

# Introduction to Neural Computation

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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)

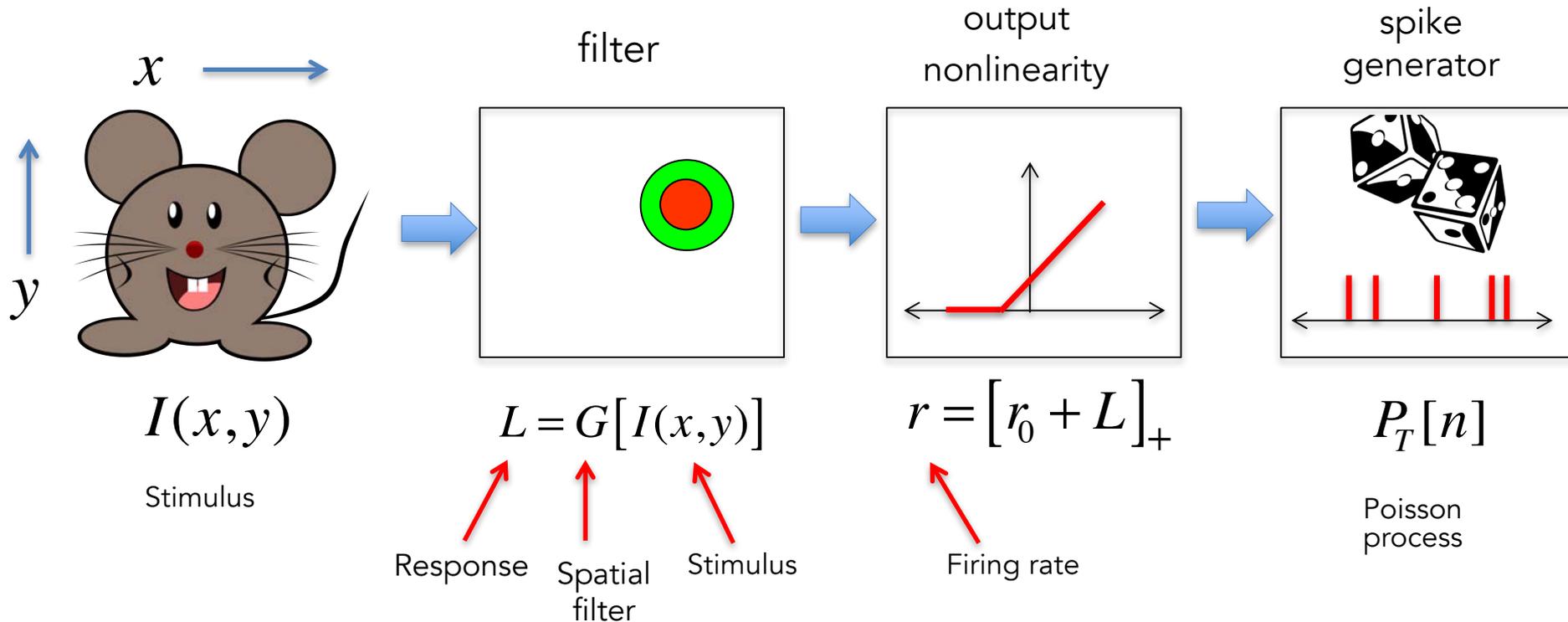


Image of mouse in public domain.

# Spatial receptive fields

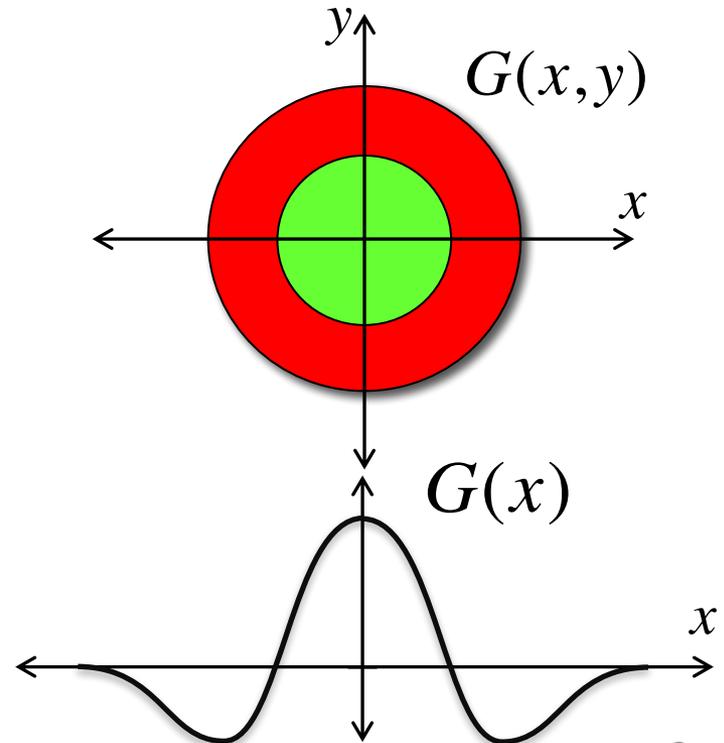
- How do we represent receptive fields mathematically?

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.

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

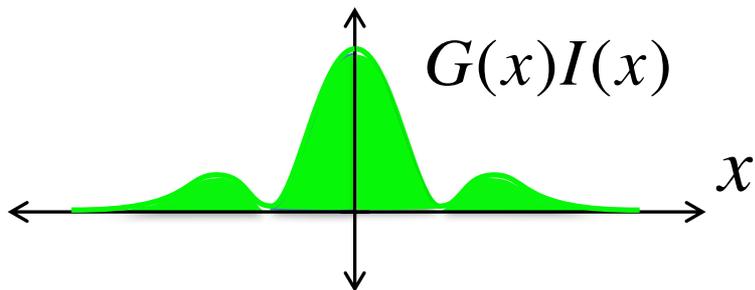
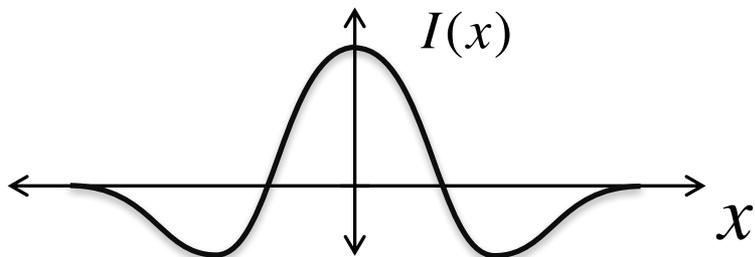
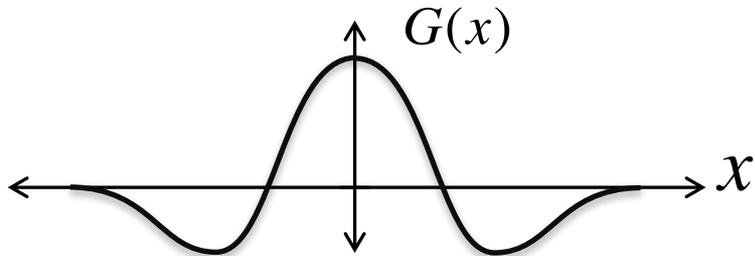
Let's look at this in one dimension

