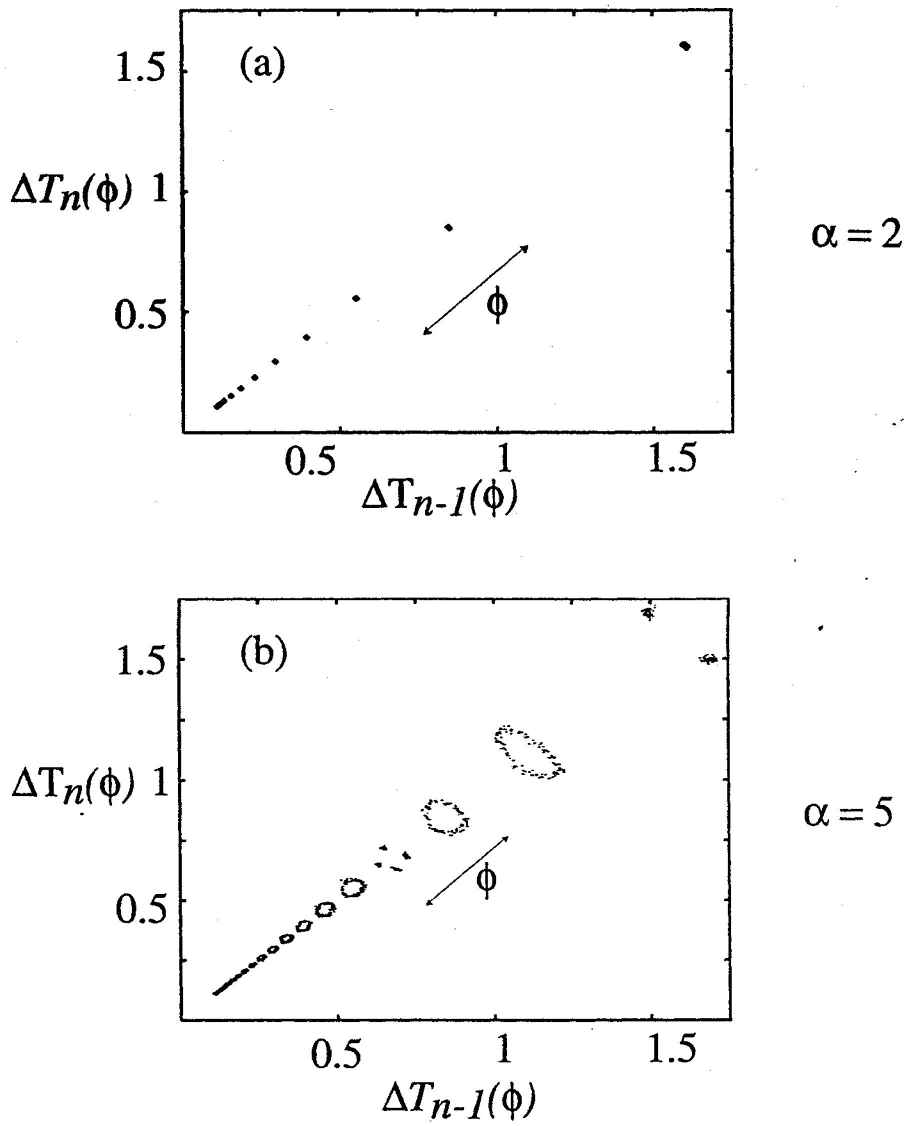
• What determines ϕ_0?

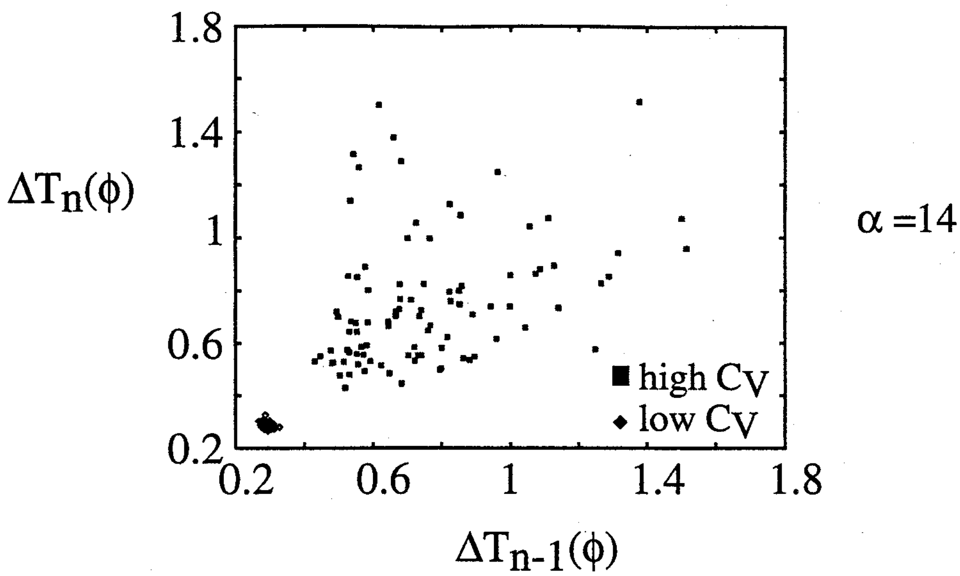
ϕ_0 is arbitrary in the absence of any biased LGN input – this reflects hidden rotation symmetry of the ring

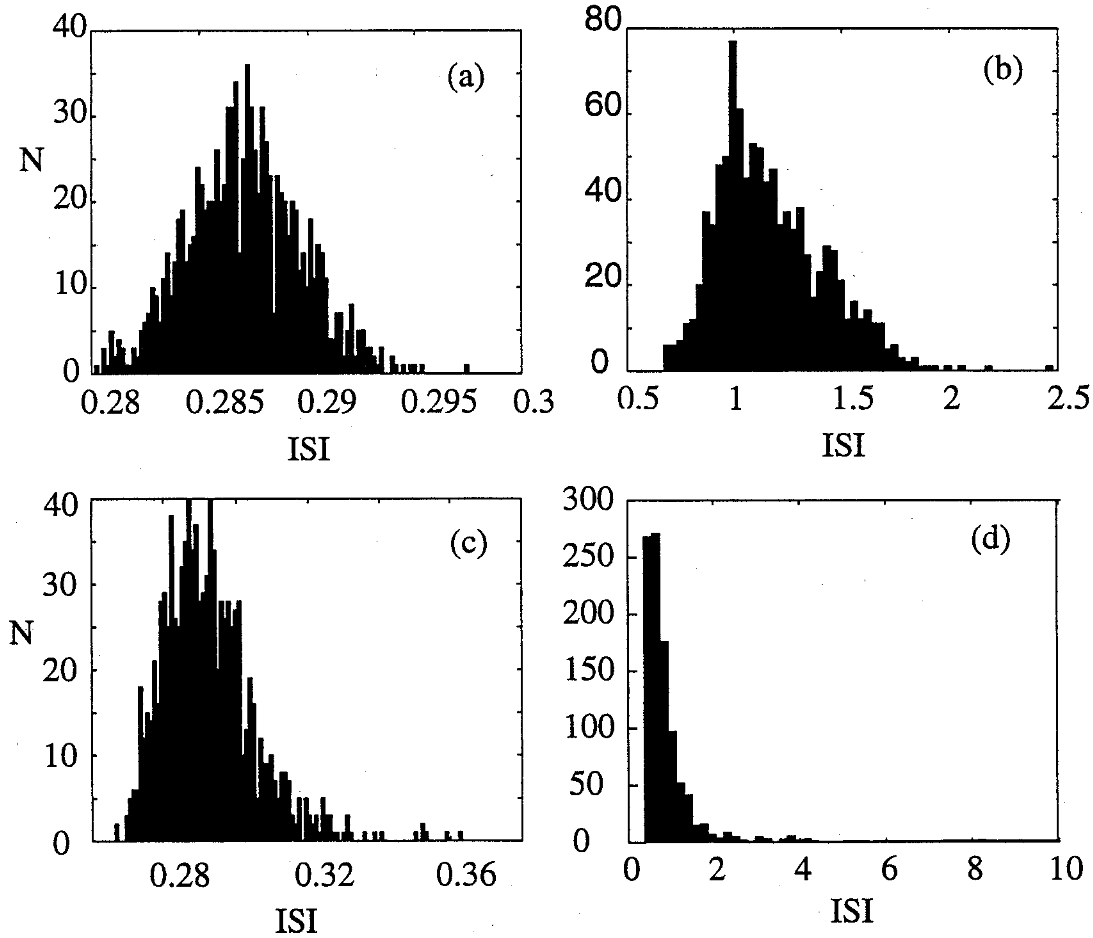
a weakly biased LGN input fixes ϕ_0 by explicitly breaking the symmetry



