

Introduction to Neural Computation

Prof. Michale Fee
MIT BCS 9.40 — 2018

Lecture 10 - Time Series

Spatial receptive fields

- How do we represent receptive fields mathematically?

Linear-Nonlinear Model (LN Model)

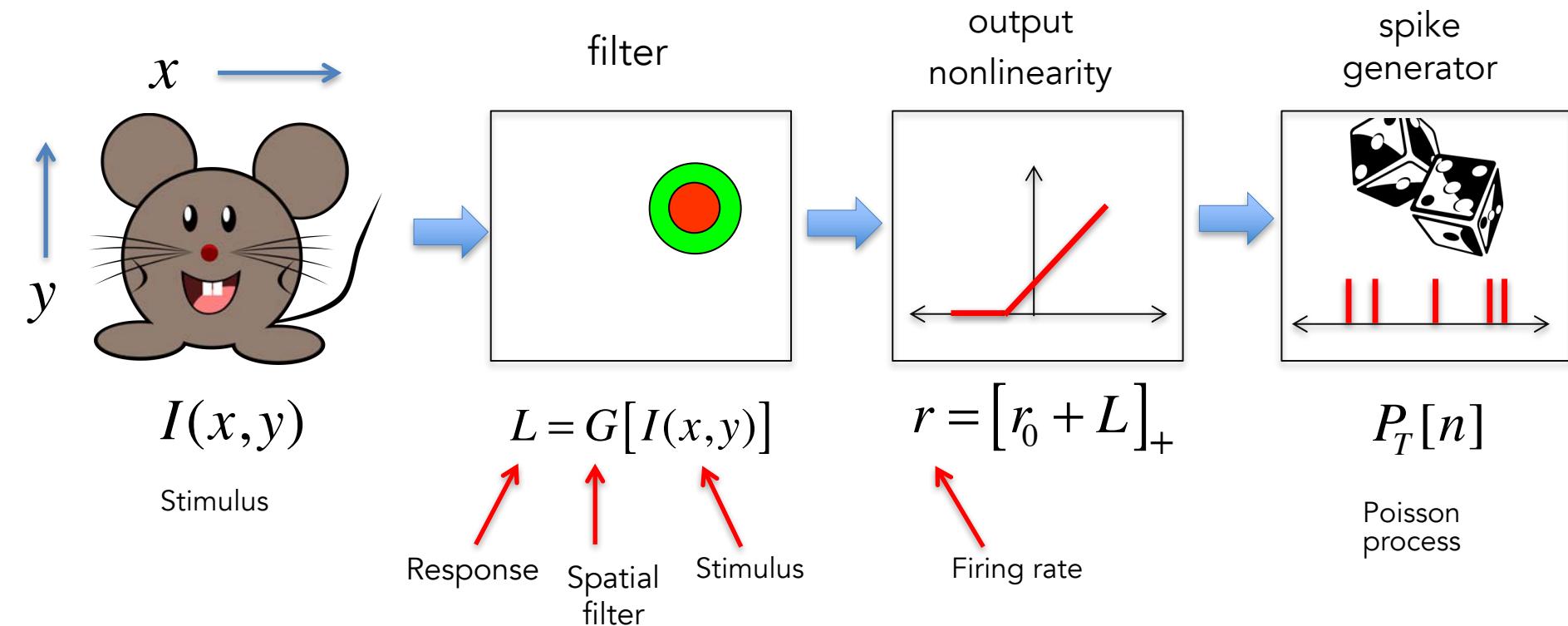


Image of mouse in public domain.

Spatial receptive fields

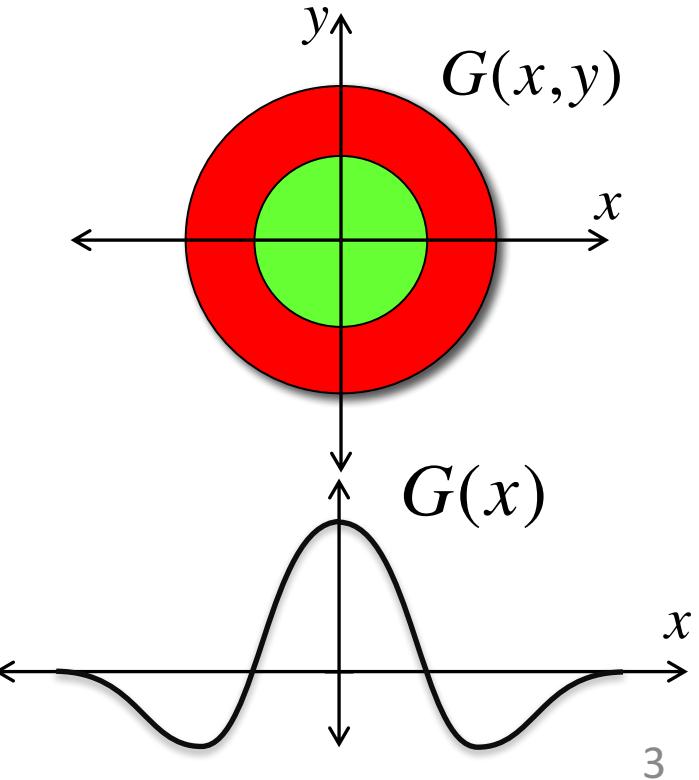
- How do we represent receptive fields mathematically?

We are going to consider the simplest case in which the response of a neuron is given by a linear filter acting on the stimulus.

$$r = r_0 + \iint G(x, y) I(x, y) dx dy$$

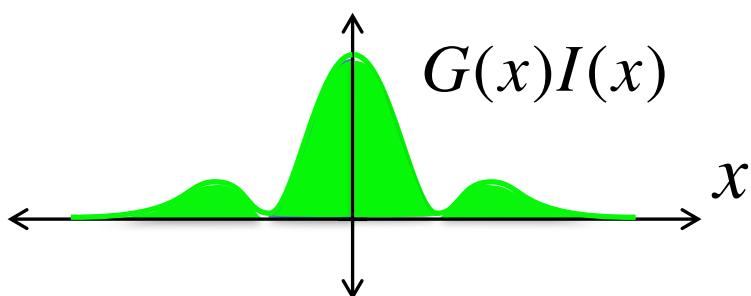
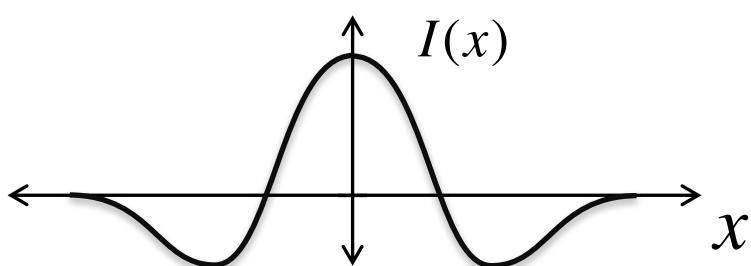
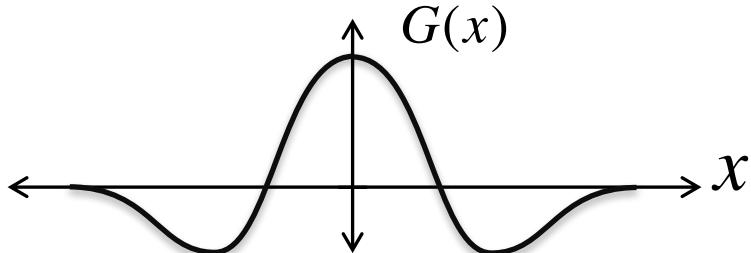
Let's look at this in one dimension

$$r = r_0 + \int G(x) I(x) dx$$

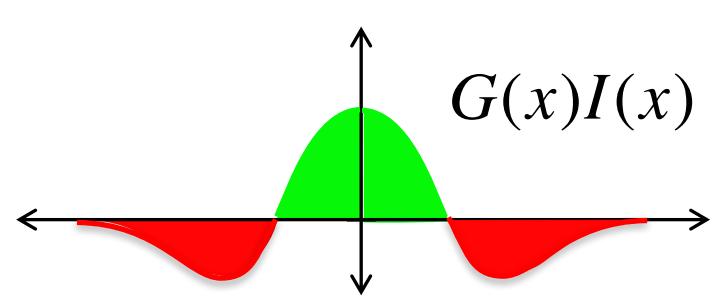
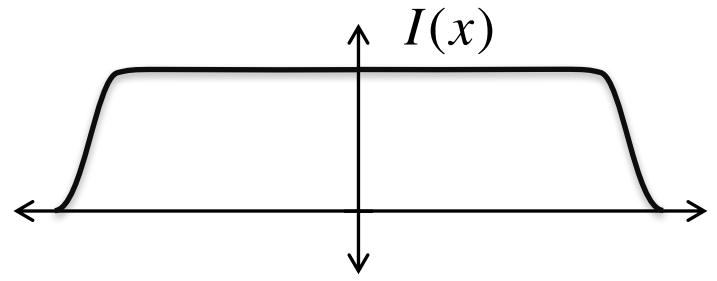
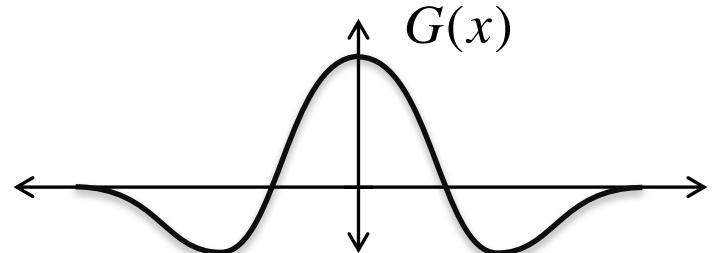


Spatial receptive fields

- How do we represent receptive fields mathematically?



$$\int G(x)I(x)dx \text{ big}$$



$$\int G(x)I(x)dx \text{ small}$$

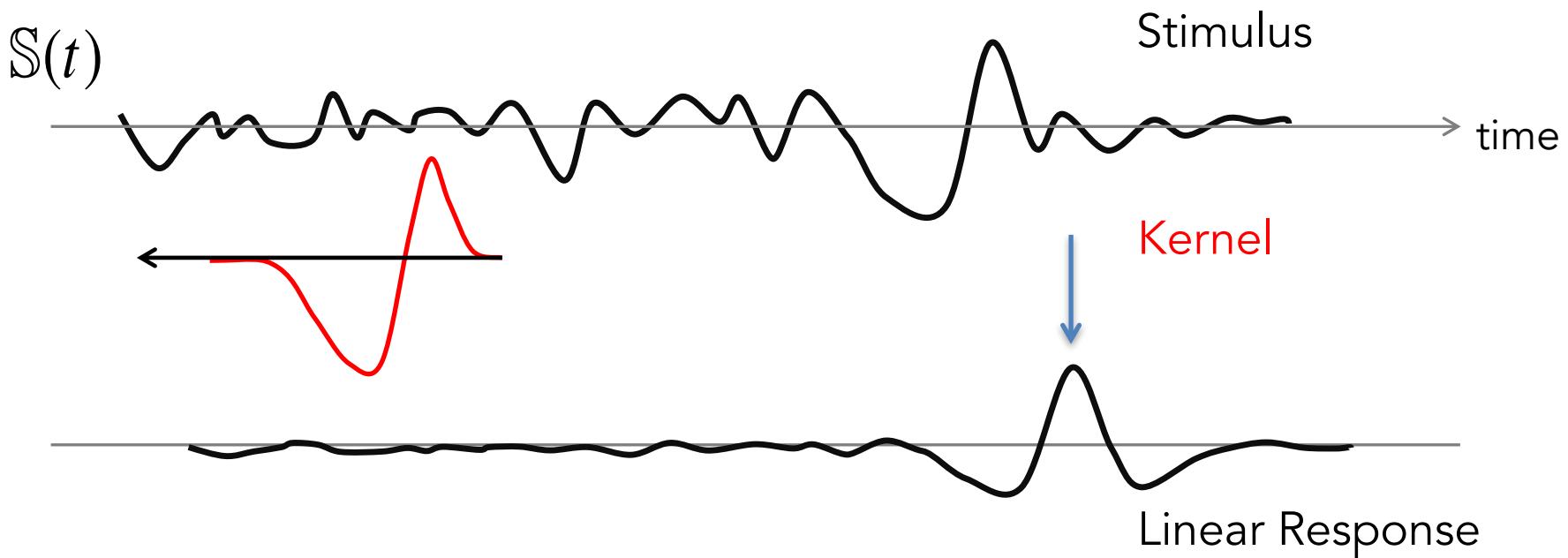
Temporal receptive fields

- We can also think of the response of a neuron as some function of the temporal variations in the stimulus.