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

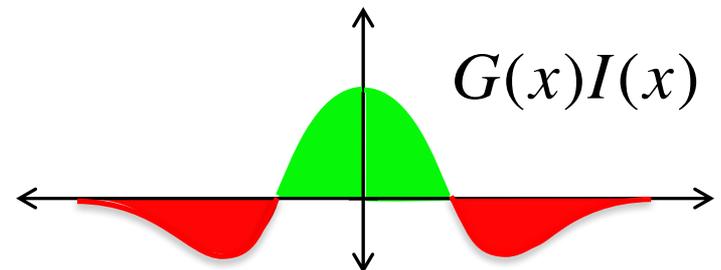
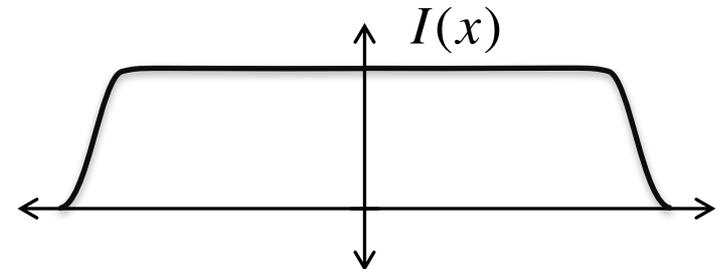
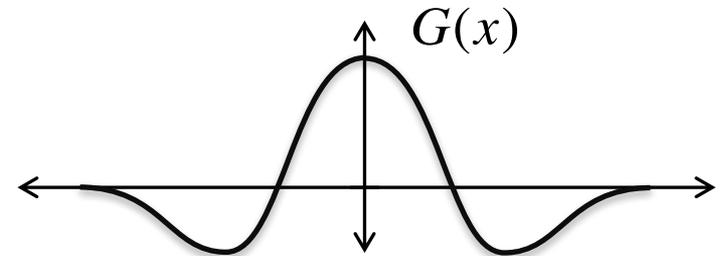


# Spatial receptive fields

- How do we represent receptive fields mathematically?