• Find fluctuations in the ISIs grow with the speed of the synapses α

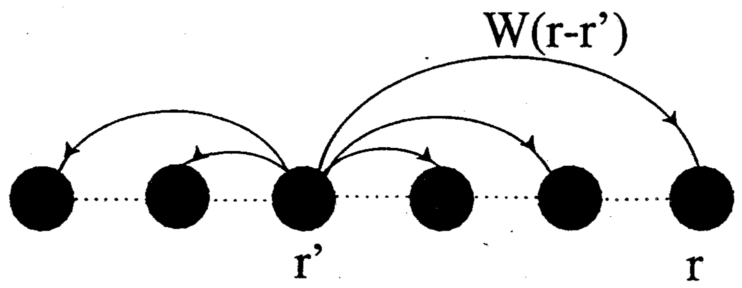



$\Delta T_n(\phi)$
$\Delta T_{n-1}(\phi)$
$\alpha = 14$
high C_V
low C_V


(a)
(b)
(c)
(d)
N
ISI

V. Synaptic waves

- Consider a one-dimensional network of synaptically coupled excitatory IF neurons:



- Linear evolution

$$\boxed{\frac{\partial V(r,t)}{\partial t} = I_0 - V(r,t) + \epsilon X(r,t)}$$

- Nonlinear reset: $V(r,t^+) = 0$ whenever $V(r,t) = 1$

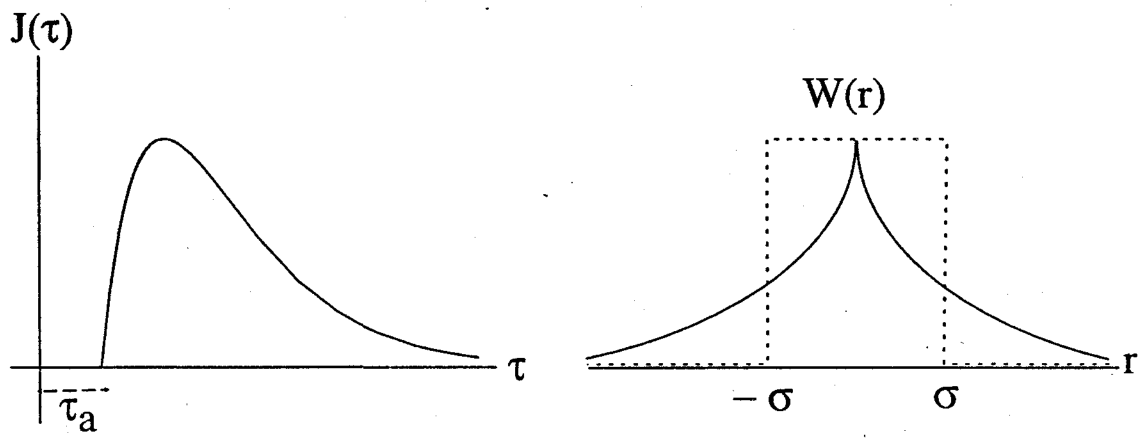
- Synaptic input:

$$\boxed{X(r,t) = \int_{-\infty}^{\infty} W(r-r') \sum_n J(t - T_n(r'))dr'}$$

• Take $W(r)$ to be an exponential weight distribution

$$\boxed{W(r) = (2\sigma)^{-1}\mathrm{e}^{-|r|/\sigma}}$$

Basic results will not depend on the precise form of $W(r)$.



• For $\epsilon = 0$ we can distinguish between two regimes:

Oscillatory regime ($I_0 > 1$) – each neuron independently fires at regular intervals of period $T_0 = \ln(I_0/[I_0 - 1])$

Excitable regime ($I_0 < 1$) – each neuron requires an additional stimulus before it can fire.

Solitary pulses: $I_0 = 0$

- Define a solitary wave solution as one where each neuron fires once with $T(r) = r/c$ (up to an arbitrary constant). Here c is the speed of the pulse.

- Threshold condition

$$V(r, T(r)) = 1$$

generates a self-consistency condition for c:

$$\boxed{1 = \int_{-\infty}^{T(r)} \mathrm{e}^t \left[\int_{-\infty}^{\infty} W(r - r') J(t - T(r')) dr' \right] dt}$$

which simplifies to

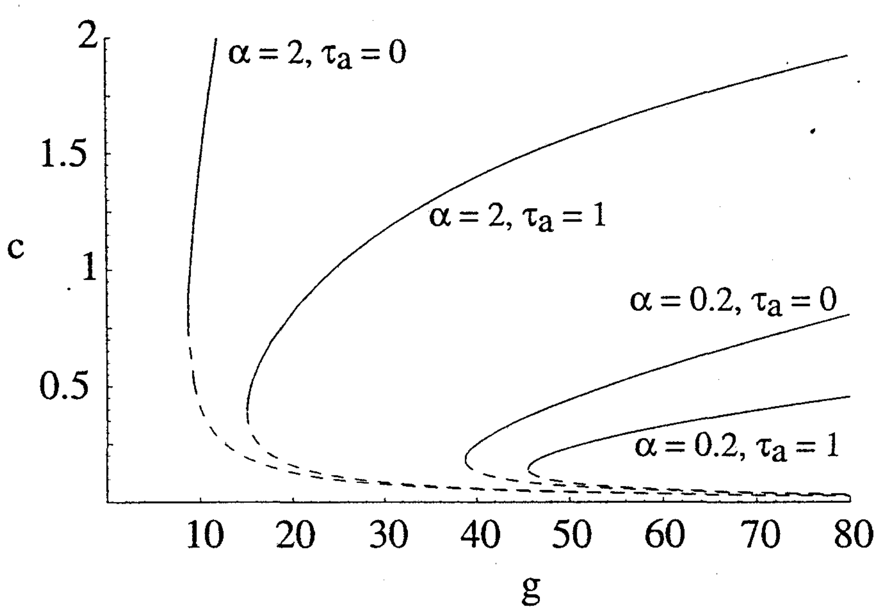
$$\boxed{1 = \int_0^{\infty} W(r) \mathrm{e}^{-r/c} \int_0^{r/c} \mathrm{e}^t J(t) dt dr}$$

• For synaptic and axonal delays $J(\tau)$

$$\boxed{1 = \frac{g\alpha^2 c}{2(1+c)} \frac{e^{-c\tau_a}}{(\alpha+c)^2}.}$$

• For large c and $\tau_a = 0$, the velocity scales according to a power law $c \sim \alpha\sigma\sqrt{g/2}$. If $\tau_a > 0$ then $c \sim \ln g$.

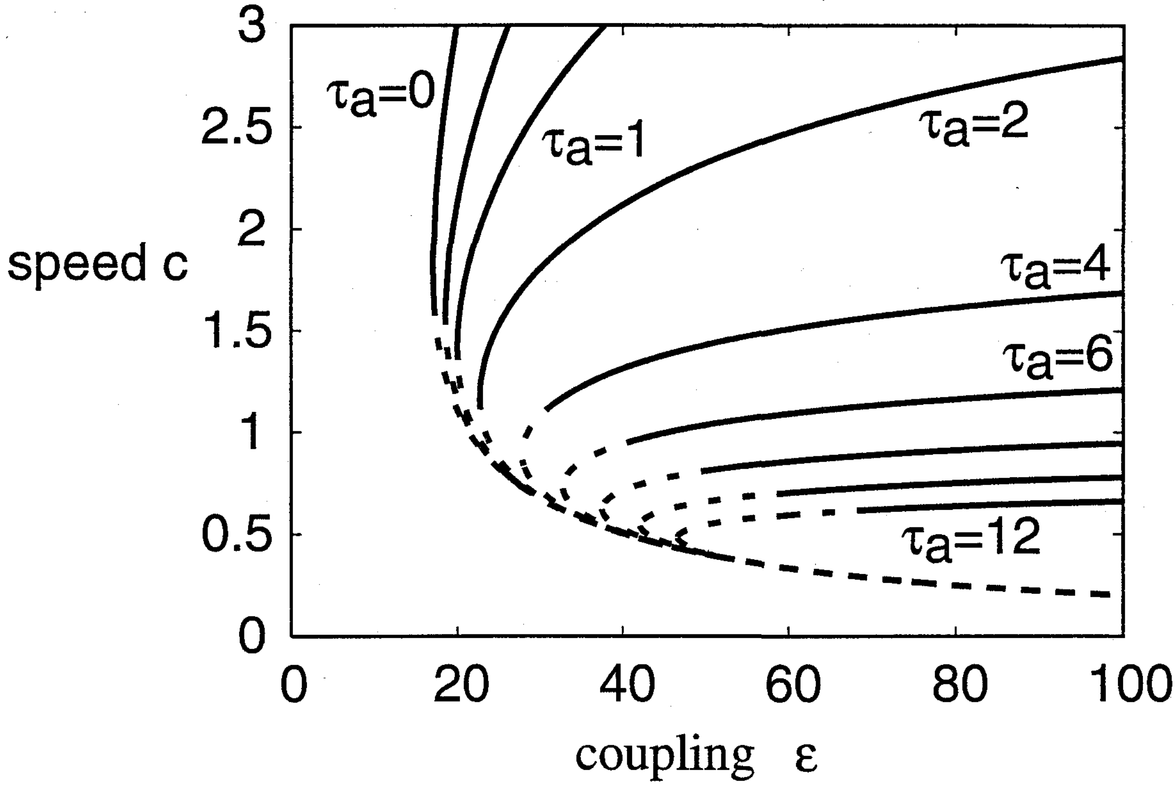
• There exists a critical coupling g_s such that there are no traveling pulse solutions for $g < g_s$ and two solutions for $g > g_s$.