$$r(t) = r_0 + D[\mathbb{S}(t)]$$

Temporal receptive fields

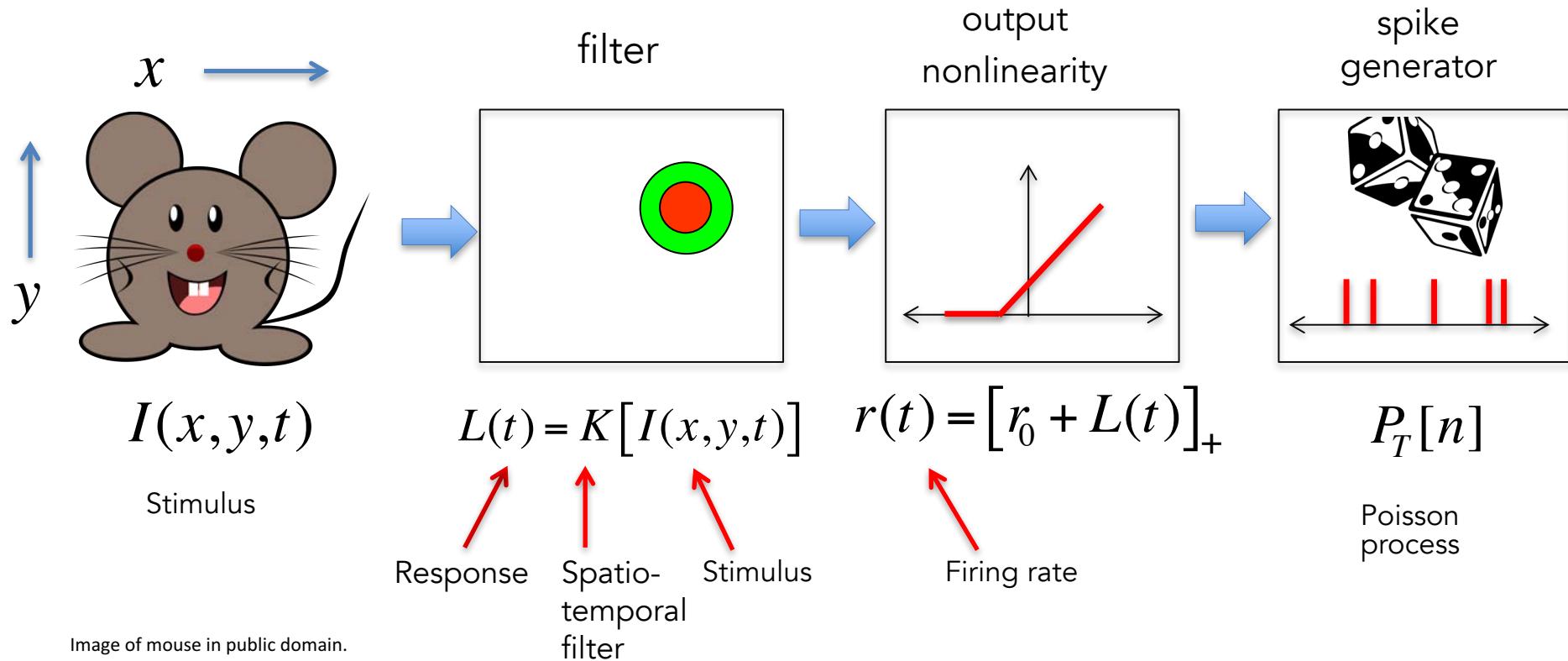
- We can think of 'overlap' in the time domain! That there is a particular 'temporal profile' of a stimulus that makes a neuron spike.



Spatio-temporal receptive fields

- How do we represent receptive fields mathematically?

Combine neural responses into a single kernel that captures both spatial and temporal sensitivity.



Learning objectives for Lecture 10

- Spike trains are probabilistic (Poisson Process)
- Be able to use measures of spike train variability
 - Fano Factor
 - Interspike Interval (ISI)
- Understand convolution, cross-correlation, and autocorrelation functions
- Understand the concept of a Fourier series

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Neuronal responses are variable

- Spike trains are often quite variable. The precise pattern of spikes on each presentation of a stimulus is different.

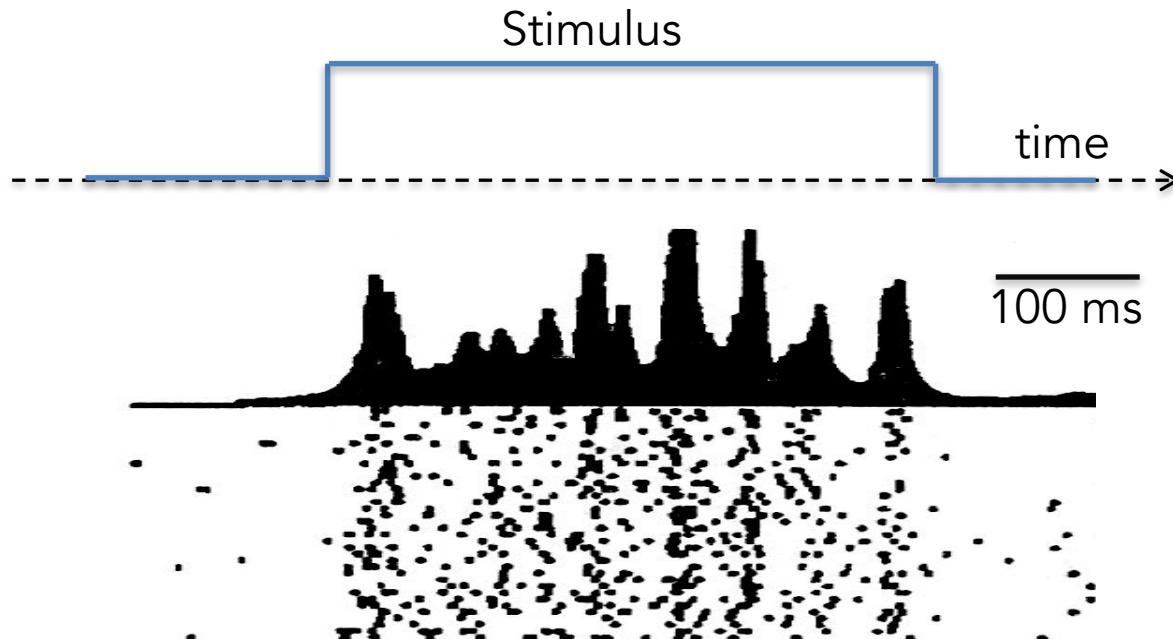
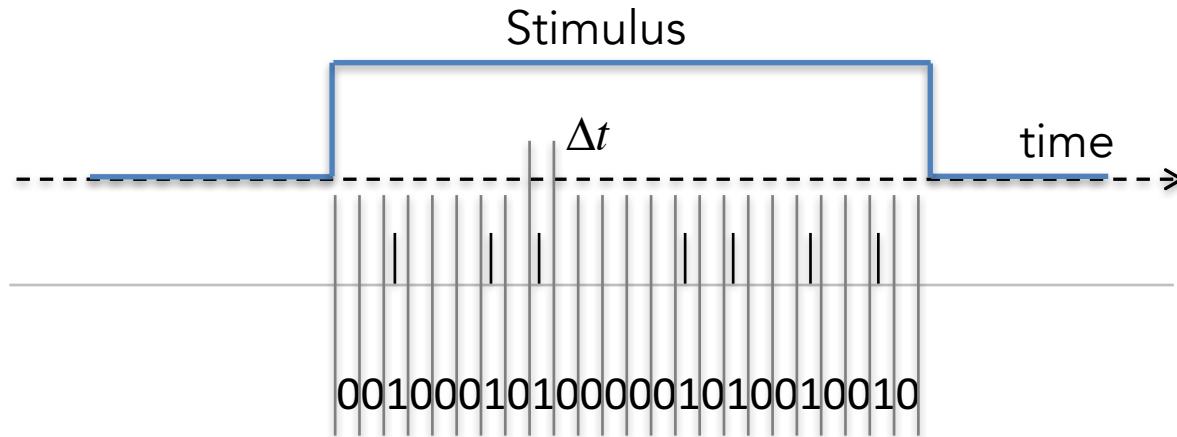


Figure courtesy MIT Press. From Dayan, P. and L. Abbott. *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems*. 2001. Original source: Bair, W. and C. Koch. "Temporal Precision of Spike Trains in Extrastriate Cortex of the Behaving Macaque Monkey." *Neural Computation* 8 no 6 (1996): 1185-1202.

Response of a neuron in area MT of the monkey to the exact same stimulus replayed on each trial.

Neuronal responses are variable



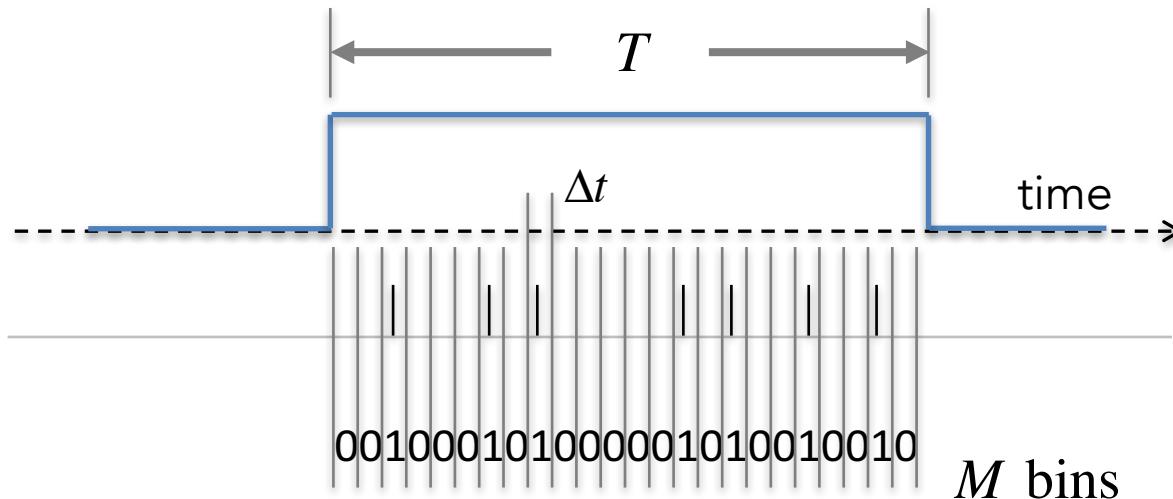
Imagine a random process that produces spikes at an average rate of μ spikes per second during the stimulus presentation.

Break up the spike train into small time bins of some duration Δt . Each spike is generated independently of other spikes and with equal probability in each bin. then we can write the probability that a spike occurs in any bin as

If Δt is small enough that most of the bins have zero spikes, we can write the probability that a spike occurs in any bin as: $\mu \cdot \Delta t$

The probability that no spike occurs in the bin is: $1 - \mu \cdot \Delta t$

Poisson process



How many spikes land in the interval T ?

What is the probability that n spikes land in the interval T ? $P_T[n]$

This is just the product of three things:

- The probability of having n bins with a spike $= (\mu \Delta t)^n$
- The probability of having $M-n$ bins with no spike $= (1 - \mu \Delta t)^{M-n}$
- The number of different ways to distribution n spikes in M bins $= \frac{M!}{(M-n)!n!}$

Poisson process

What is the probability that n spikes land in the interval T ?

$$P_T[n] = \lim_{\Delta t \rightarrow 0} \frac{M!}{(M-n)!n!} (\mu \Delta t)^n (1 - \mu \Delta t)^{M-n}$$

In the limit that: $\Delta t \rightarrow 0$ $M = \frac{T}{\Delta t} \rightarrow \infty$

$$P_T[n] = \frac{(\mu T)^n}{n!} e^{-\mu T}$$

Poisson distribution!

Poisson distribution

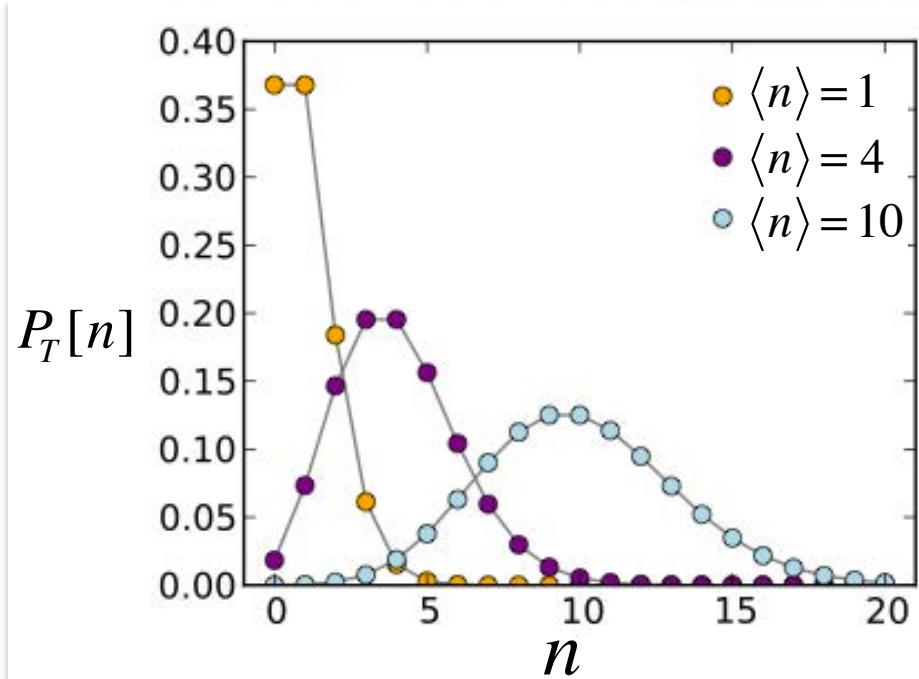
The Poisson Distribution gives us the probability that n spikes land in the interval T

$$P_T[n] = \frac{(\mu T)^n}{n!} e^{-\mu T}$$

Average (expected) number of spikes

$$\langle n \rangle = \sum_{n=0}^{\infty} n P_T[n] = \mu T$$

Thus, $\mu = \frac{\langle n \rangle}{T}$ is also the average spike rate! (going to use variable r)



Poisson distribution plot courtesy of [Skbekkas](#) on Wikimedia. License: CC BY.