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



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

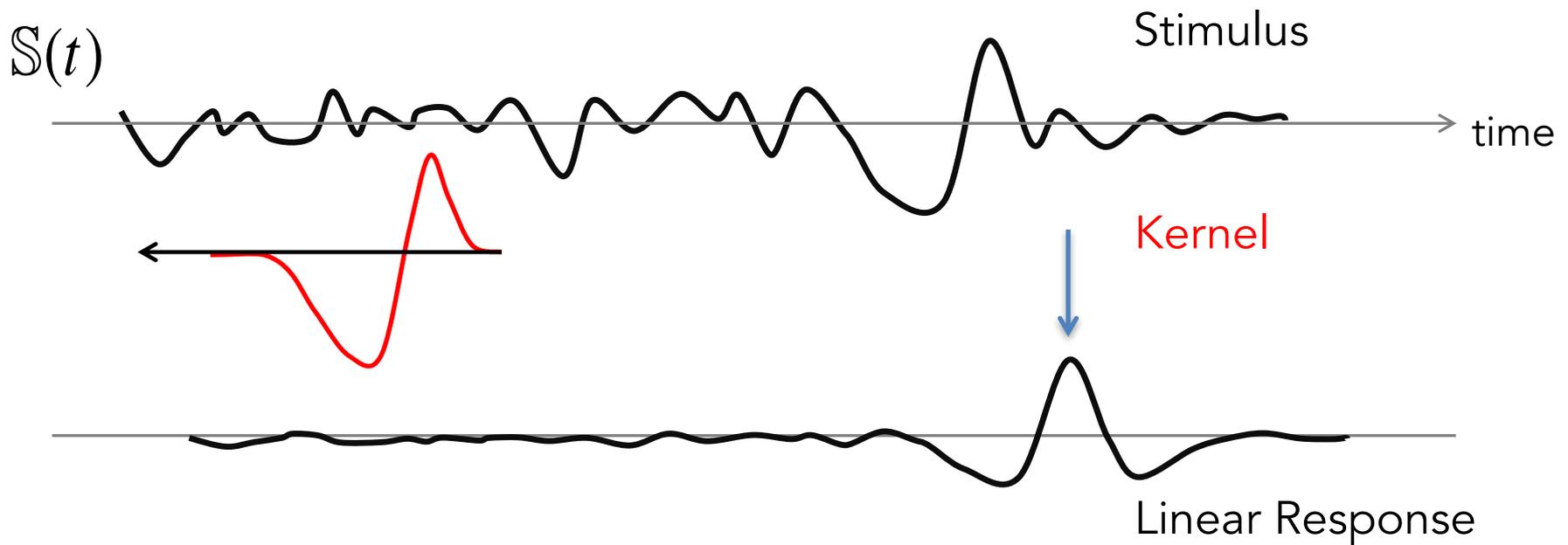
# Temporal receptive fields

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

$$r(t) = r_0 + D[S(t)]$$

# 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.

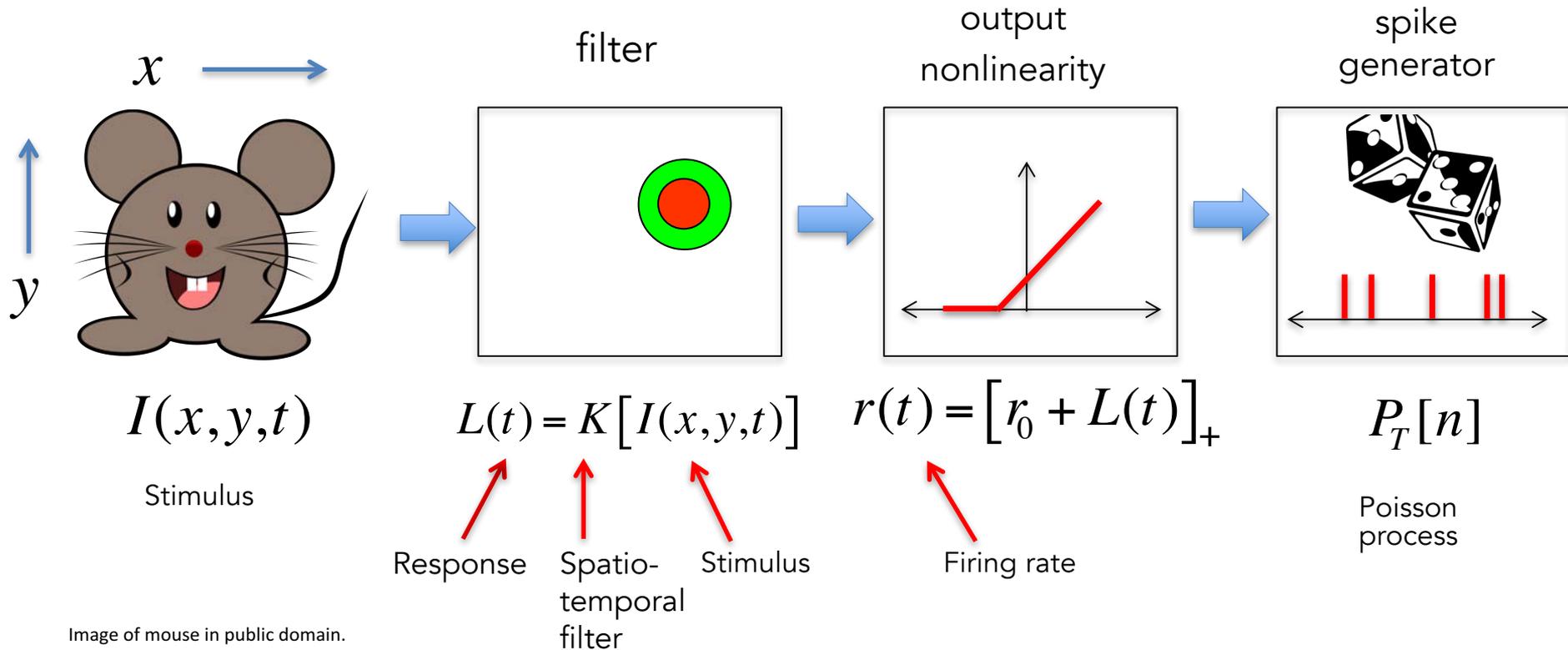


Image of mouse in public domain.

# 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.

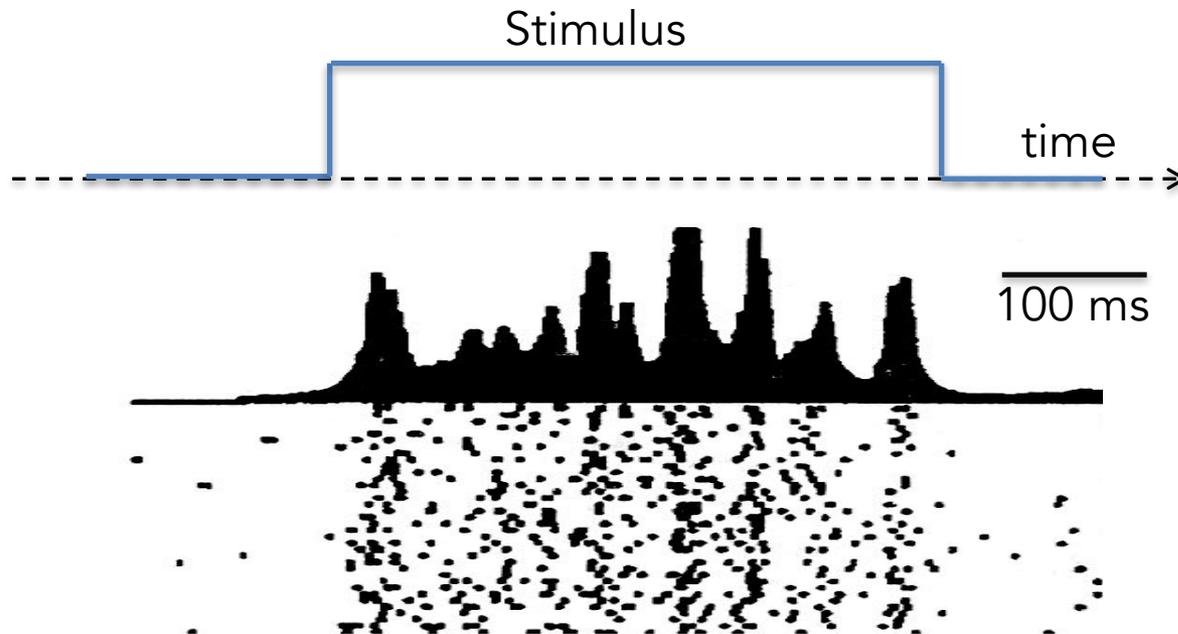
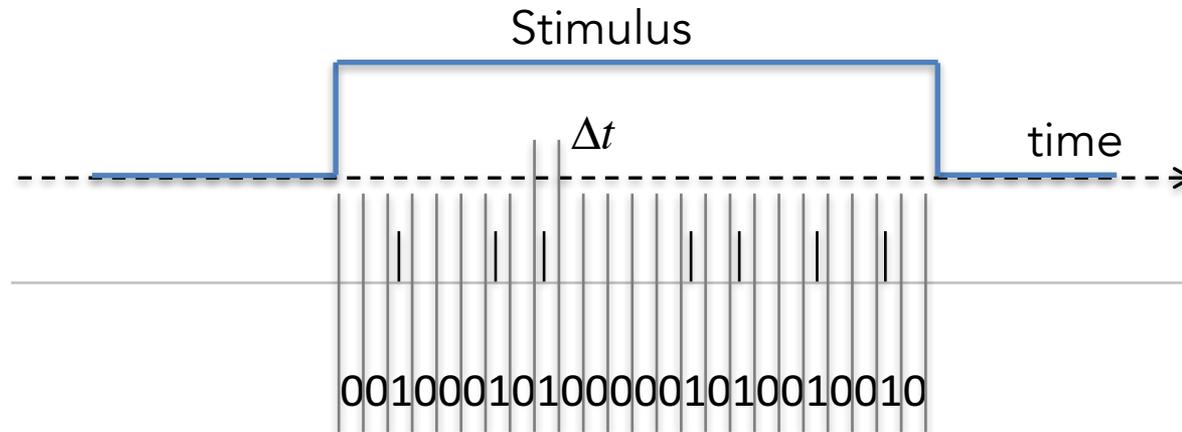