• The lower (upper) solution branch is unstable (stable) when $\tau_a = 0$.

Lurching waves

• For fixed α and ϵ the continuous solitary pulse can become unstable at a critical value of the delay τ_{ac}.

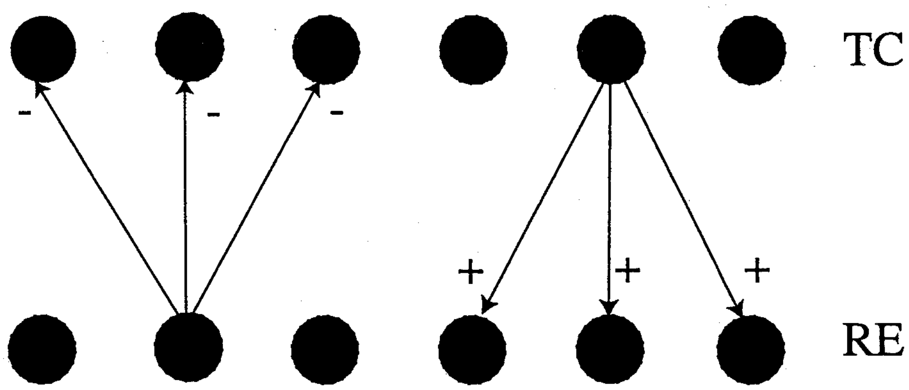


• In the regime where the continuous wave is unstable, $\tau_a > \tau_{ac}$, *lurching* pulses propagate with discontinuous, periodic spatio-temporal characteristics (Golomb and Ermentrout 1999).

Cortical versus thalamic waves

• In computational and experimental studies of disinhibited neocortical slices, one finds that neuronal discharges propagate continuously at a velocity $c \sim 10 - 15$ cm/sec (Golomb and Amitai 1997). Axonal delays are relatively small.

• In models of thalamic slices, composed of excitatory thalamocortical neurons and inhibitory reticular thalamic neurons, waves propagate in a lurching manner at a velocity $c \sim 1$ cm/sec. Thought to form the basic mechanism for the generation of 7- to 14-Hz spindle oscillations during the onset of sleep.



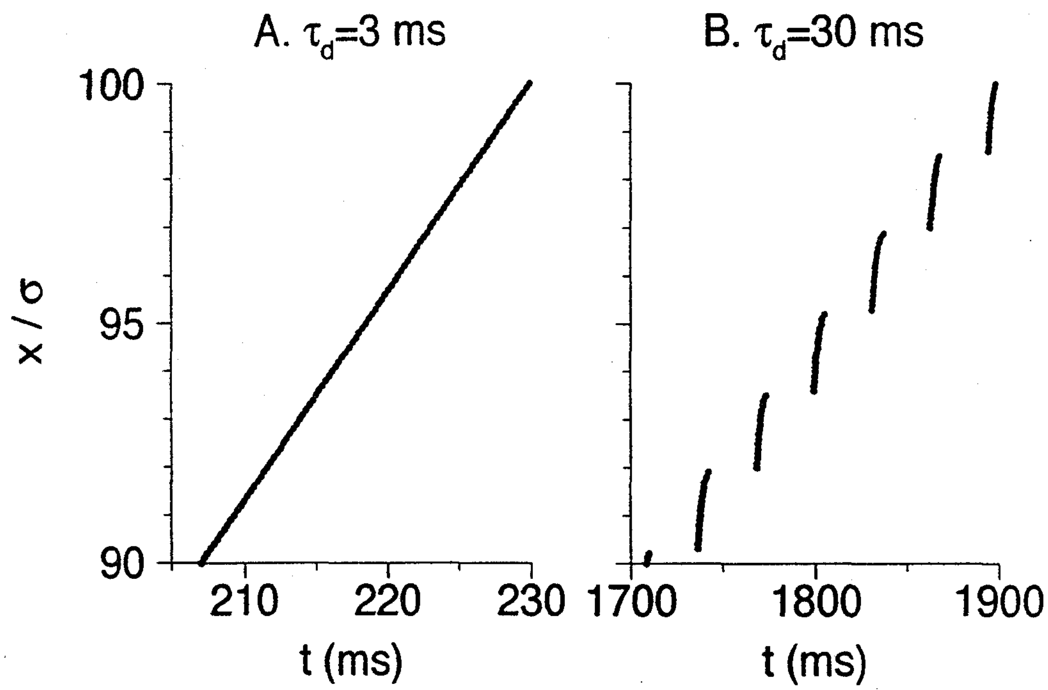
• Each recruitment cycle has two stages:

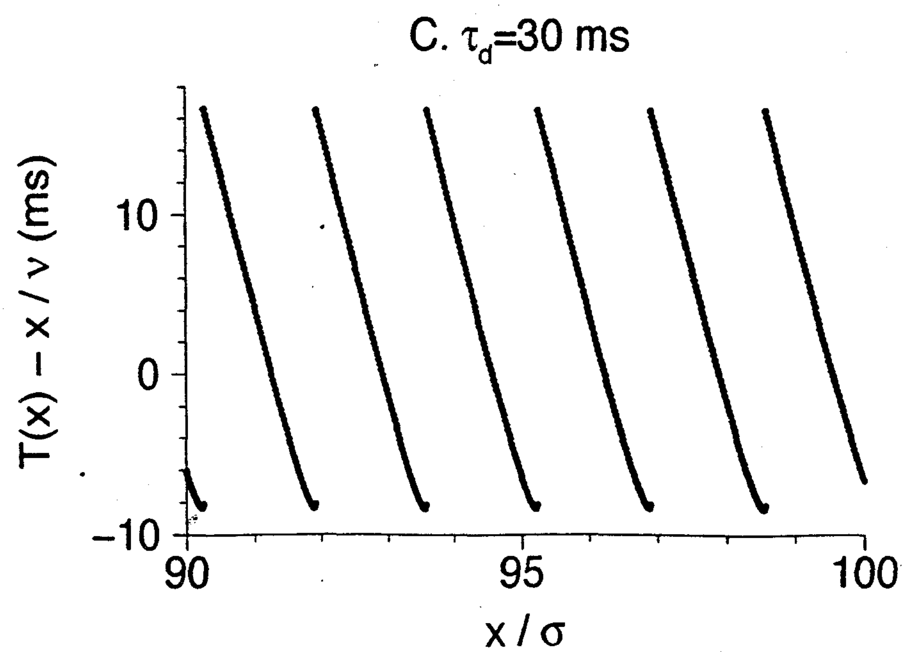
I. A new group of inhibitory RE cells is excited by synapses from TC cells, and this RE group then inhibits a new group of TC cells.

II. The new recruited TC cells rebound from hyperpolarization and fire a burst of spikes, which further recruit more RE cells during next cycle.

• Can reduce the two-layer thalamic model to a single-layer excitatory network with a large effective delay ($\tau_a \approx 100$ msec) caused by the time needed for a TC cell to rebound from inhibition.