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Spike count variability

What is the variance in the number of spikes that land in the interval T ?

$$P_T[n] = \frac{(\mu T)^n}{n!} e^{-\mu T}$$

Variance in spike count

$$\begin{aligned}\sigma_n^2(T) &= \langle (n - \langle n \rangle)^2 \rangle \\ &= \langle n^2 \rangle - 2\langle n \rangle^2 + \langle n \rangle^2 \\ &= \langle n^2 \rangle - \langle n \rangle^2\end{aligned}$$

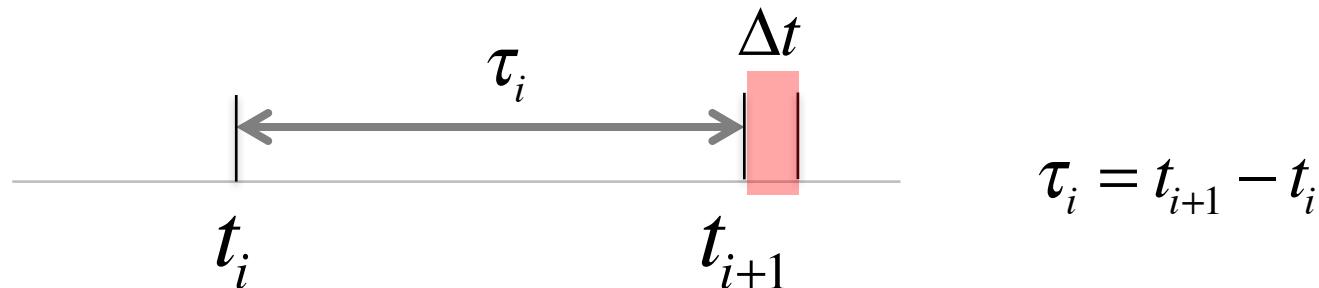
Fano Factor

$$F = \frac{\sigma_n^2(T)}{\langle n \rangle} = 1$$

$$\sigma_n^2(T) = \mu T$$

Interspike interval (ISI) distribution

What is the distribution of intervals between spikes?



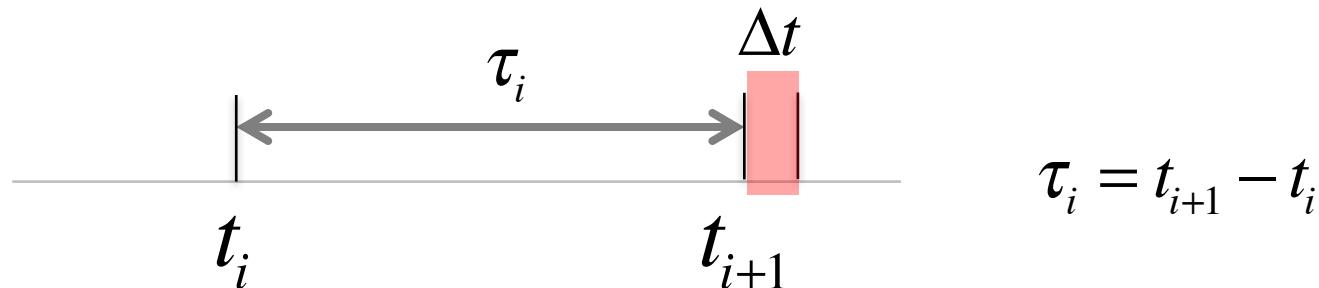
The probability of having the next spike land in the interval between t_{i+1} and $t_{i+1} + \Delta t$ is:

$$P_\tau[n=0] = \frac{(r\tau)^0}{0!} e^{-r\tau} = e^{-r\tau}$$

$$P[\tau \leq t_{i+1} - t_i < \tau + \Delta t] = e^{-r\tau} r \Delta t$$

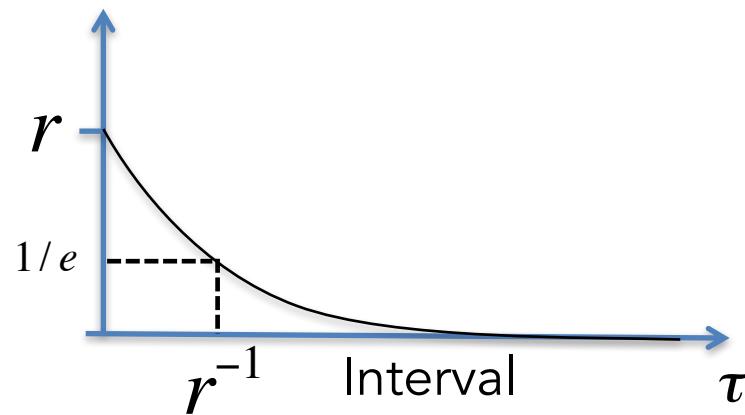
Interspike interval (ISI) distribution

What is the distribution of intervals between spikes?

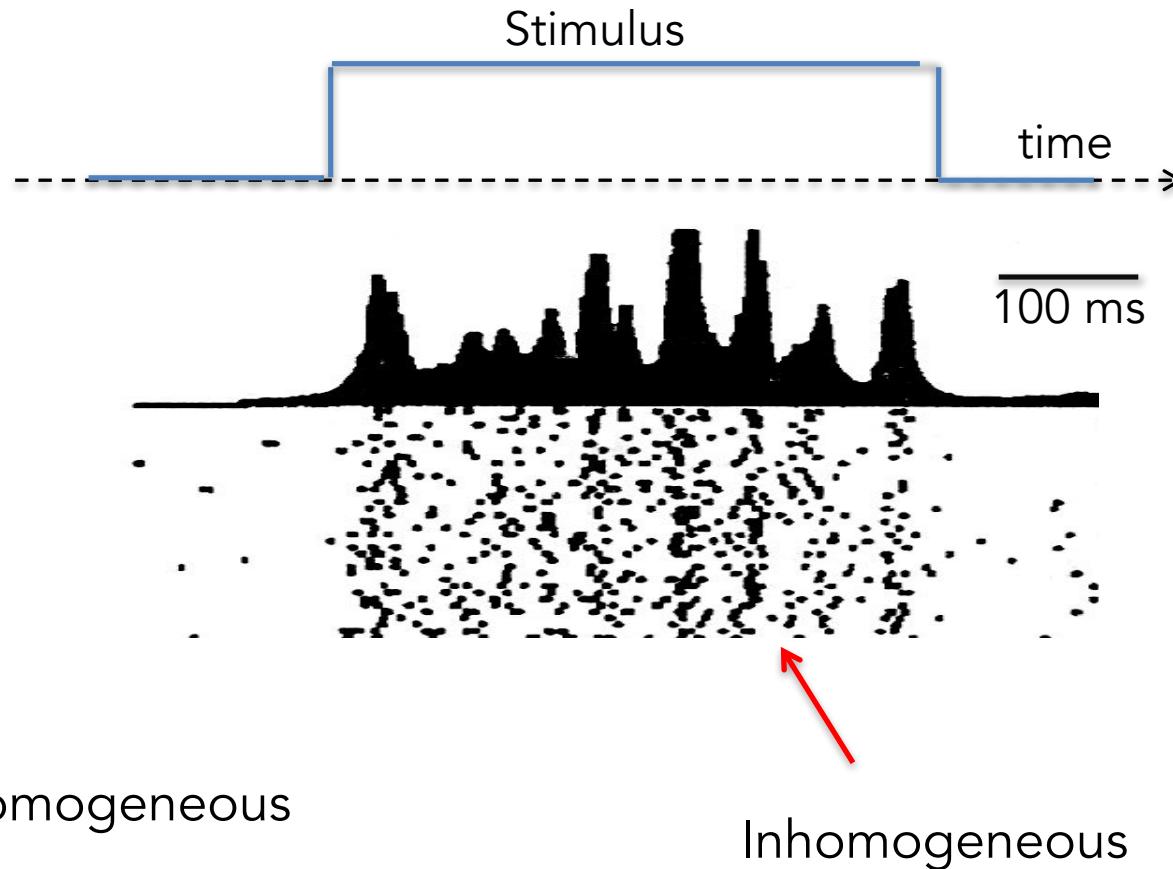


The probability density (probability per unit time) is just

$$\frac{1}{\Delta t} P[\tau] = r e^{-r\tau}$$



Homogeneous vs inhomogeneous Poisson process



$$rate = \mu$$

$$rate = \mu(t)$$

Annotated figure from Dayan, P. and L. Abbott. *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems*. 2001. Original source: Bair, W. and C. Koch. "Temporal Precision of Spike Trains in Extrastriate Cortex of the Behaving Macaque Monkey." *Neural Computation* 8 no 6 (1996): 1185-1202. All rights reserved. This content is excluded from our Creative Commons license. For more information, see <https://ocw.mit.edu/help/faq-fair-use/>.

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Convolution

- We have discussed the idea of convolution

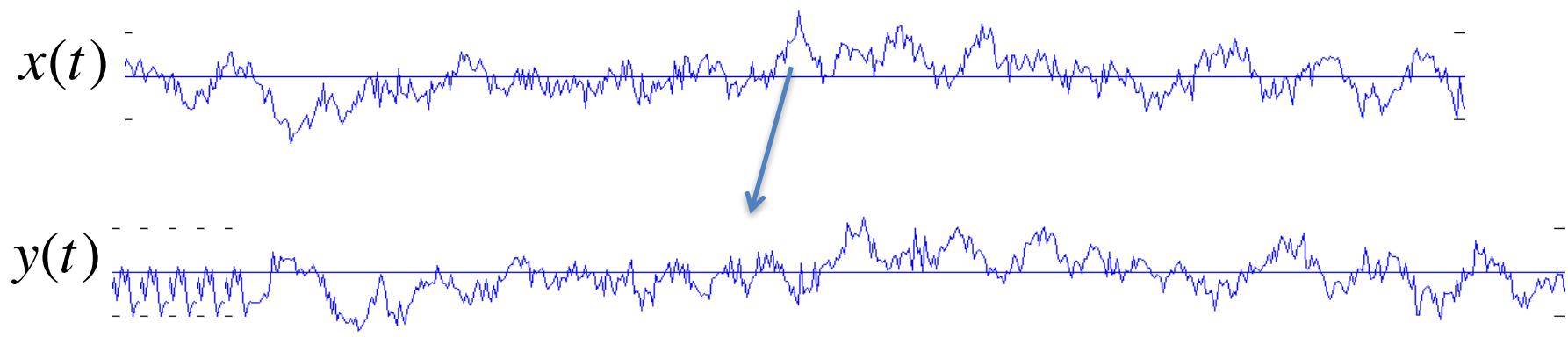
$$y(t) = \int_{-\infty}^{\infty} d\tau G(\tau)x(t - \tau)$$

- To model the response of membrane potential to synaptic input
- To model the response of neurons to a time-dependent stimulus
- To implement a low-pass or high-pass filter
- In general, convolution allows us to model the output of a system as a linear filter acting on its input.

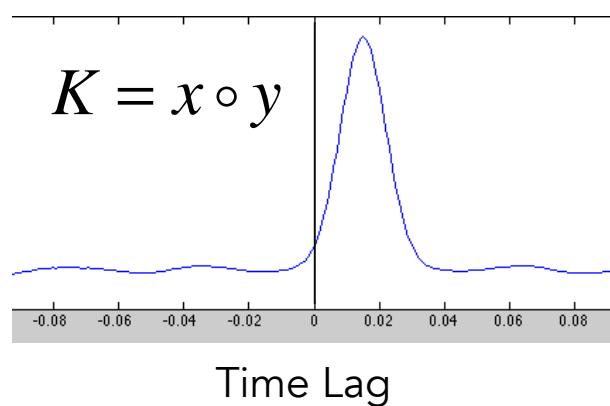
Cross-correlation function

- A way to examine the temporal relation between signals.

$$K(\tau) = \int_{-\infty}^{\infty} dt x(t)y(t + \tau)$$



`xc=xcorr(ShftNoisyData, NoisyData, Nlags);`



Relation between Convolution and Cross-correlation

- These are mathematically very similar, but are used differently.

Convolution

$$y(t) = \int_{-\infty}^{\infty} d\tau K(\tau)x(t - \tau)$$

Take input signal $x(t)$ and convolve it with kernel K to get output signal $y(t)$.

Cross-correlation

$$K(\tau) = \int_{-\infty}^{\infty} dt x(t)y(t + \tau)$$

Take two signals, $x(t)$ and $y(t)$, and cross-correlate to extract a temporal 'kernel' K .