Figure courtesy MIT Press. From Dayan, P. and L. Abbott. *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems*. 2001. Original source: Bair, W. and C. Koch. "Temporal Precision of Spike Trains in Extrastriate Cortex of the Behaving Macaque Monkey." *Neural Computation* 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



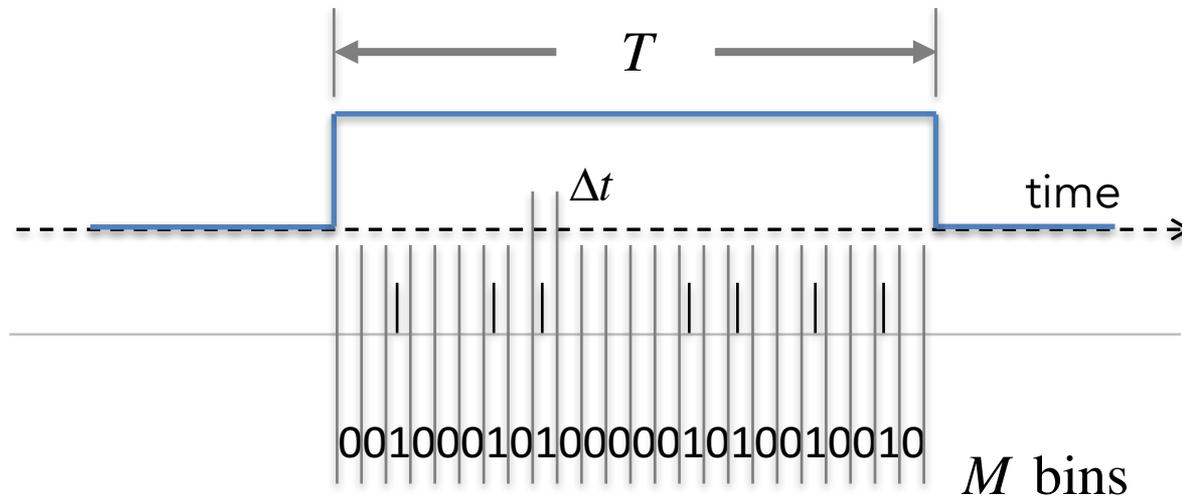
Imagine a random process that produces spikes at an average rate of  $\mu$  spikes per second during the stimulus presentation.

Break up the spike train into small time bins of some duration  $\Delta t$ . 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  $\Delta t$  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

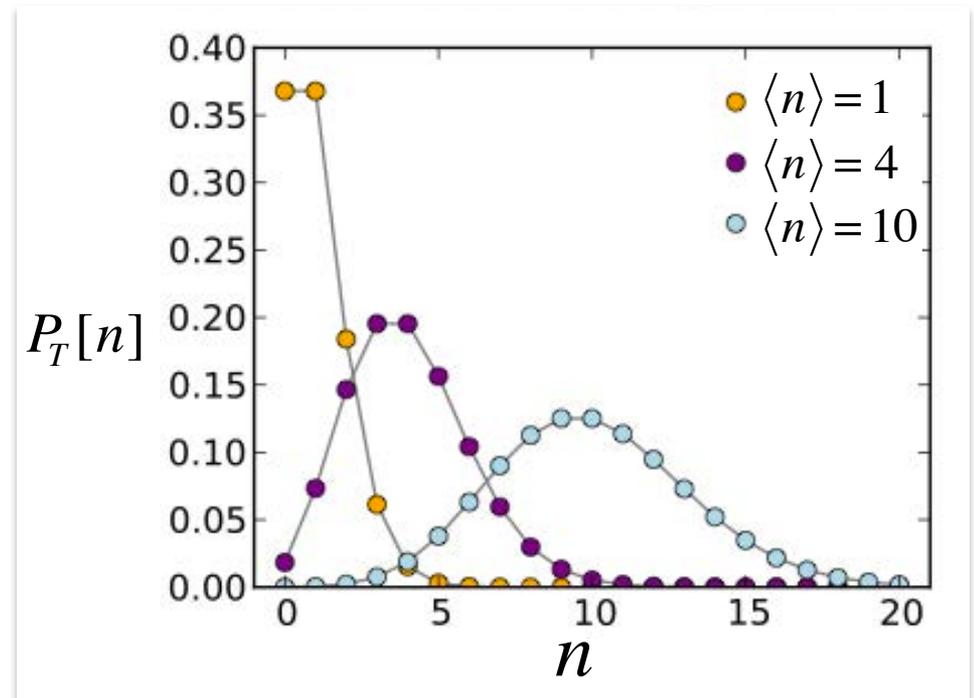
The Poisson Distribution gives us the probability that  $n$  spikes land in the interval  $T$

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

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 [Skbkekas](#) 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

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

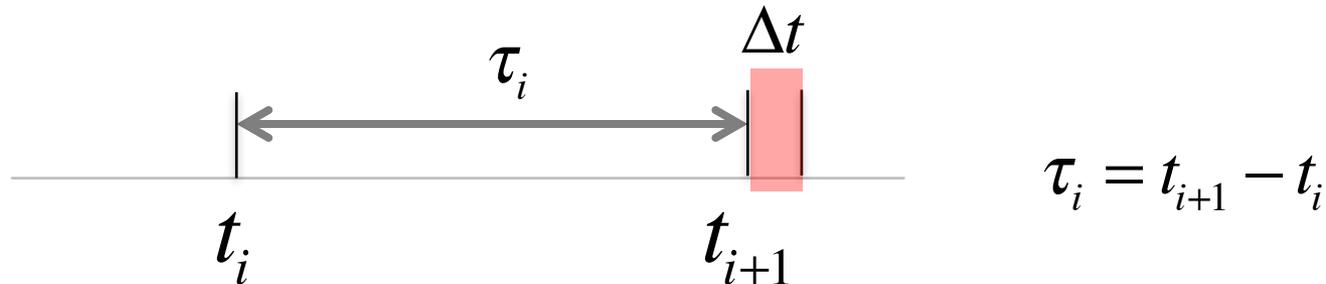
$$\sigma_n^2(T) = \mu T$$

Fano Factor

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

# Interspike interval (ISI) distribution

What is the distribution of intervals between spikes?