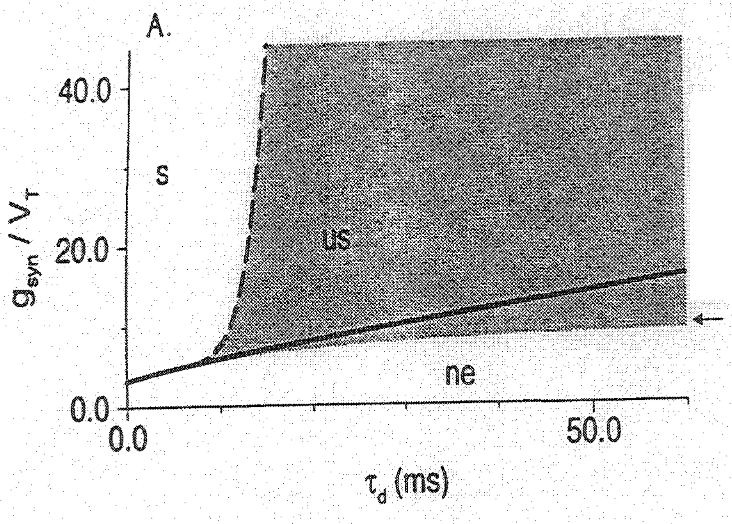
• In the regime where the continuous wave is unstable, $\tau_a > \tau_{ac}$, *lurching* pulses propagate with discontinuous, periodic spatio-temporal characteristics (Golomb and Ermentrout 1999).



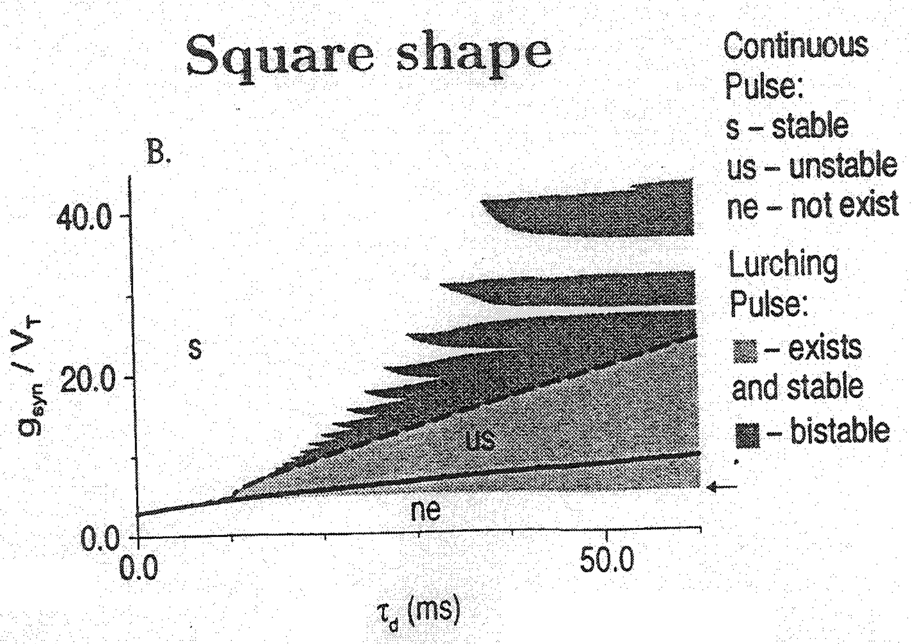


• The lurching wave can occur in regions where continuous wave does not exist. For certain choices of weight kernel $W(x)$ the two types of wave may co-exist (bistability).

Exp shape



Square shape



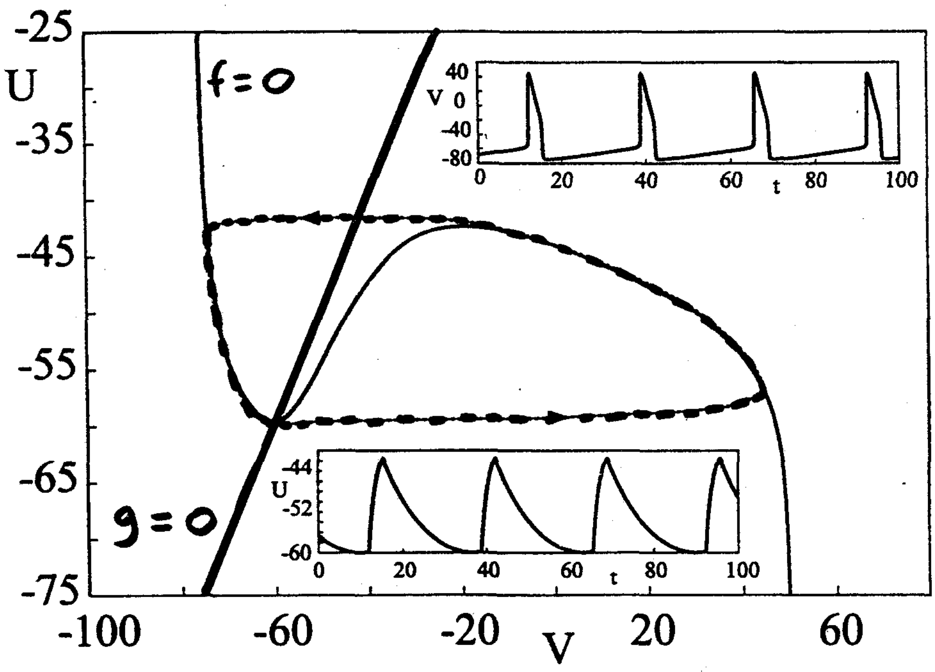
Neural phase oscillators

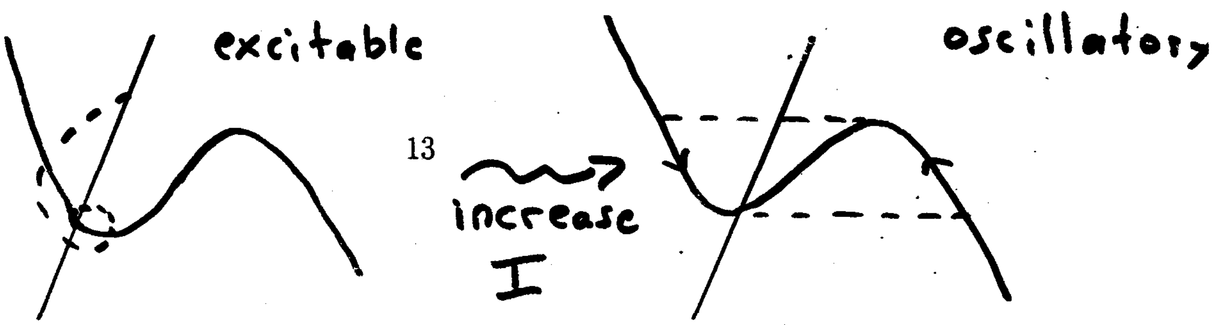
- A simple model of a spiking neuron is

$$\boxed{C\frac{dV}{dt} = I + f(V,U), \quad \frac{dU}{dt} = g(V,U)}$$

where V is cell membrane potential and U is a recovery variable.

- Using phase-plane analysis one can show how a Hopf bifurcation occurs as current I increases





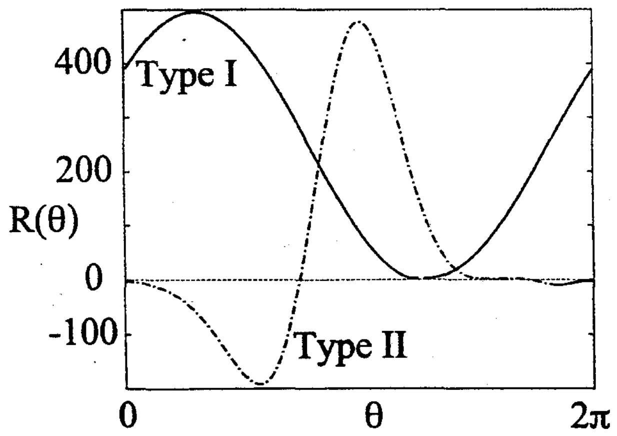
13

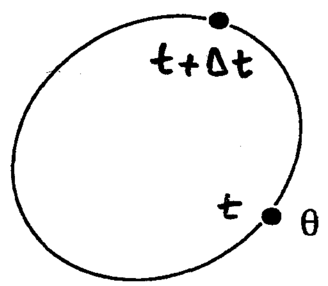
Phase resetting curve

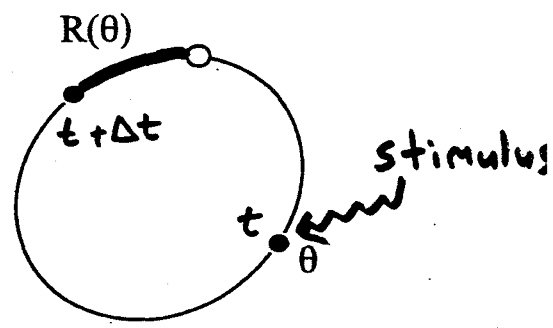
• Can perform a change of coordinates $(U, V) \rightarrow (y, \theta)$ such that dynamics on limit-cycle becomes

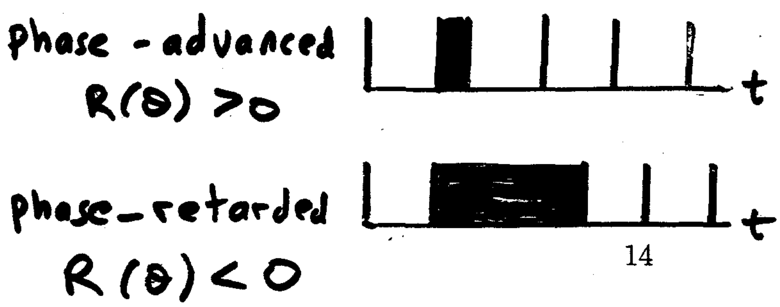
$$\frac{d\theta}{dt} = \Omega_0$$

• A small perturbation temporarily moves neuron off limit-cycle generating an effective phase-shift $R(\theta)$ where θ is point on limit cycle where disturbance occurs.