Think of $x(t)$ and $y(t)$ as long vectors (signals)

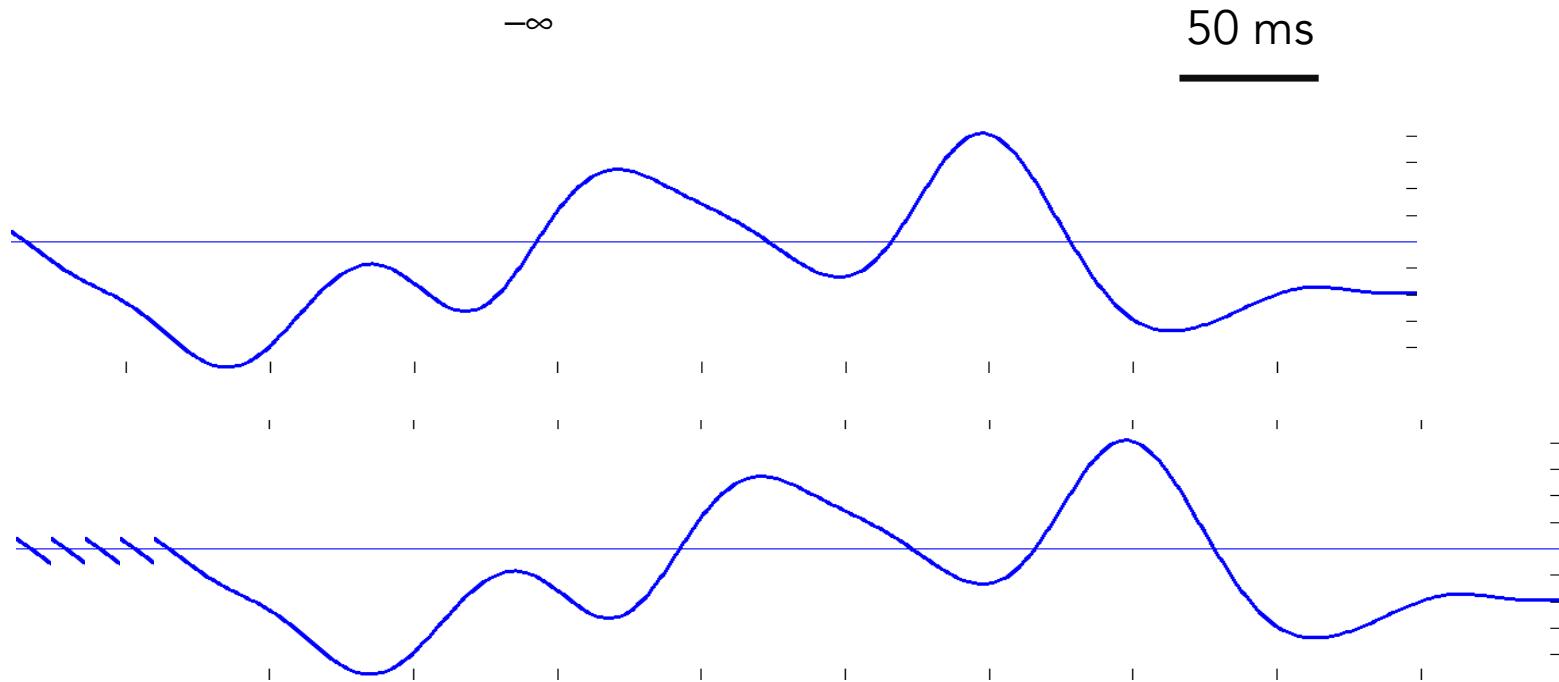
Think of $K(\tau)$ as a short vector (kernel)

Relation to STA

Autocorrelation

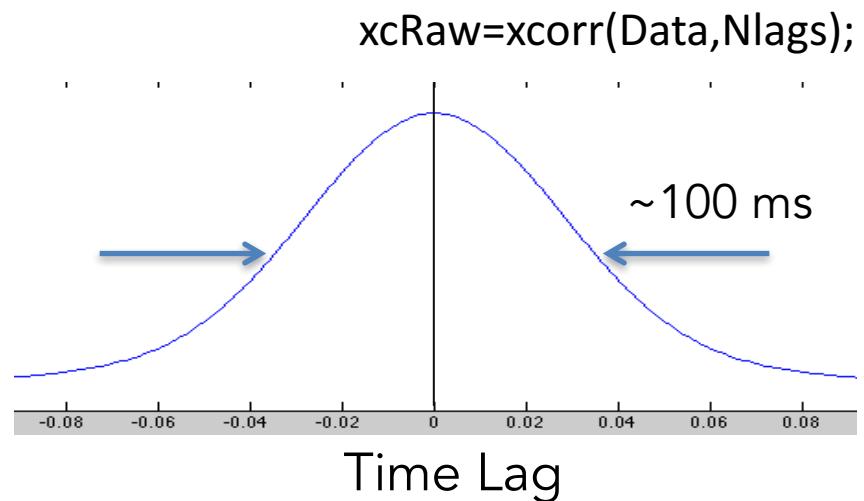
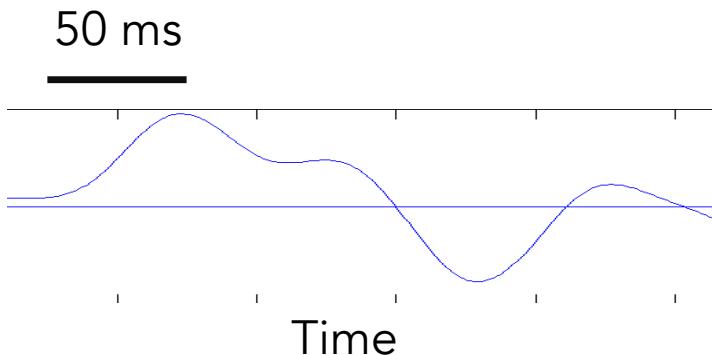
- A way to examine the temporal structure within a signal.

$$K(\tau) = \int_{-\infty}^{\infty} dt x(t)x(t + \tau)$$



Autocorrelation

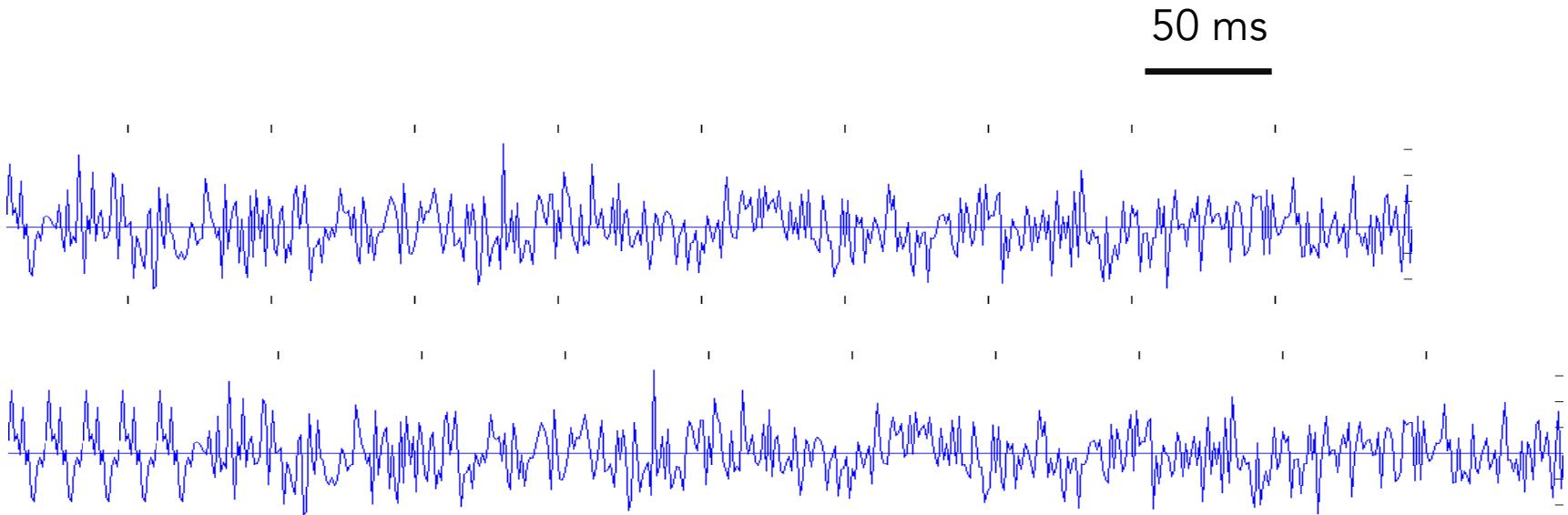
- A way to examine the temporal structure within a signal.



Autocorrelation

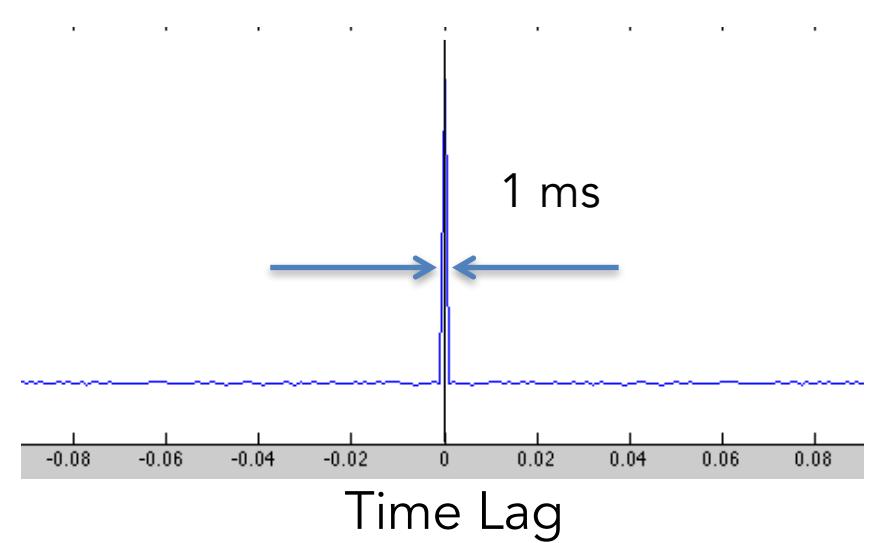
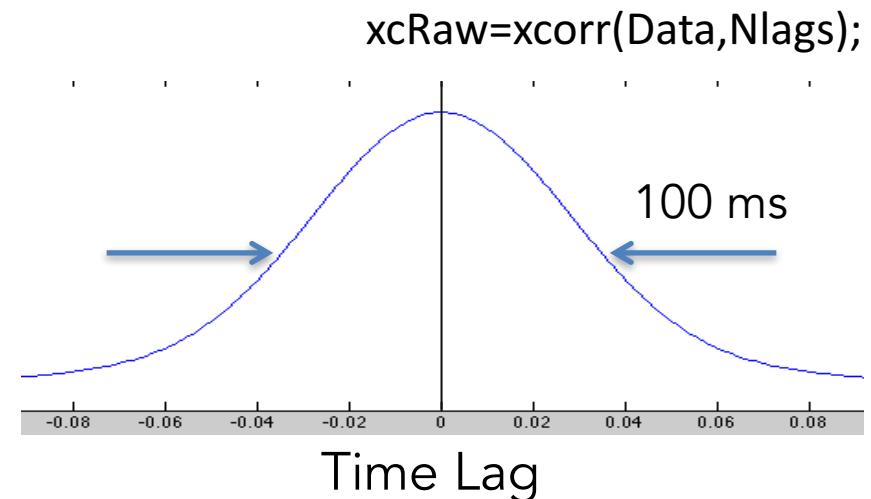
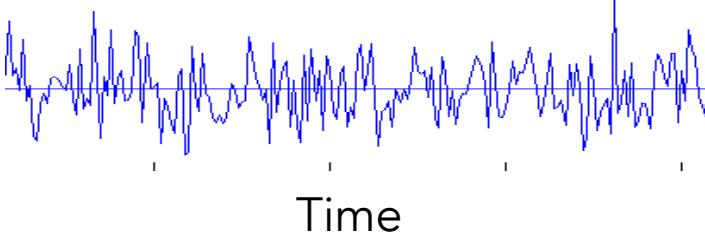
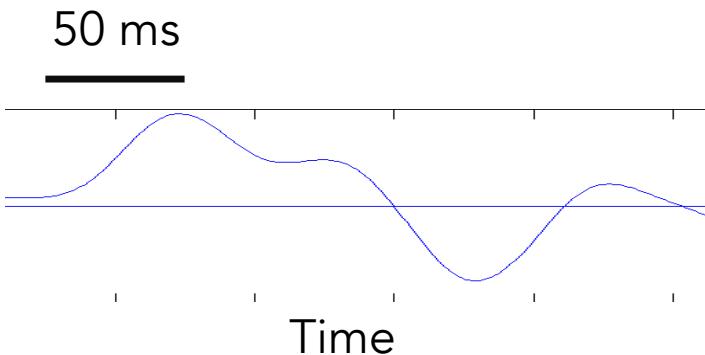
- A way to examine the temporal structure within a signal.