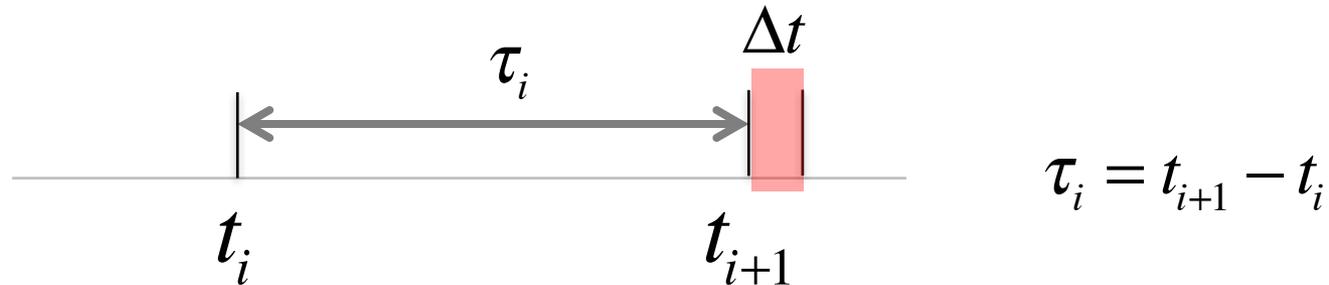
The probability of having the next spike land in the interval between  $t_{i+1}$  and  $t_{i+1} + \Delta t$  is:

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

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

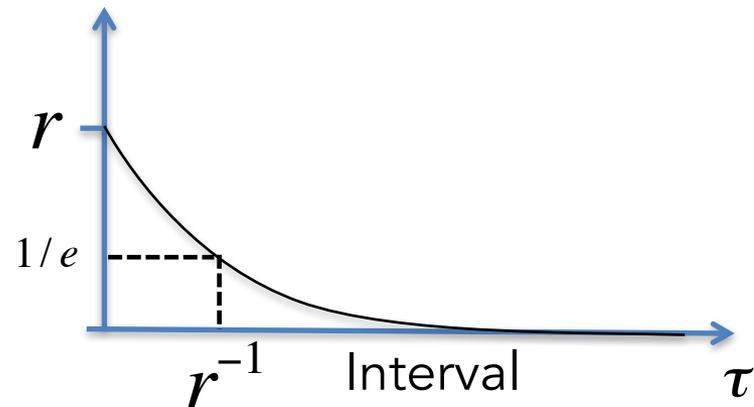
# Interspike interval (ISI) distribution

What is the distribution of intervals between spikes?

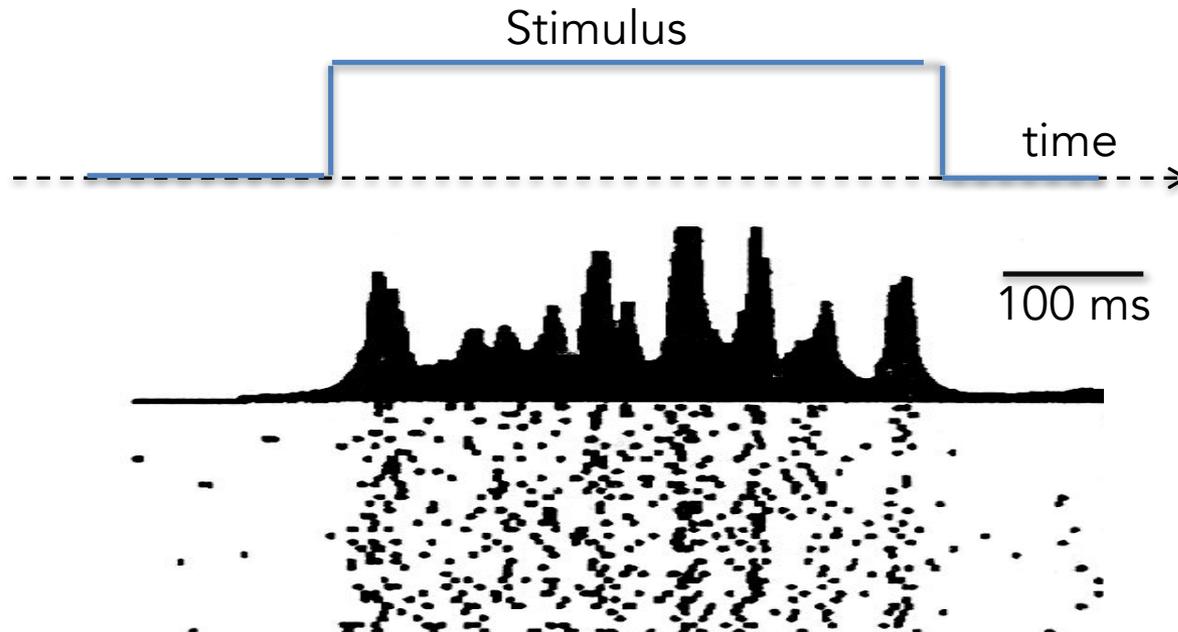


The probability density (probability per unit time) is just

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



# Homogeneous vs inhomogeneous Poisson process



Homogeneous

Inhomogeneous

$$rate = \mu$$

$$rate = \mu(t)$$

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# Convolution

- We have discussed the idea of convolution

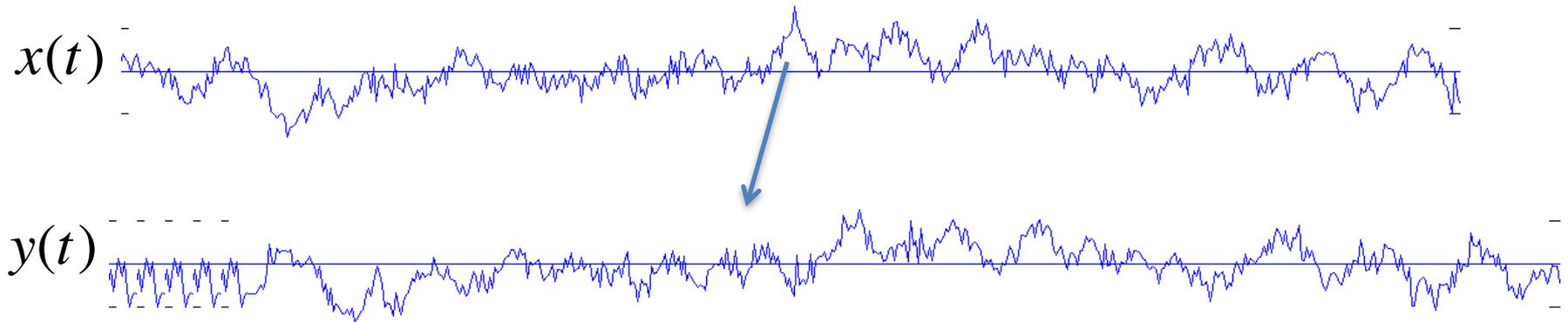
$$y(t) = \int_{-\infty}^{\infty} d\tau G(\tau)x(t - \tau)$$

- 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.