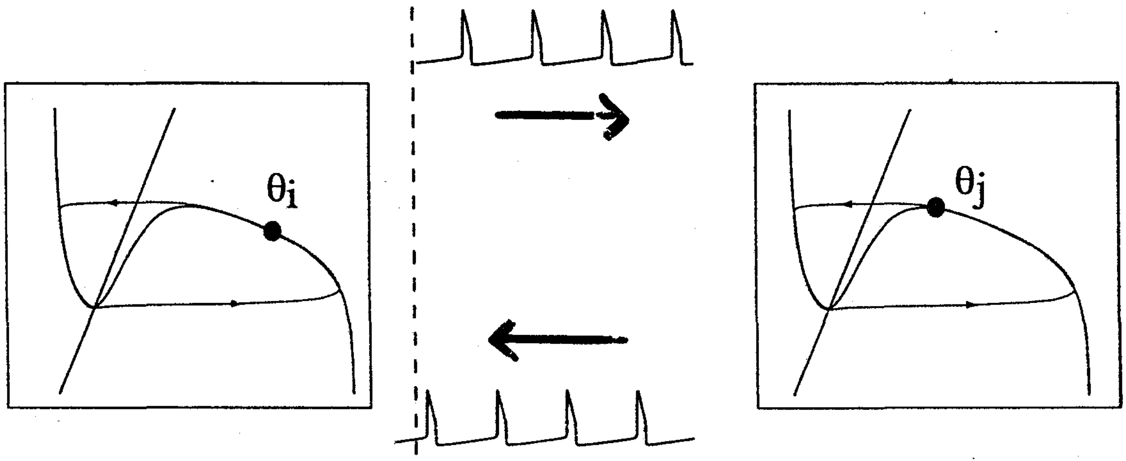


Network model

- Network of N neural oscillators with phases θ_i, $i = 1, \ldots, N$. Each neuron periodically sends spikes to all the neurons in the network:

$$\boxed{\frac{d\theta_i}{dt} = \Omega_0 + \epsilon R(\theta_i) X_i(t)}$$

where ϵW_{ij} is the coupling strength from $j \to i$.



$$\boxed{X_i(t) = \sum_n \sum_{j=1}^{N} W_{ij} J(t - T_j^n)}$$

synaptic drive

- Threshold condition

$$\boxed{\theta(T_j^n) = 2\pi n, \; \frac{d\theta}{dt}(T_j^n) > 0}$$

Averaging theorem for weak coupling $\epsilon \ll 1$

- Set $\theta_i(t) = \Omega_0 t + \psi_i(t)$ so that

$$\boxed{\frac{d\psi_i}{dt} = \epsilon \sum_{j=1}^{N} W_{ij} P(\psi_j + \Omega_0 t) R(\psi_i + \Omega_0 t)}$$

where $P(\Omega_0 t) = \sum_n J(t - 2\pi n/\Omega_0)$

Averaging theorem: there exists a change of variables $\psi \to \psi + \epsilon b(\psi, t, \epsilon)$ that maps to solutions of

$$\boxed{\frac{d\psi_i}{dt} = \epsilon \sum_{j=1}^{N} W_{ij} H(\psi_j - \psi_i) + \mathcal{O}(\epsilon^2)}$$

where

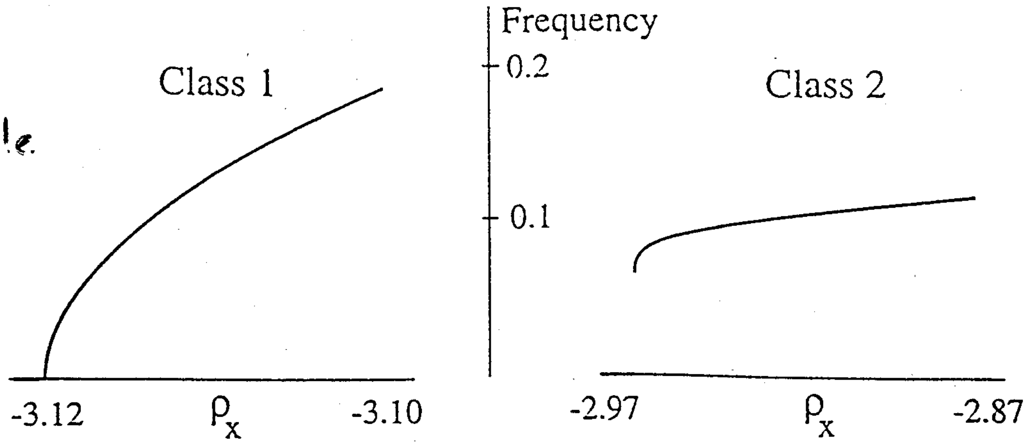
$$H(\psi) = \frac{1}{2\pi} \int_0^{2\pi} P(\theta) R(\theta - \psi) d\theta$$

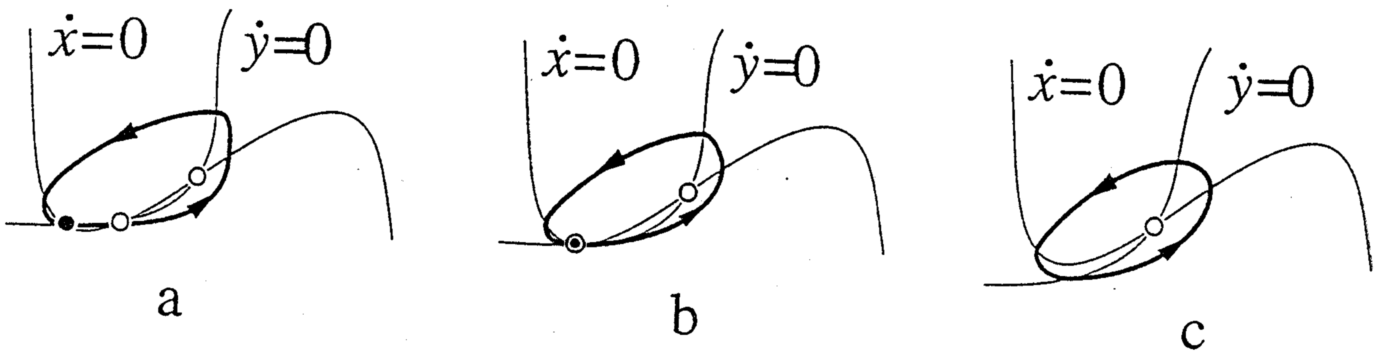
- In terms of original phase-variables,

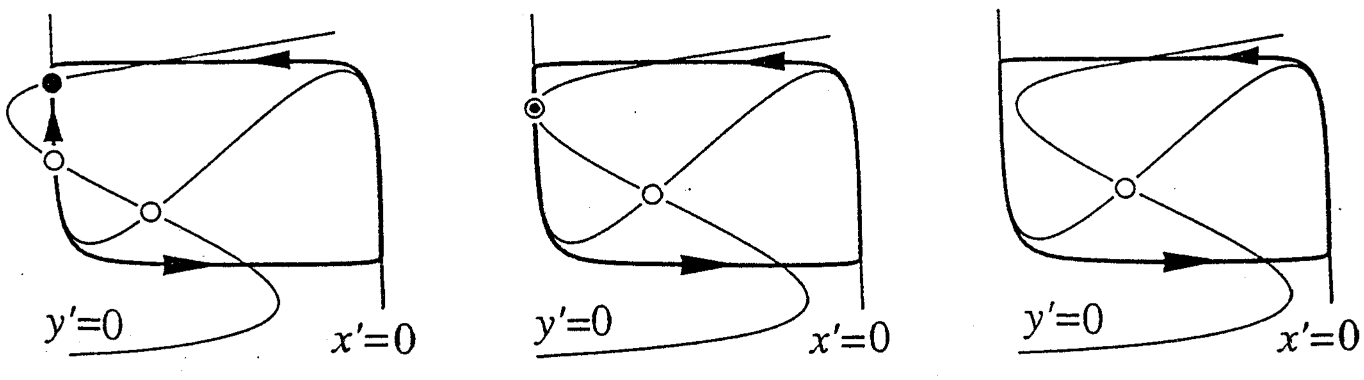
$$\boxed{\frac{d\theta_i}{dt} = \Omega_0 + \epsilon \sum_{j=1}^{N} W_{ij} H(\theta_j - \theta_i)}$$

Two classes of excitable cell.