$$K(\tau) = \int_{-\infty}^{\infty} dt x(t)x(t + \tau)$$



Autocorrelation

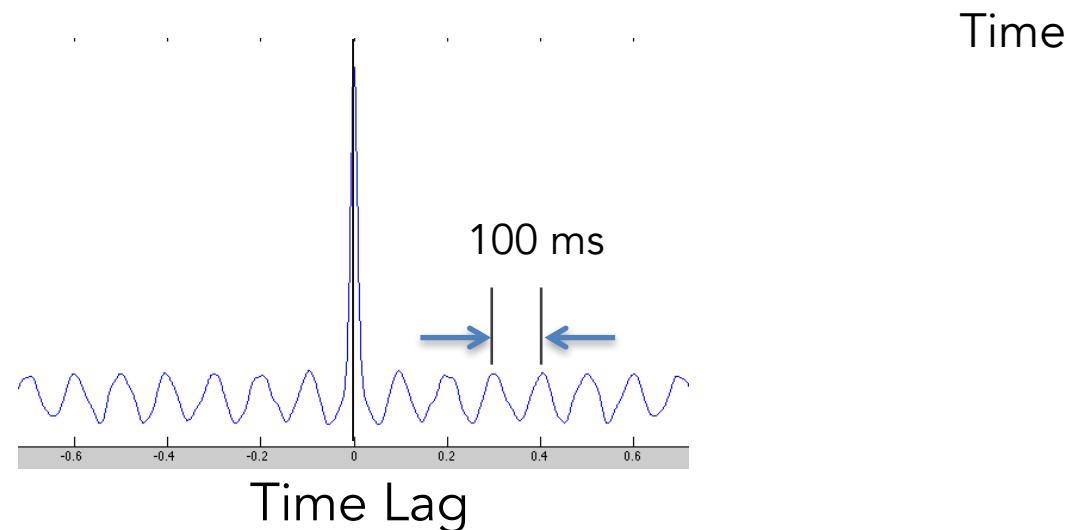
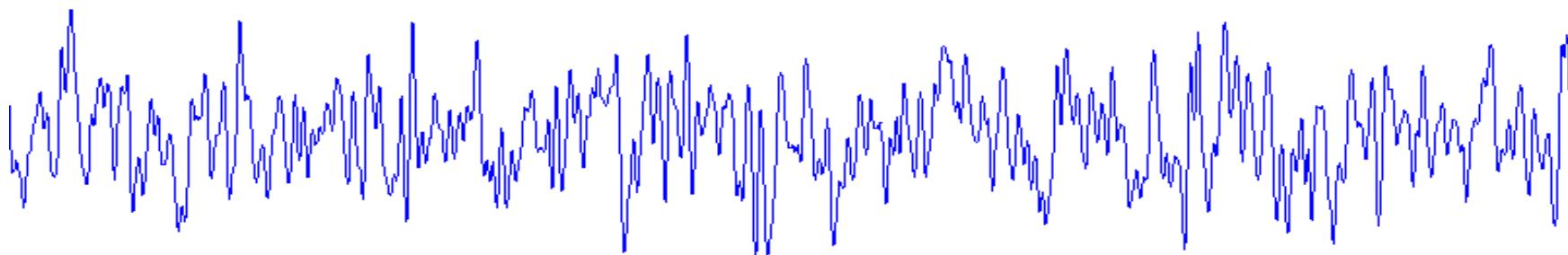
- A way to examine the temporal structure within a signal.



Autocorrelation

- A way to examine the temporal structure within a signal.

Data = randn(1,N)+0.1*cos(2*pi*10*time);



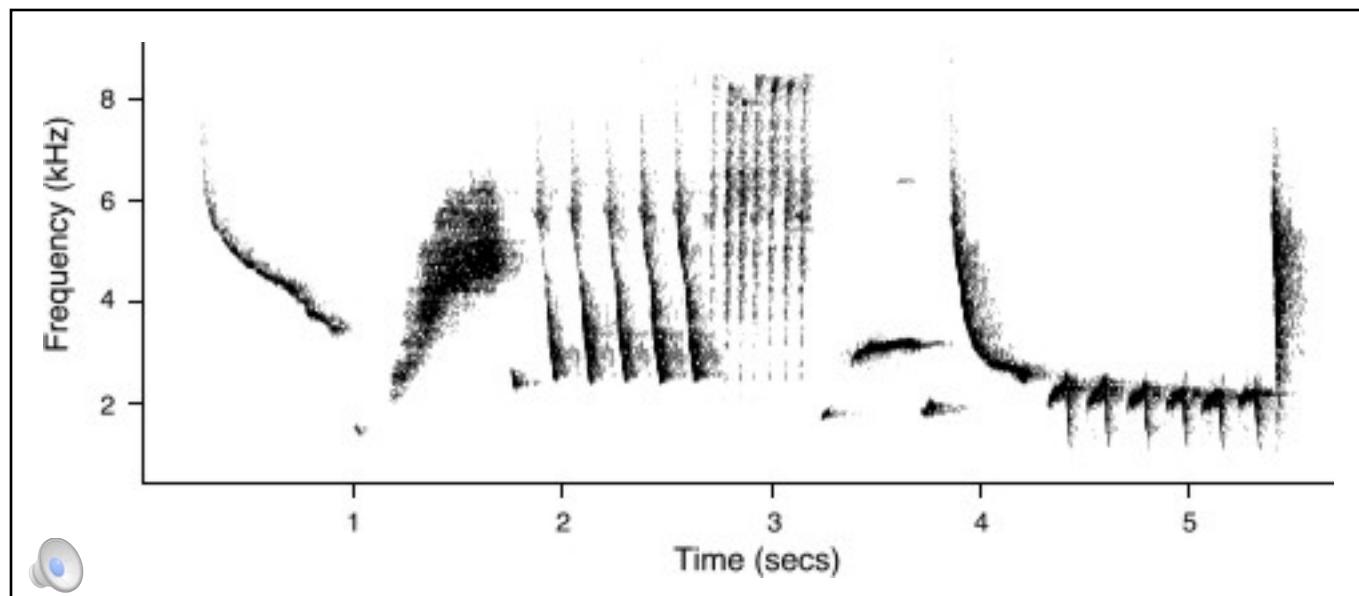
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Spectral Analysis

A spectrogram shows how much power there is in a sound at different frequencies and at different times.

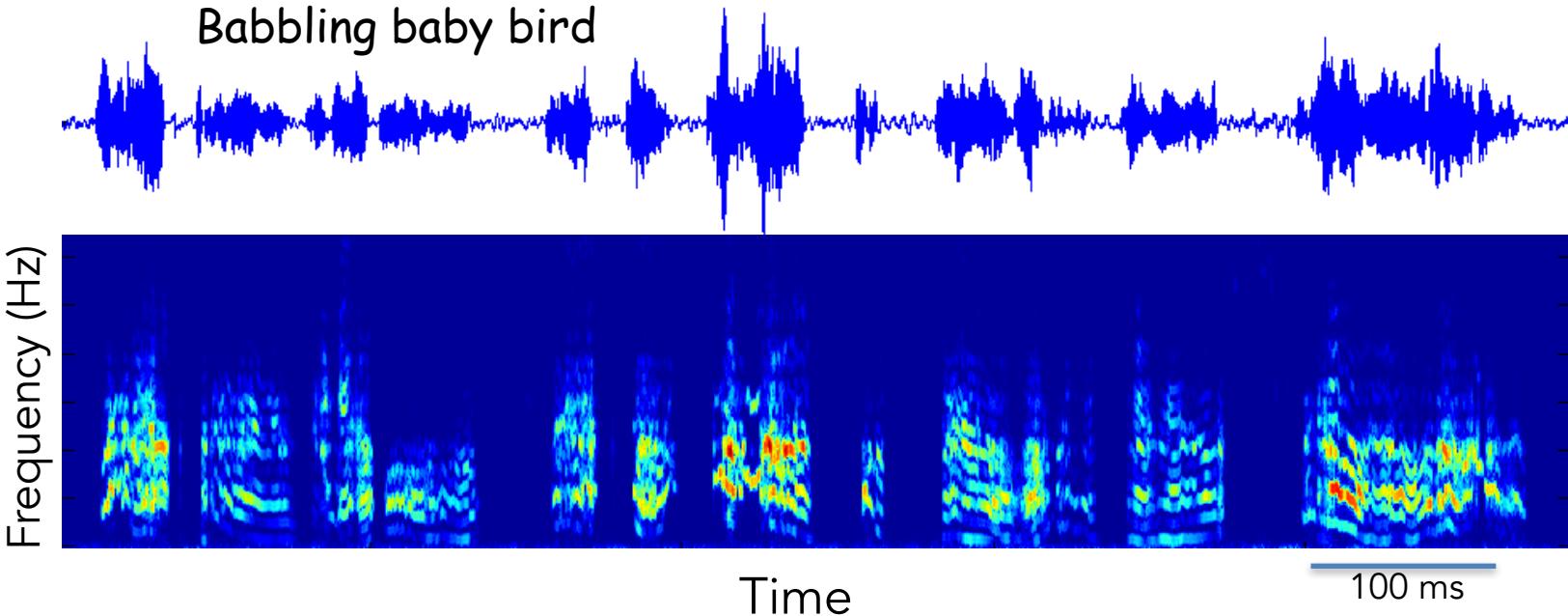
$$S(f,t)$$



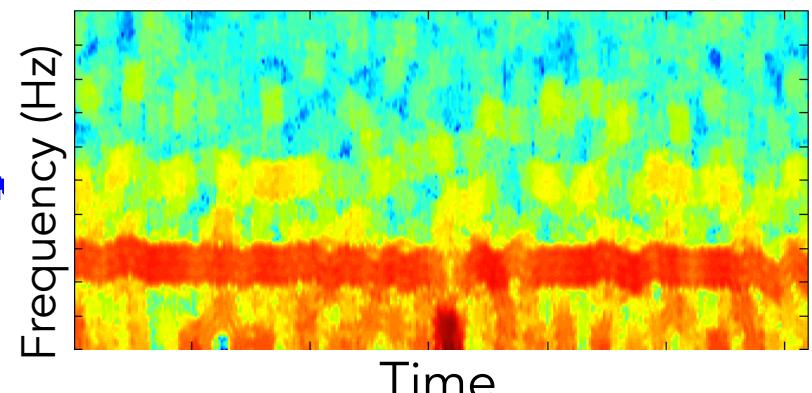
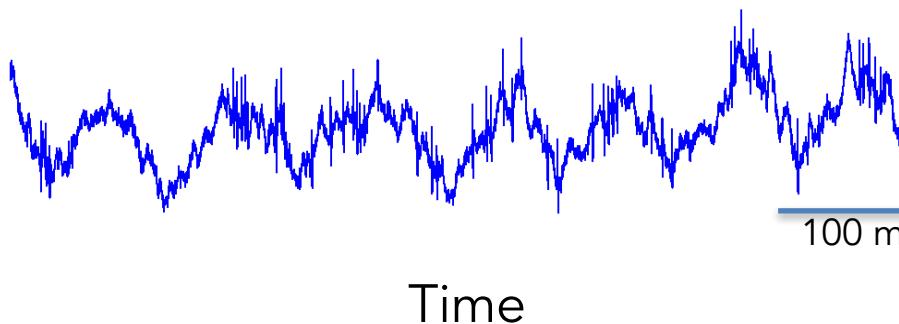
Spectral Analysis



Babbling baby bird

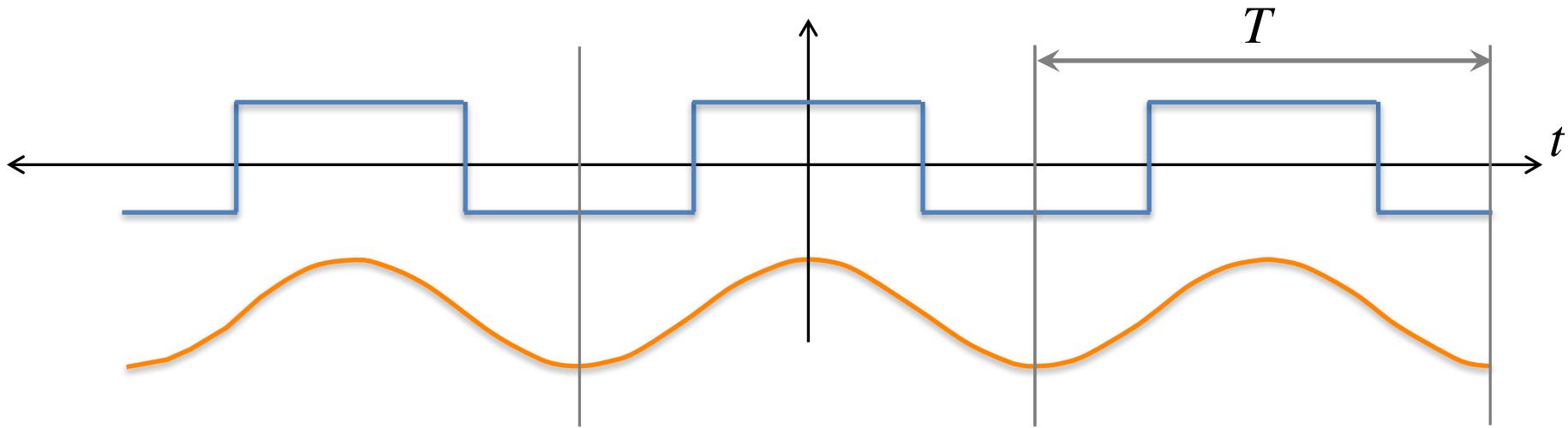


Hippocampal theta rhythm



Fourier Series

- We can express any periodic function of time as sums of sine and cosine functions.
- Let's start with an even function that is periodic with a period T