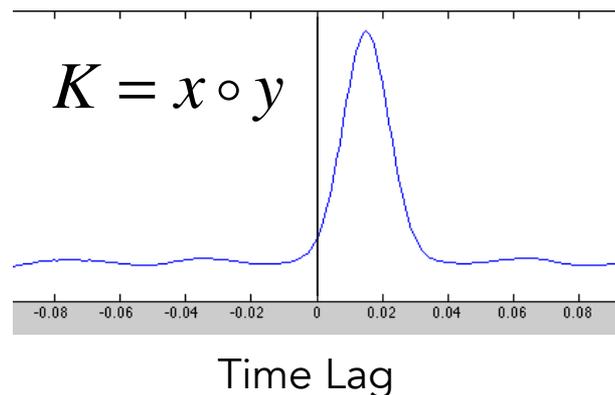
# Cross-correlation function

- 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)

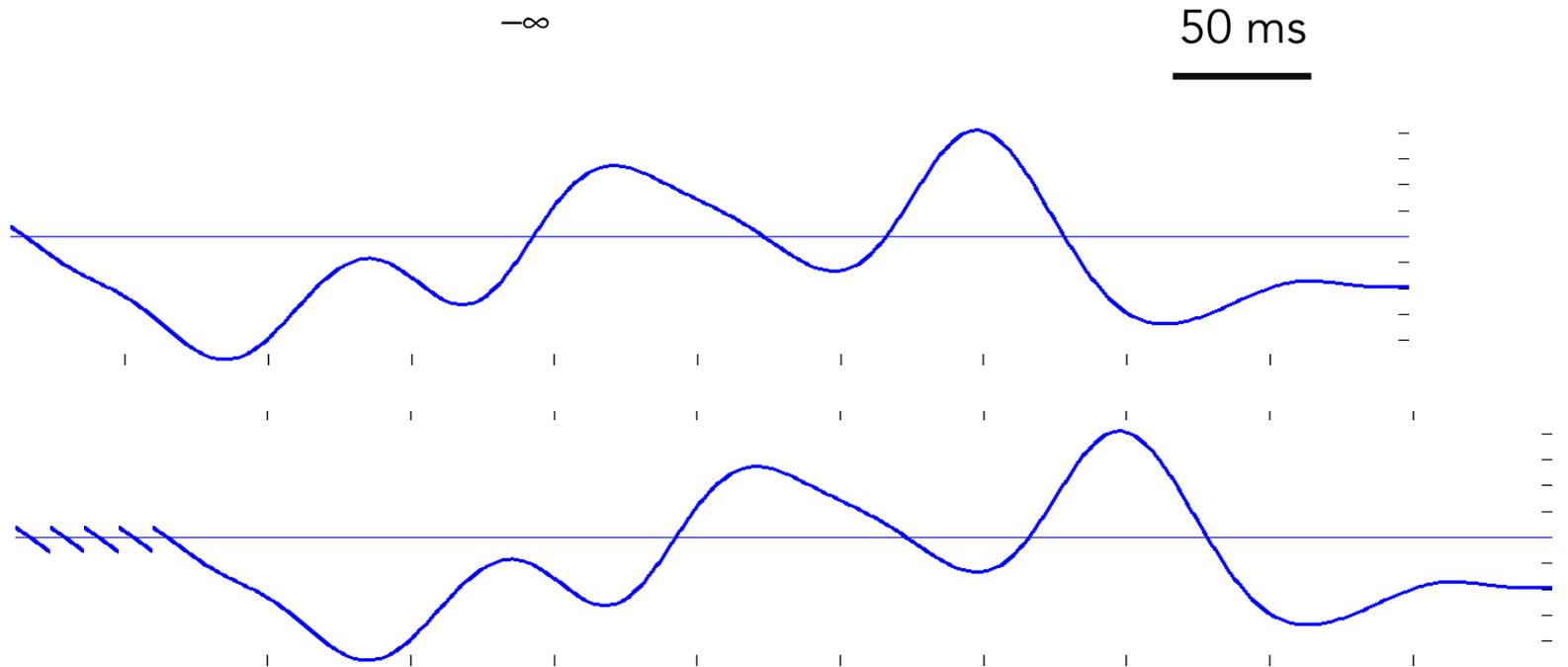
Think of  $K(\tau)$  as a short vector (kernel)

Relation to STA

# Autocorrelation

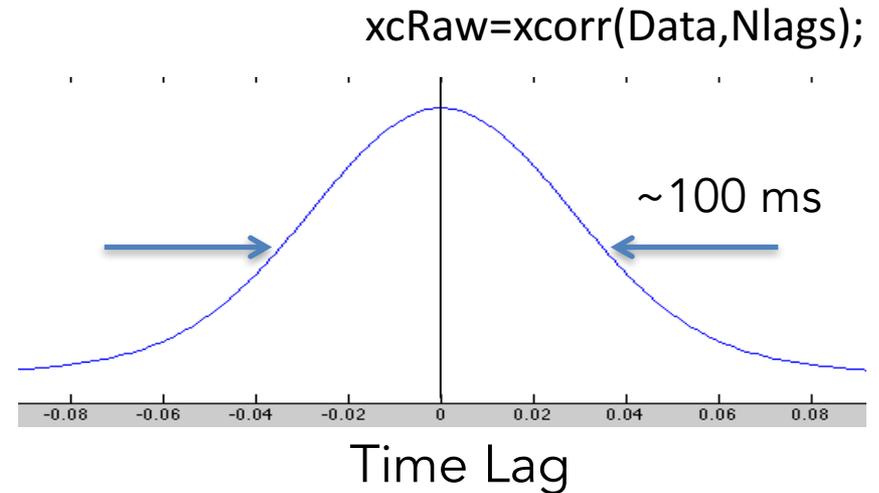
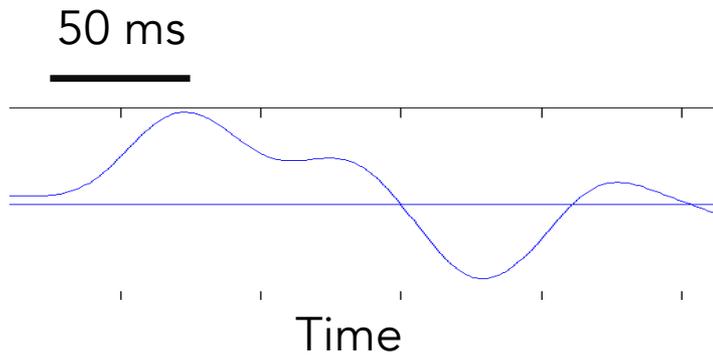
- A way to examine the temporal structure within a signal.