ρ_x is applied current.







Two examples of a "saddle-node on a limit cycle" bifurcation generating a class I excitable cell.

- Class 1 excitable cells have Type I phase resetting curves $R(\theta)$.

- A PRC is of Type I if $R(\theta) > 0$ for all θ, otherwise it is Type II

- Type I and Type II can lead to different synchronization properties.

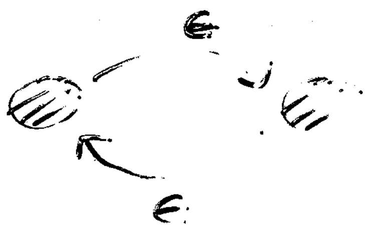
- Averaging over one period we have

$$\frac{d\theta_i}{dt} = \omega_0 + \epsilon \sum_j W_{ij} H(\theta_j - \theta_i)$$

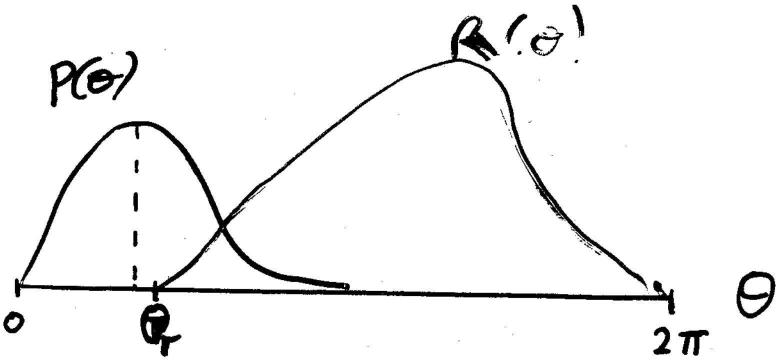
- A pair of identical neurons will synchronize if

$$H(0) = 0$$

$$\epsilon H'(0) > 0$$



A pair of Type I neural oscillators with excitatory coupling will NOT synchronize if rise-time of synaptic response is short relative to the refractory period (Hansel, Mato + Meunier, Neural Comput. 1995)



$$H'(0) = \frac{1}{2\pi} \int_{\theta_r}^{2\pi} R(\theta) P'(\theta)\, d\theta$$

Let θ^* be the phase at which $P(\theta)$ reaches its peak. Then

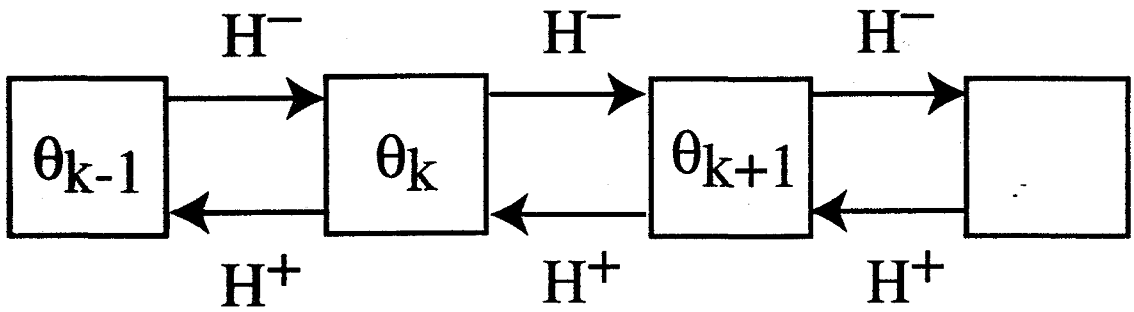
$$H'(0) = \frac{1}{2\pi} \int_{\theta_r}^{\theta^*} R(\theta) P'(\theta)\, d\theta \qquad +\text{ve}$$

$$+ \frac{1}{2\pi} \int_{\theta^*}^{2\pi} R(\theta) P'(\theta)\, d\theta \qquad -\text{ve}$$

If $\theta^* < \theta_r$ (Short rise-time) then +ve contribution vanishes so that $H'(0) < 0$ and synchronous state is unstable (for $\epsilon > 0$).

- For type II oscillators $R(\theta)$ can be negative such that synchronous state stabilizes

Traveling waves on a chain I



$$\boxed{\frac{d\theta_k}{dt} = \omega_n + \epsilon\left[H^+(\theta_{k+1} - \theta_k) + H^-(\theta_{k-1} - \theta_k)\right]}$$

- Phase-locked solution $\theta_k(t) = \Omega t + \overline{\theta}_k$ for collective period Ω.
- Phase-differences $\phi_k = \overline{\theta}_{k+1} - \overline{\theta}_k$.
- Traveling wave up chain: $\phi_k > 0 \ \forall \ k$
- Traveling wave down chain: $\phi_k < 0 \ \forall \ k$

Traveling waves on a chain II

- Conditions for phase-locking are

$$\boxed{\begin{aligned} 0 \;=\; & \Delta_k + H^+(\phi_{k+1}) - H^+(\phi_k) \\ & + H^-(-\phi_k) - H^-(-\phi_{k-1}) \end{aligned}}$$

for $k = 1, \ldots, N$ with $\epsilon\Delta_n = \omega_{n+1} - \omega_n$ and boundary conditions

$$\boxed{H^-(-\phi_0) = 0 = H^+(\phi_{N+1})}$$

- Collective frequency satisfies

$$\boxed{\Omega = \omega_1 + \epsilon H^+(\phi_1)}$$

- Two basic mechanisms for traveling waves:

A. Gradient of frequencies: Δ_k varies monotonically with k.

B. Anisotropic coupling: $H^+ \neq H^-$, $H^\pm(0) \neq 0$.

Ⓐ For isotropic coupling $\boxed{H^{\pm}(\phi) = H(\phi) = \sin 2\pi\phi}$

a phase-locked solution $\Phi = (\phi_1, \dots, \phi_N)$ satisfie

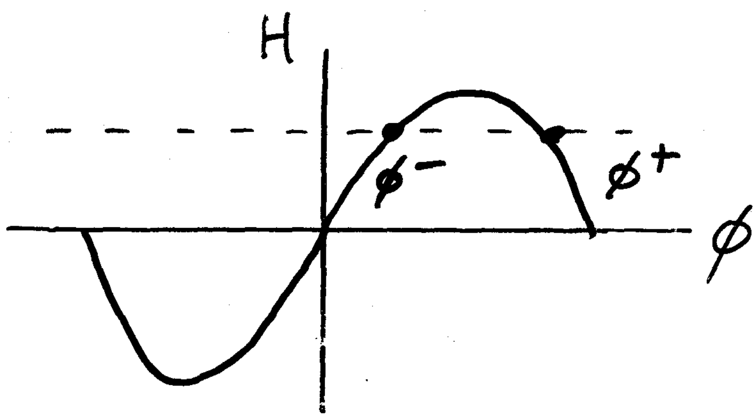
$$\boxed{\hat{H}(\Phi) = -A^{-1} D}$$

$$[\hat{H}(\Phi)]_n = H(\phi_n), \quad [D]_n = \Delta_n$$

$$A_{nm} = -2\,\delta_{n,m} + \delta_{n,m+1} + \delta_{n,m-1}$$

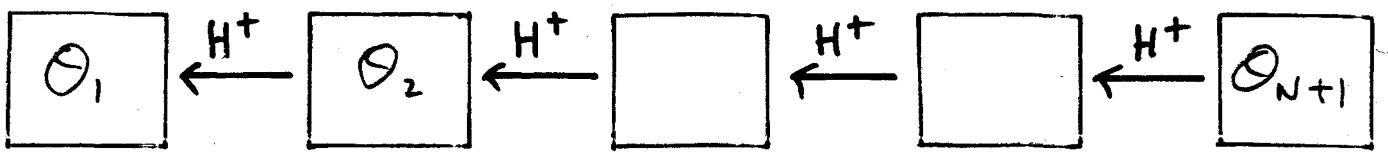
Let $\boxed{a_0 = \max_n \{ |[A^{-1}D]_n| \}}$

If $a_0 < 1$ then for each $n = 1, \dots, n$ there exists two distinct solutions $\phi_n^{\pm} \in [-\frac{1}{2}, \frac{1}{2}]$ with $H'(\phi_n^-) > 0$ and $H'(\phi_n^+) < 0$.