We could approximate this square wave with a cosine wave of the same period T and amplitude.

$$a_1 \cos(2\pi f_0 t)$$

Oscillation frequency

$$f_0 = \frac{1}{T}$$

Cycles per second (Hz)

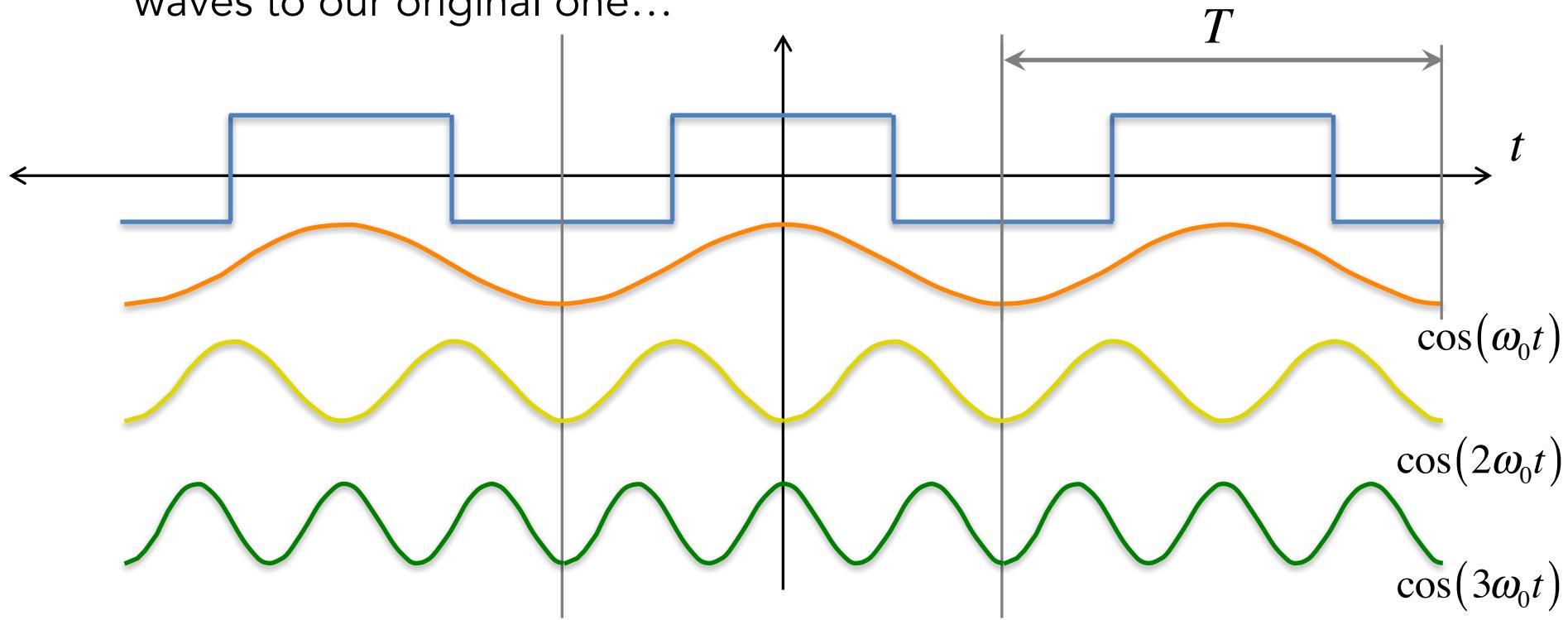
Angular frequency

$$\omega_0 = \frac{2\pi}{T}$$

Radians per second

Fourier Series

- But we can get a better approximation if we add some more cosine waves to our original one...

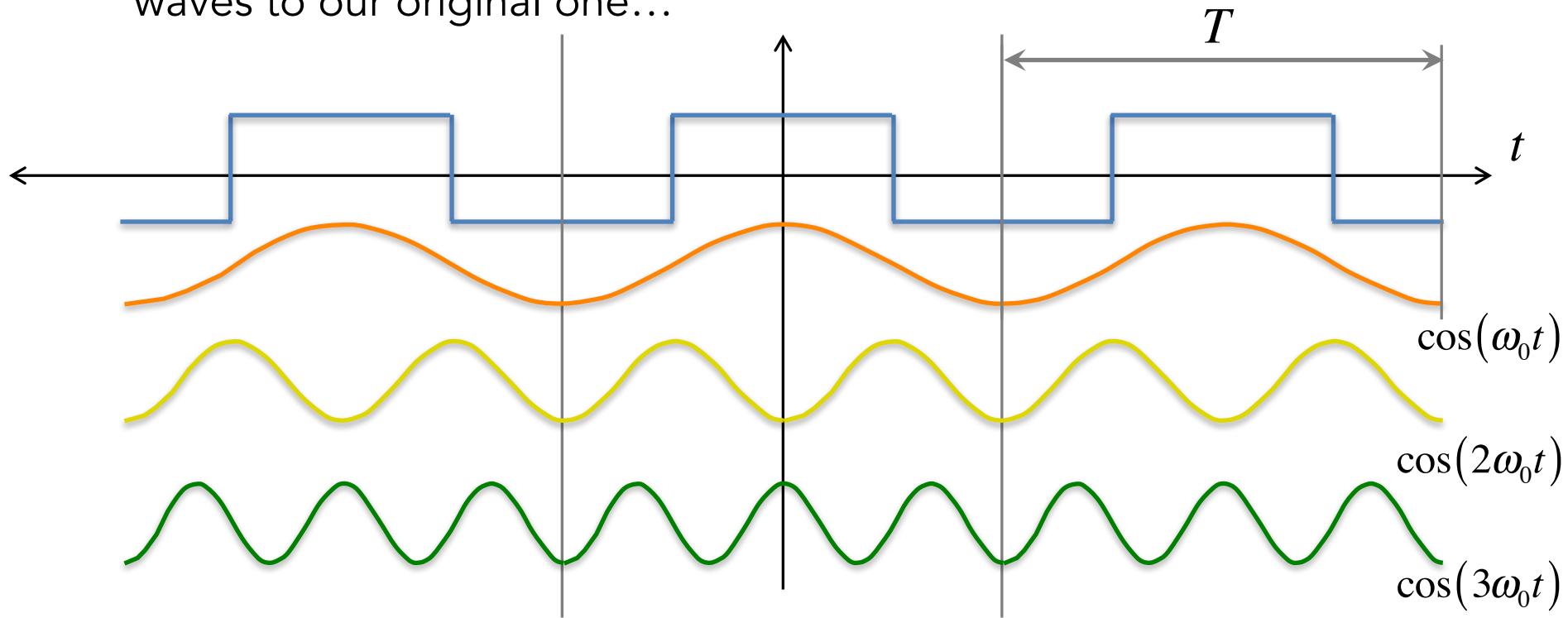


Why can we restrict ourselves to only frequencies that are integer multiples of ω_0 ?

Because only cosines that are integer multiples of ω_0 are periodic with a period T !

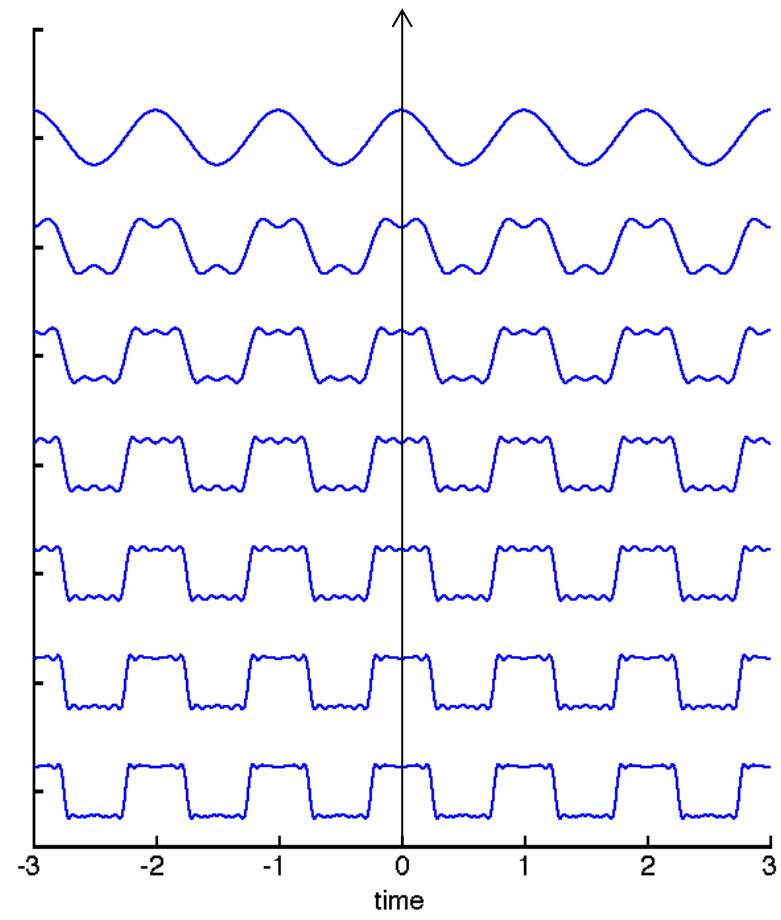
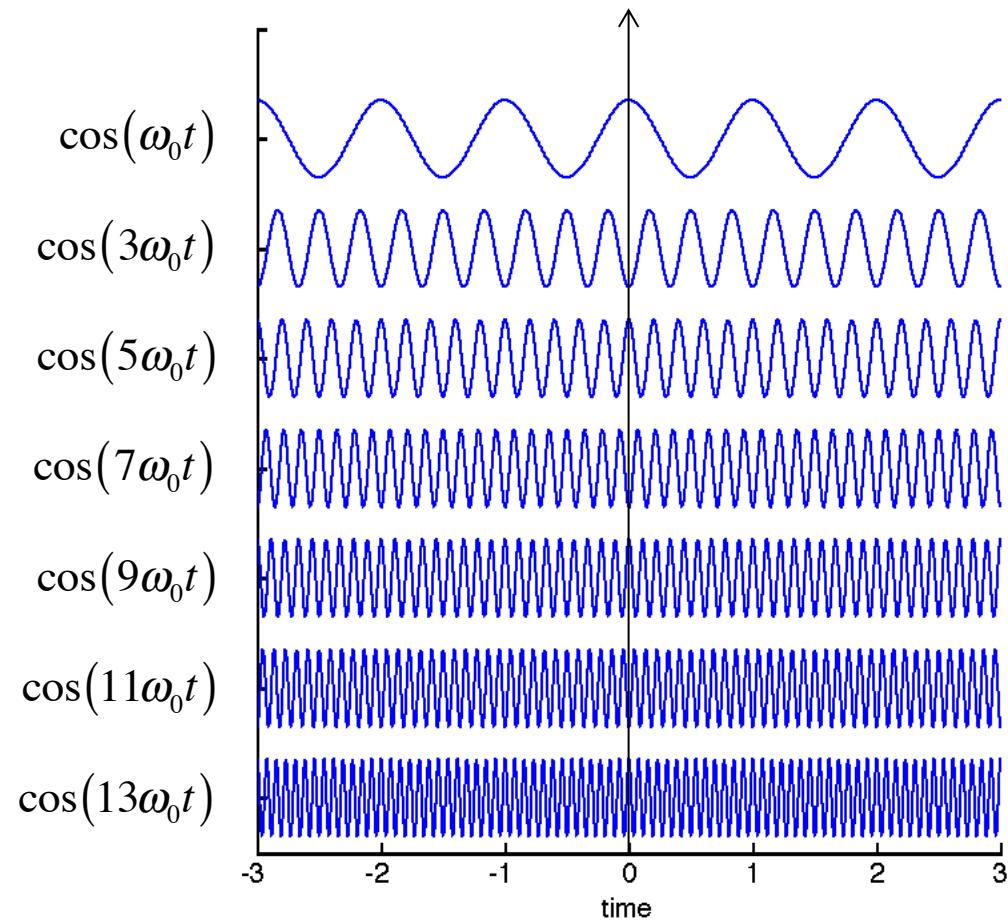
Fourier Series