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



# Autocorrelation

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

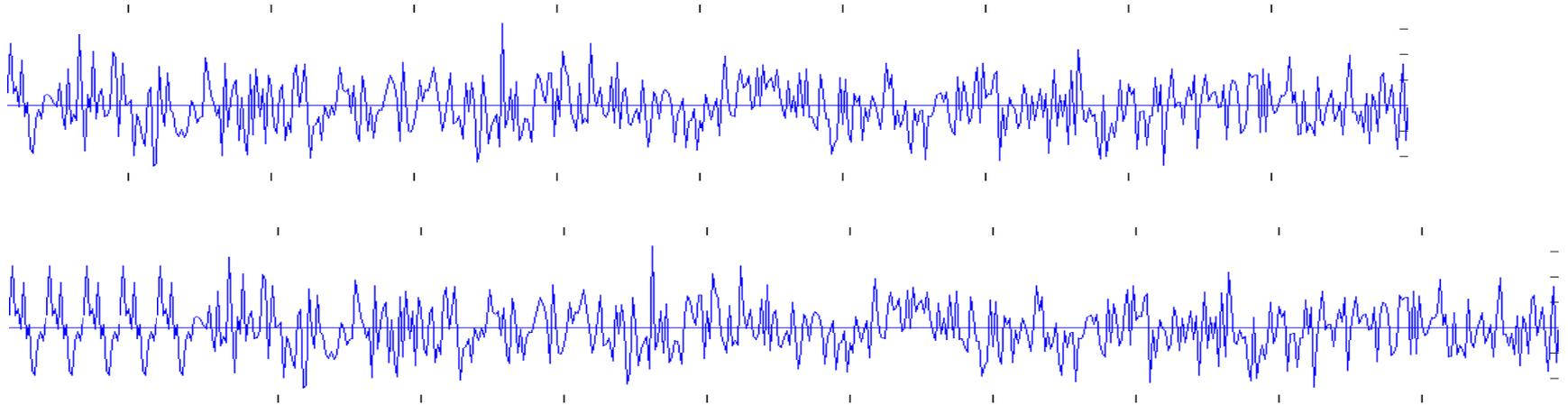


# Autocorrelation

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

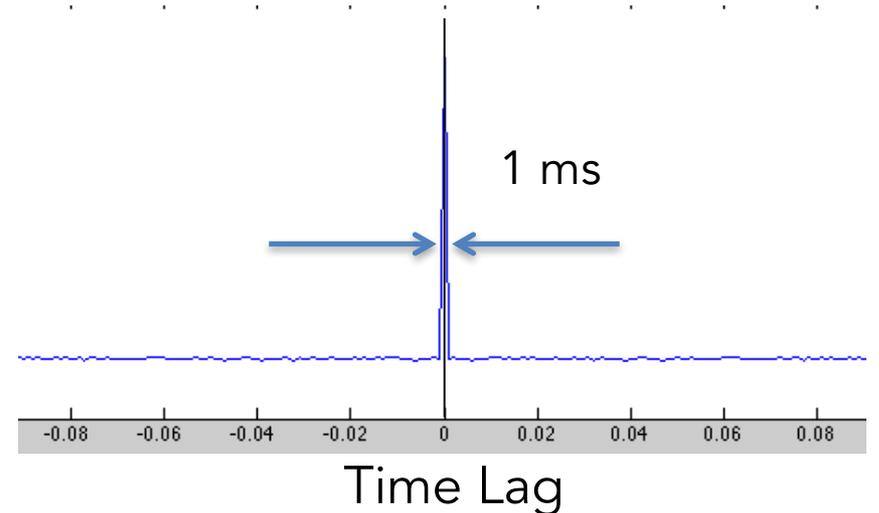
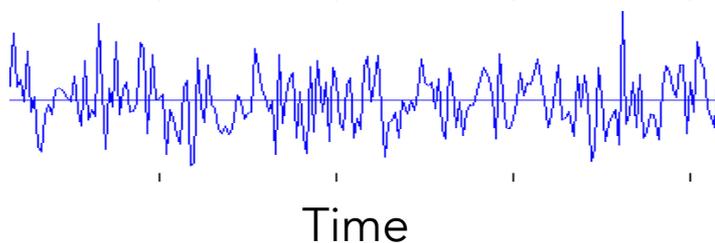
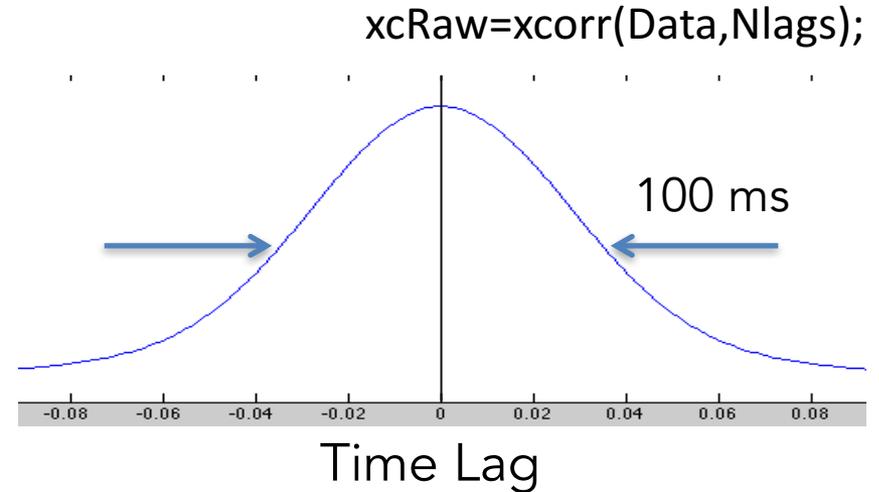
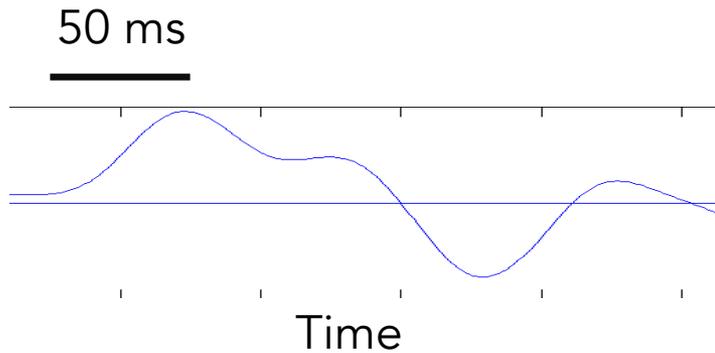
$$K(\tau) = \int_{-\infty}^{\infty} dt x(t)x(t + \tau)$$