Unique stable sol$^=$ $\Phi = (\phi_1^-, \dots, \phi_N^-)$

(B) Consider a chain with one-way coupling



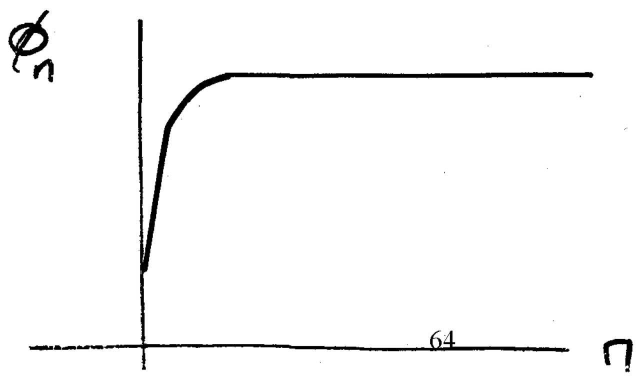
- For zero frequency gradient a phase-locked solution satisfies

$$\boxed{\begin{aligned} &H^+(\phi_{n+1}) = H^+(\phi_n), \qquad n = 1, \dots N \\ &H^+(\phi_{N+1}) = 0 \end{aligned}}$$

This has a stable travelling wave sol$^{\underline{n}}$

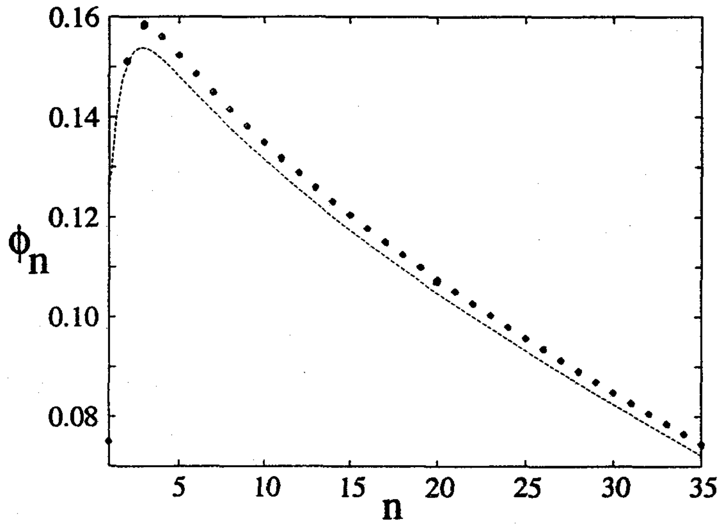
$$\boxed{\begin{aligned} &\phi_n = \bar{\phi} \qquad \text{for all } n \\ &H^+(\bar{\phi}) = 0, \quad H^{+\prime}(\bar{\phi}) > 0 \end{aligned}}$$

- For anisotropic two-way coupling there exists a stable travelling wave with constant phase-lag (except in a small boundary layer)



Traveling waves on a chain III

- Typically, the phase-lag is slowly-varying across the chain except in a boundary layer.



- For large networks one can approximate phase-locking equations by a *singularly perturbed two-point (continuum) boundary value problem* (Ermentrout and Kopell).

- Can extend analysis to a chain of IF oscillators with arbitrary coupling:

$$\boxed{H^{\pm}(\phi) \to H_T^{\pm}(\phi), \;\; \omega_k \to I_k}$$

for a self-consistent collective period T.

BRESSLOFF + COOMBES (PHYSICA D 1999)
(PHYS. REV. LETT. 1997)

Kuramoto model

• Mean-field model for a system of weakly-coupled, near-identical limit-cycle oscillators:

$$\boxed{\frac{d\theta_i}{dt} = \omega_i + \frac{K}{N}\sum_{j=1}^{N}\sin(\theta_j - \theta_i)}$$

for $i = 1, \ldots N$, where $K \geq 0$ is the coupling strength and ω_i is natural frequency of ith oscillator.

• Frequencies ω_i are distributed according to a probability density $g(\omega)$ with

i) $g(-\omega) = g(\omega)$

ii) $g(0) \geq g(\omega)$ for all $w \in [0, \infty)$ (unimodal)

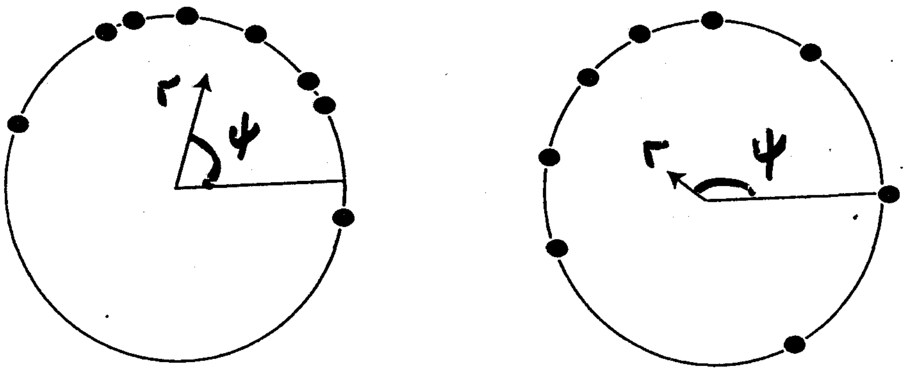
• Can assume $g(\omega)$ has zero mean by going to a rotating frame if necessary.

Order parameter

- Introduce complex order parameter

$$re^{i\psi} = \frac{1}{N}\sum_{j=1}^{N} e^{i\theta_j}$$

- Geometric interpretation as centroid of phases:



The radius $r(t)$ measures the phase-coherence and $\psi(t)$ is the average phase.

- Using a trigonometric identity,

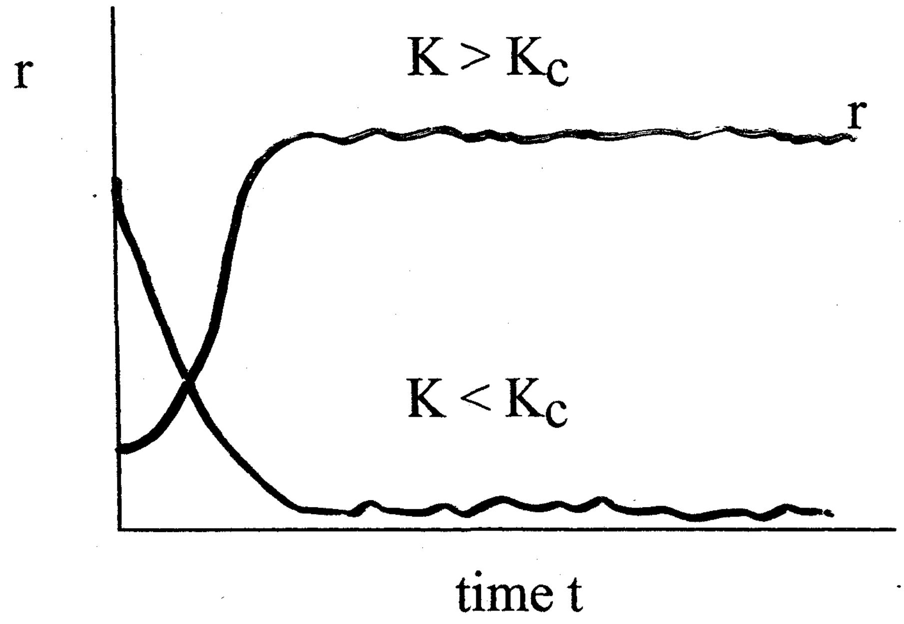
$$\frac{d\theta_i}{dt} = \omega_i + Kr\sin(\psi - \theta_i)$$

• Oscillators only couple through mean-field quantities r, ψ

• Coupling tends to synchronize oscillators – each phase θ_i is pulled toward ψ with restoring force of strength Kr (positive feedback)

$\boxed{\text{Numerical results}}$

Suppose $g(\omega)$ is a Gaussian.