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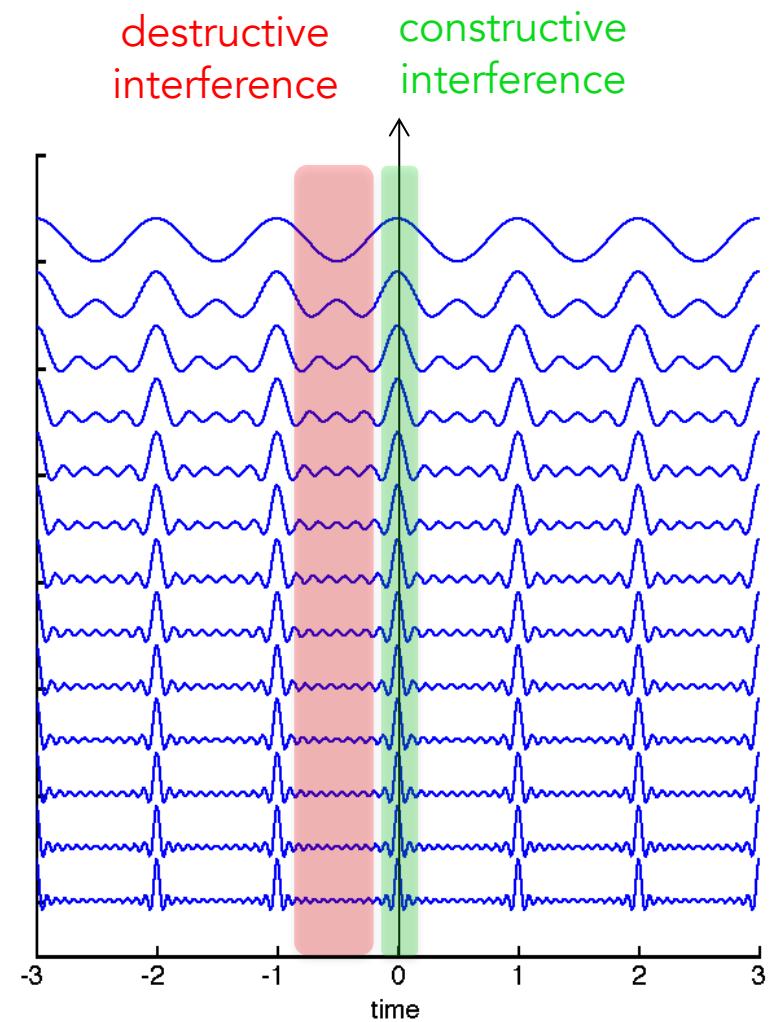
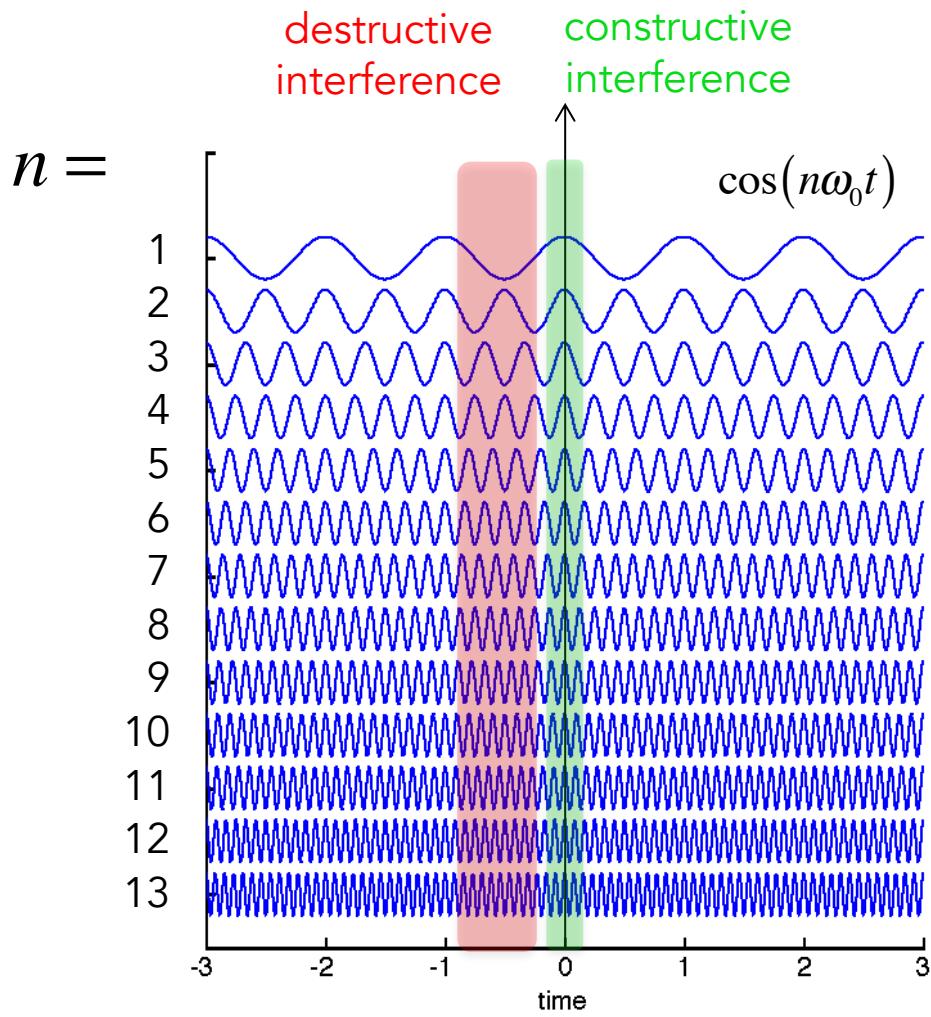


$$y(t) = a_1 \cos(\omega_0 t) + a_2 \cos(2\omega_0 t) + a_3 \cos(3\omega_0 t) + \dots$$

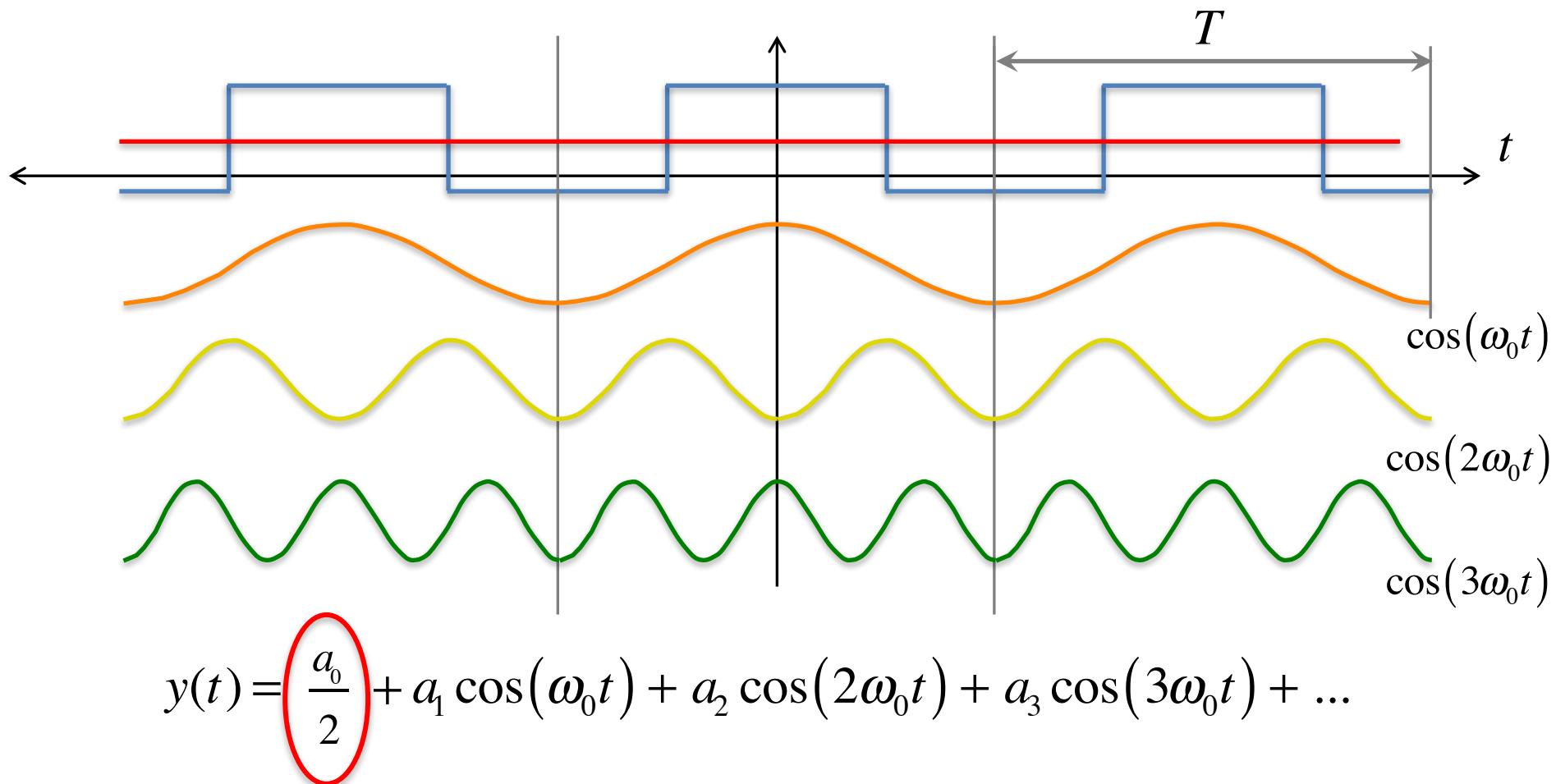
Fourier Series



Fourier Series



Fourier Series



$$y_{even}(t) = \frac{a_0}{2} + \sum_{n=1}^{\infty} a_n \cos(n\omega_0 t)$$

How do we find the coefficients?

- The a_0 coefficient is just like the average of our function $y(t)$.

$$\frac{a_0}{2} = \frac{1}{T} \int_{-T/2}^{T/2} y(t) dt$$

$$a_0 = \frac{2}{T} \int_{-T/2}^{T/2} y(t) \cos(0\omega_0 t) dt$$

- The a_1 coefficient is just the overlap of our function $y(t)$ with $\cos(\omega_0 t)$

$$a_1 = \frac{2}{T} \int_{-T/2}^{T/2} y(t) \cos(\omega_0 t) dt \quad \text{Correlation!}$$

- The a_2 coefficient is just the overlap of our function $y(t)$ with $\cos(2\omega_0 t)$

$$a_2 = \frac{2}{T} \int_{-T/2}^{T/2} y(t) \cos(2\omega_0 t) dt$$

- The a_n coefficient is just the overlap of our function $y(t)$ with $\cos(n\omega_0 t)$

$$a_n = \frac{2}{T} \int_{-T/2}^{T/2} y(t) \cos(n\omega_0 t) dt$$

How do we find the coefficients?

$$a_0 = \frac{2}{T} \int_{-T/2}^{T/2} y(t) dt$$

$$a_1 = \frac{2}{T} \int_{-T/2}^{T/2} y(t) \cos(\omega_0 t) dt$$

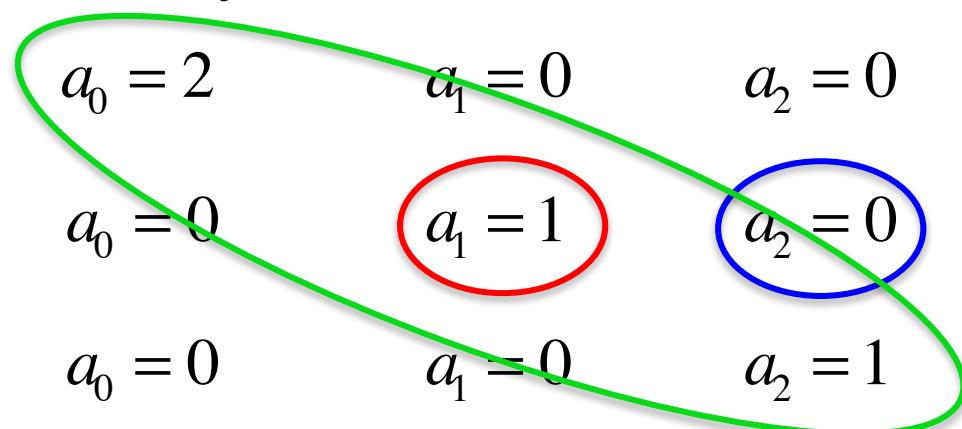
$$a_2 = \frac{2}{T} \int_{-T/2}^{T/2} y(t) \cos(2\omega_0 t) dt$$

Consider the following functions $y(t)$:

$$y(t) = 1$$

$$y(t) = \cos(\omega_0 t)$$

$$y(t) = \cos(2\omega_0 t)$$



$$a_0 = 0$$

$$a_1 = 1$$

$$a_2 = 0$$

$$a_0 = 0$$

$$a_1 = 0$$

$$a_2 = 1$$

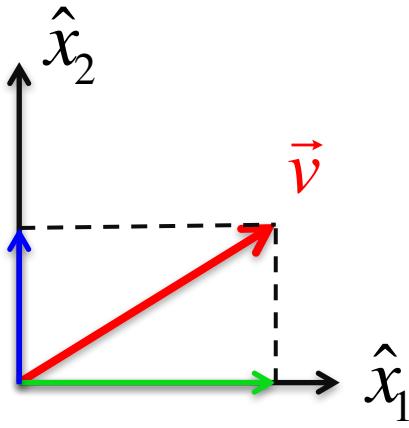
$$\int_{-T/2}^{T/2} [\cos(\omega_0 t)]^2 dt = \frac{T}{2}$$

$$\int_{-T/2}^{T/2} \cos(\omega_0 t) \cos(2\omega_0 t) dt = 0$$

$$y(t) = \frac{a_0}{2} + a_1 \cos(\omega_0 t) + a_2 \cos(2\omega_0 t) + \dots$$

Fourier Series

- If a function has maximal overlap with one of our cosine functions, then it has zero overlap with all the others!
- We say that our set of cosine functions form an orthogonal basis set...



$$\vec{v} = a_1 \hat{x}_1 + a_2 \hat{x}_2$$

$a_1 \hat{x}_1$

$a_2 \hat{x}_2$

$$u_n(t) = \cos(n\omega_0 t)$$

$$\hat{x}_1 = [0, 1]$$

$$\hat{x}_2 = [1, 0]$$

$$\vec{v} = [a_1, a_2]$$

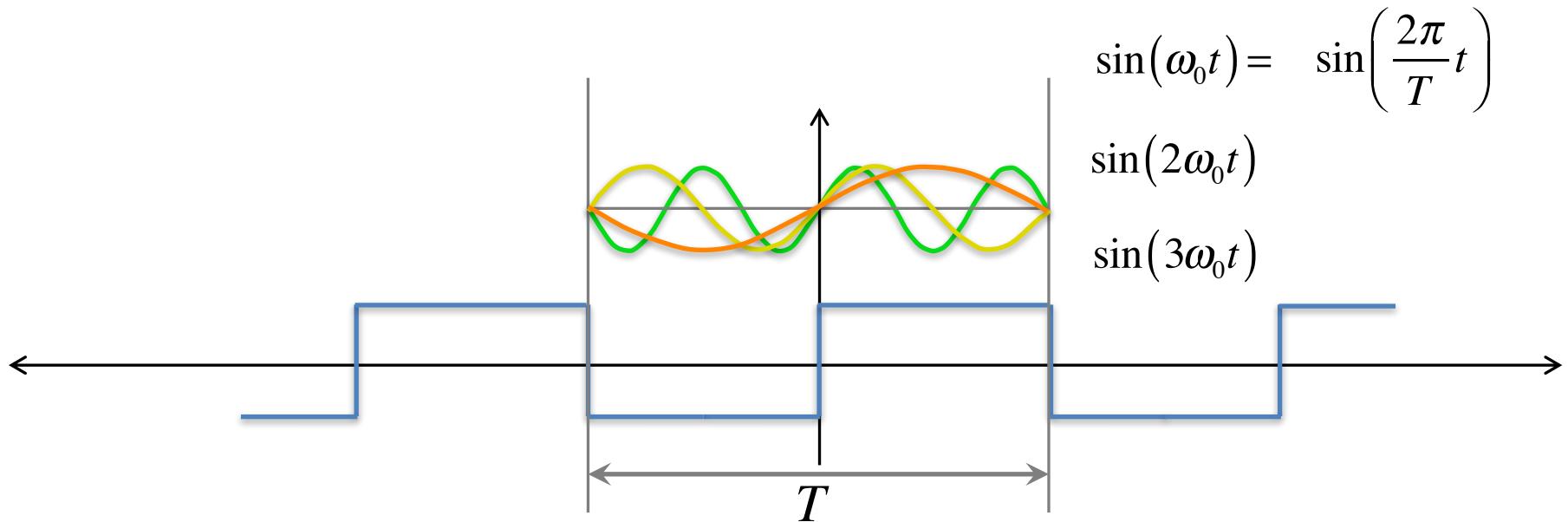
How do we find the coefficients a_1 and a_2 ?

$$a_1 = \vec{v} \cdot \hat{x}_1 = \sum_i v^i x_1^i \quad a_2 = \vec{v} \cdot \hat{x}_2 = \sum_i v^i x_2^i$$

$$a_1 = \frac{2}{T} \int_{-T/2}^{T/2} y(t) \cos(\omega_0 t) dt$$

Fourier Series

- Now let's look at an odd (antisymmetric) function...



$$y_{odd}(t) = b_1 \sin(\omega_0 t) + b_2 \sin(2\omega_0 t) + b_3 \sin(3\omega_0 t) + \dots$$

$$y_{odd}(t) = \sum_{n=1}^{\infty} b_n \sin(n\omega_0 t)$$

Why is there no DC term here?

Fourier Series

- For an arbitrary function, we can write it down as the sum of a symmetric and an antisymmetric part.

$$y(t) = \frac{a_0}{2} + \sum_{n=1}^{\infty} a_n \cos(n\omega_0 t) + \sum_{n=1}^{\infty} b_n \sin(n\omega_0 t)$$

The equation shows the Fourier series decomposition of a function $y(t)$. It consists of three parts: a constant term $\frac{a_0}{2}$, a sum of cosine terms $\sum_{n=1}^{\infty} a_n \cos(n\omega_0 t)$, and a sum of sine terms $\sum_{n=1}^{\infty} b_n \sin(n\omega_0 t)$. The first two terms are grouped by a blue brace and labeled 'symmetric'. The third term is grouped by a blue brace and labeled 'antisymmetric'.

Complex Fourier Series

- We can express any periodic function of time as sums of complex exponentials.

Euler's formula

$$e^{i\omega t} = \cos \omega t + i \sin \omega t$$

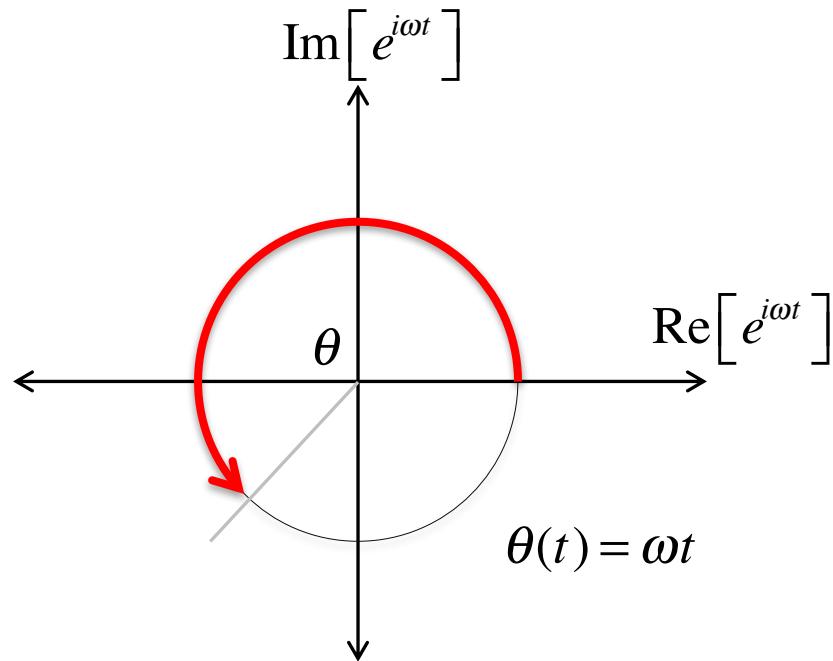
$$e^{-i\omega t} = \cos \omega t - i \sin \omega t$$

Rewrite as follows...

$$\cos \omega t = \frac{1}{2} (e^{i\omega t} + e^{-i\omega t})$$

$$\sin \omega t = \frac{1}{2i} (e^{i\omega t} - e^{-i\omega t}) = -\frac{i}{2} (e^{i\omega t} - e^{-i\omega t})$$

$$\frac{1}{i} = -i$$



Fourier Series

$$y(t) = \frac{a_0}{2} + \sum_{n=1}^{\infty} a_n \cos(n\omega_0 t) + \sum_{n=1}^{\infty} b_n \sin(n\omega_0 t)$$

$$y(t) = \frac{a_0}{2} + \sum_{n=1}^{\infty} \frac{a_n}{2} \left(e^{in\omega t} + e^{-in\omega t} \right) + \sum_{n=1}^{\infty} \frac{-ib_n}{2} \left(e^{in\omega t} - e^{-in\omega t} \right)$$

$$y(t) = A_0 + \sum_{n=1}^{\infty} A_n e^{i n \omega_0 t} + \sum_{n=1}^{\infty} A_{-n} e^{-i n \omega_0 t}$$

'DC' or
'constant'
term

positive
frequencies

negative
frequencies

$$A_0 = \frac{a_0}{2} \quad A_n = \frac{1}{2}(a_n - ib_n) \quad A_{-n} = \frac{1}{2}(a_n + ib_n) \quad A_n = (A_{-n})^*$$

complex conjugates

Complex Fourier Series

$$y(t) = A_0 + \sum_{n=1}^{\infty} A_n e^{in\omega_0 t} + \sum_{n=1}^{\infty} A_{-n} e^{-in\omega_0 t}$$

- We can write this more compactly as follows:

$$= \sum_{n=0}^{\infty} A_n e^{in\omega_0 t} + \sum_{n=1}^{\infty} A_n e^{in\omega_0 t} + \sum_{n=-1}^{-\infty} A_n e^{in\omega_0 t}$$

For $n = 0$,

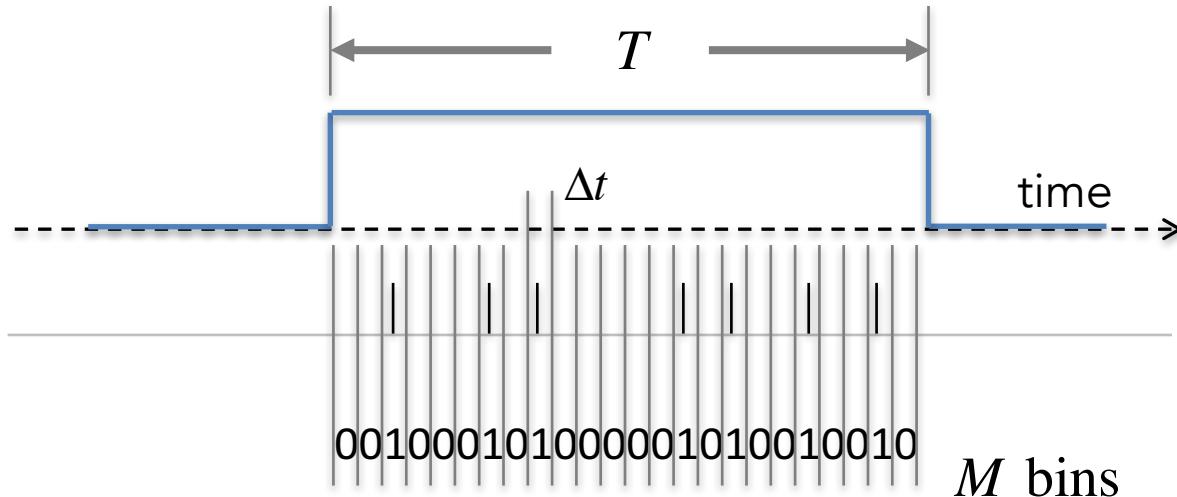
$$e^{in\omega_0 t} = e^0 = 1$$

$$y(t) = \sum_{n=-\infty}^{\infty} A_n e^{in\omega_0 t}$$

Learning objectives for Lecture 10

- Spike trains are probabilistic (Poisson Process)
- Be able to use measures of spike train variability
 - Fano Factor
 - Interspike Interval (ISI)
- Understand convolution, cross-correlation, and autocorrelation functions
- Understand the concept of a Fourier series

Extra Slides on Poisson process



How many spikes land in the interval T ?

What is the probability that n spikes land in the interval T ? $P_T[n]$

This is just the product of three things:

- The probability of having n bins with a spike = $(\mu \Delta t)^n$
- The probability of having $M-n$ bins with no spike = $(1 - \mu \Delta t)^{M-n}$
- The number of different ways to distribution n spikes in M bins = $\frac{M!}{(M-n)!n!}$

Extra Slides on Poisson process

What is the probability that n spikes land in the interval T ?

$$P_T[n] = \lim_{\Delta t \rightarrow 0} \frac{M!}{(M-n)!n!} (\mu \Delta t)^n (1 - \mu \Delta t)^{M-n}$$

Note that as $\Delta t \rightarrow 0$: $M = \frac{T}{\Delta t} \rightarrow \infty$ $M - n \approx M$

$$\varepsilon = -\mu \Delta t \quad \frac{1}{\Delta t} = \frac{-\mu}{\varepsilon}$$

$$\lim_{\Delta t \rightarrow 0} (1 - \mu \Delta t)^{M-n} = \lim_{\Delta t \rightarrow 0} (1 - \mu \Delta t)^{\frac{T}{\Delta t}} = \lim_{\varepsilon \rightarrow 0} (1 + \varepsilon)^{\frac{-\mu T}{\varepsilon}} = \lim_{\varepsilon \rightarrow 0} \left[(1 + \varepsilon)^{\frac{1}{\varepsilon}} \right]^{-\mu T}$$



$$= e^{-\mu T}$$

Extra Slides on Poisson process

What is the probability that n spikes land in the interval T ?

$$P_T[n] = \lim_{\Delta t \rightarrow 0} \frac{M!}{(M-n)!n!} (\mu \Delta t)^n e^{-\mu T}$$

Note that as $M \rightarrow \infty$:

$$\frac{M!}{(M-n)!} = \overbrace{M(M-1)(M-2) \cdots (M-n+1)}^{\text{n terms}} \approx M^n = \left(\frac{T}{\Delta t}\right)^n$$

$$P_T[n] = \frac{1}{n!} \left(\frac{T}{\Delta t}\right)^n (\mu \Delta t)^n e^{-\mu T}$$

Poisson distribution!

$$P_T[n] = \frac{(\mu T)^n}{n!} e^{-\mu T}$$

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9.40 Introduction to Neural Computation
Spring 2018

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