<u>I. For $K < K_c$</u> system converges to an incoherent state in which the phases are distributed uniformly around the circle: $r(t) \to 0$ as $t \to \infty$

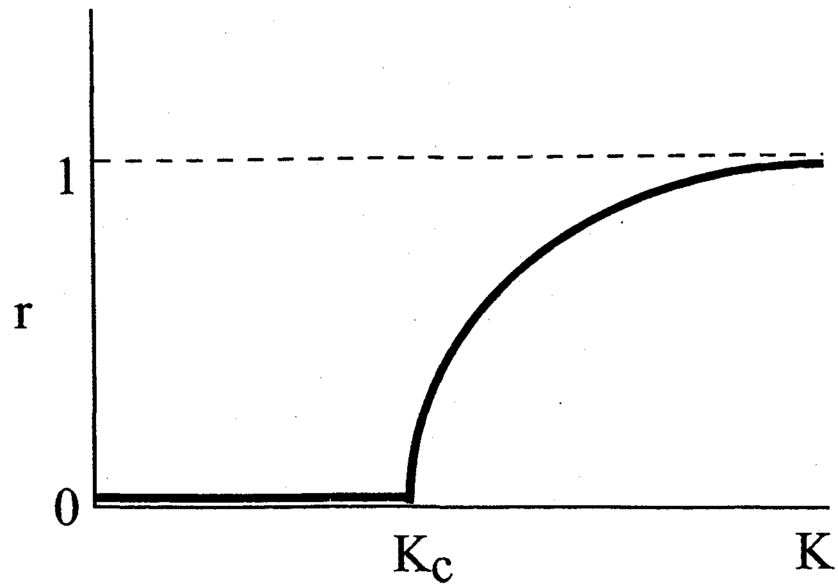
II. For $K > K_c$ the incoherent state becomes unstable and system converges to a partially synchronized state: $r(t) \longrightarrow r_\infty < 1$ as $t \to \infty$.

- In the partially synchronized state the oscillators split into two groups:

a) those near center of frequency distribution lock together and co-rotate with average phase $\psi(t)$

b) those in tail of distribution run near their natural frequencies and drift relative to the synchronized cluster

- Degree of synchrony r_∞ increases with K



Problems

- Derive expressions for threshold coupling K_c and for the coherence $r_\infty(K)$.

  – solved by Kuramoto (1984)

- Determine the local stability of the incoherent and partially synchonized states in the large-N limit.

  – stability of incoherent state determined by Mirollo and Strogatz (1991)

  – stability of coherent branch close to K_c solved by Crawford (1994)

- Global stability and convergence.

- Finite-size effects: away from the bifurcation point fluctuations are $\mathcal{O}(N^{-1/2})$ but they can be amplified when $K \approx K_c$.

- Strong-coupling and breakdown of phase description (Bressloff + Coombes)

$\boxed{K_c \text{ and } r_\infty(K)}$

• Look for steady-state solutions $r(t) = r$ and $\psi(t) = \Omega t$. (Can set $\Omega = 0$ by going to a rotating frame).

• Now have a set of independent oscillators whose motions depend on r as a paramter

$$\boxed{\frac{d\theta_i}{dt} = \omega_i - Kr \sin\theta_i, \quad i = 1, \ldots, N}$$

$\Longrightarrow$ self-consistency condition for r.

• Two types of solution:

(a) oscillators with $|\omega_i| \leq Kr$ approach a stable fixed point defined implicitly by

$$\boxed{\omega_i = Kr\sin\theta_i}$$

and are locked at frequency Ω in original frame

(b) oscillators with $|\omega_i| > Kr$ rotate non-uniformly and drift relative to the locked population.

• POTENTIAL PROBLEM – drifting oscillators appear to contradict assumption of stationarity

• SOLUTION – require drifting oscillators to form a stationary distribution on the circle.

• Let $\rho(\theta, \omega)d\theta$ denote fraction of oscillators with natural frequency ω and phase between θ and $\theta + d\theta$. Then $\rho(\theta, \omega)$ should be inversely proportional to angular speed:

$$\boxed{\rho(\theta, \omega) = \frac{C}{|\omega - Kr\sin\theta|}}$$

with C determined by the normalization condition $\int_{-\pi}^{\pi} \rho(\theta, \omega)d\theta = 1$ for each ω.

• Self-consistency condition:

$$\boxed{r = \langle e^{i\theta}\rangle_{\mathrm{lock}} + \langle e^{i\theta}\rangle_{\mathrm{drift}}}$$

• Symmetry condition $g(-\omega) = g(\omega)$ implies that

$$\langle e^{i\theta}\rangle_{\mathrm{drift}} \equiv \int_{-\pi}^{\pi}\int_{|\omega|>+Kr} e^{i\theta}\rho(\theta, \omega)g(\omega)d\omega d\theta = 0$$

and $\langle e^{i\theta}\rangle_{\mathrm{lock}} = \langle \cos(\theta)\rangle_{\mathrm{lock}}$

• Hence

$$\boxed{\begin{aligned} r = \langle \cos(\theta) \rangle_{\text{lock}} &= \int_{-Kr}^{Kr} \cos(\theta[\omega]) g(\omega) d\omega \\ &= Kr \int_{-\pi/2}^{\pi/2} \cos^2(\theta) g(Kr \sin\theta) d\theta \end{aligned}}$$

• Zero solution $r = 0$ with $\rho(\theta, \omega) = 1/2\pi$ exists for all K

• A second branch of partially synchronized solutions satisfying

$$\boxed{1 = K \int_{-\pi/2}^{\pi/2} \cos^2(\theta) g(Kr \sin\theta) d\theta}$$

bifurcates from $r = 0$ at critical coupling

$$\boxed{K_c = \frac{2}{\pi g(0)}}$$

• Assuming that $g''(0) < 0$ then

$$\boxed{r \approx \frac{4}{K_c^2} \sqrt{\frac{K - K_c}{-\pi g''(0)}}}$$

Stability of incoherent state: continuum limit

- Imagine a continuum of oscillators distributed on the circle (cf. fluid mechanics). Let $\rho(\theta, t, \omega)$ denote fraction of these oscillators that lie between θ and $\theta + d\theta$ at time t.

- Continuity (Liouville) equation

$$\boxed{\frac{\partial \rho}{\partial t} = -\frac{\partial}{\partial \theta}(\rho v)}$$

where

$$\boxed{v(\theta, t, \omega) = \omega + K \int_{-\pi}^{\pi} \int_{-\infty}^{\infty} \sin(\theta' - \theta)\rho(\theta', t, \omega')g(\omega')d\omega' d\theta'}$$

- Consider small perturbations of incoherent state:

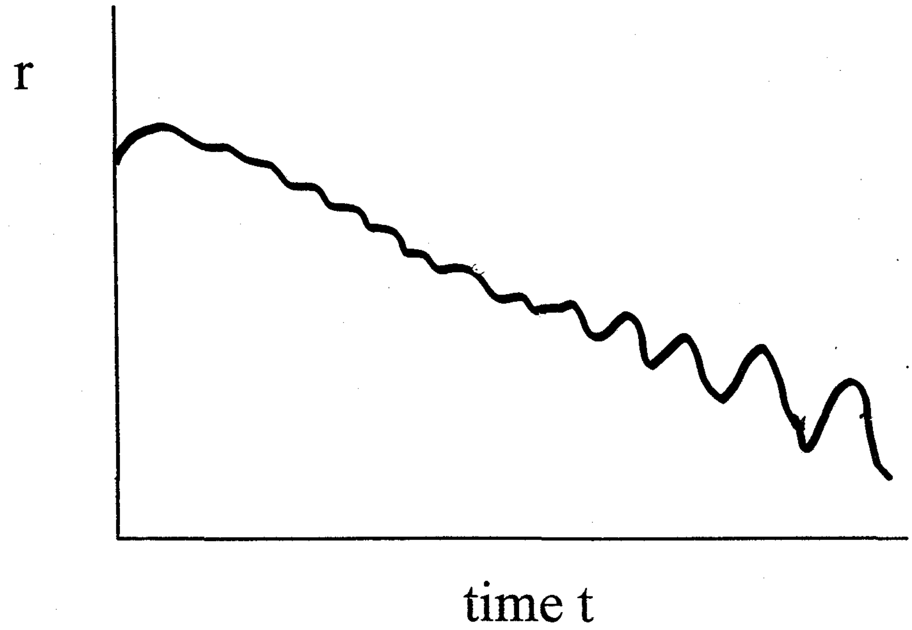
$$\boxed{\rho(\theta, t, \omega) = \frac{1}{2\pi} + \epsilon\eta(\theta, t, \omega)}$$

where $\epsilon \ll 1$ and expand η as a Fourier series

$$\boxed{\eta(\theta, t, \omega) = c(t, \omega)e^{i\theta} + c^*(t, \omega)e^{-i\theta} + \text{higher harmonics}}$$

Landau damping

• Although the incoherent state is neutrally stable (for $K < K_c$) one finds that the coherence $r(t)$ exhibits damped oscillations with $r(t) \to 0$ as $t \to \infty$



• Analogous to Landau damping in a collisionless plasma

– distribution over **velocities** (frequencies)

– self-consistent MF equation for **electric field** (coherence) generated by **charged particles** (phase oscillators)