50 ms



# Autocorrelation

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

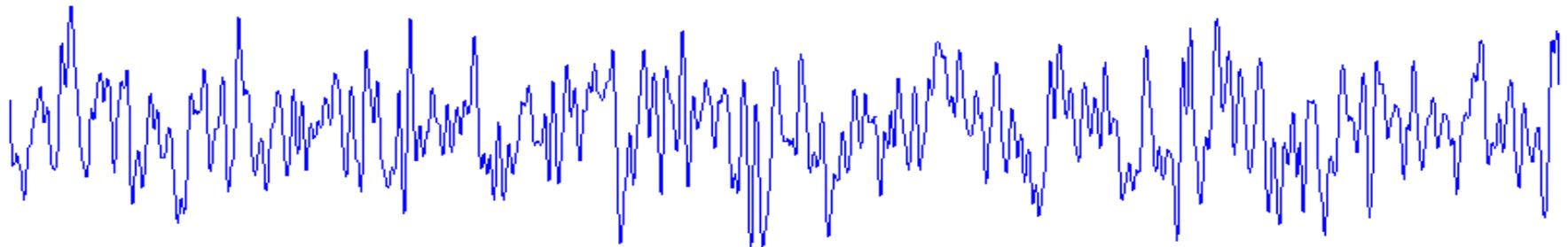


# Autocorrelation

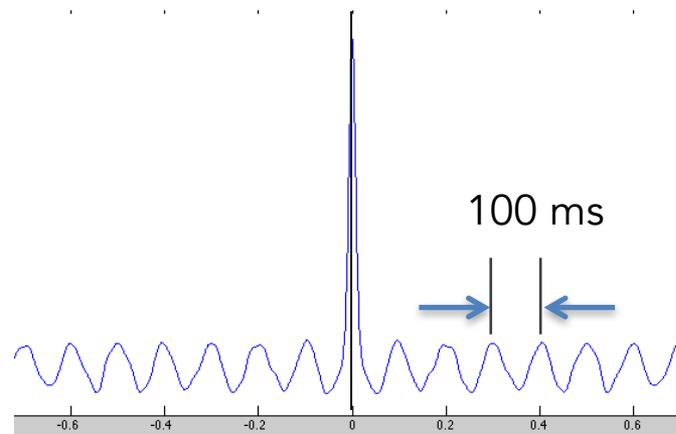
- A way to examine the temporal structure within a signal.

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

50 ms



Time



Time Lag

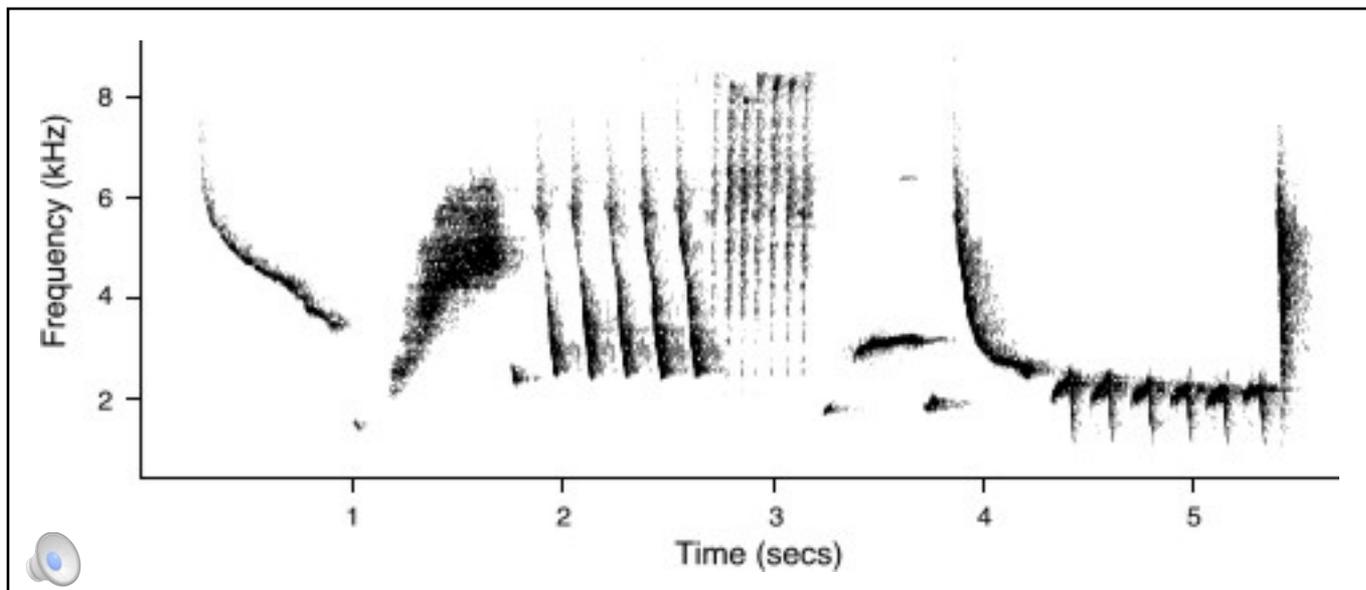
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# Spectral Analysis

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

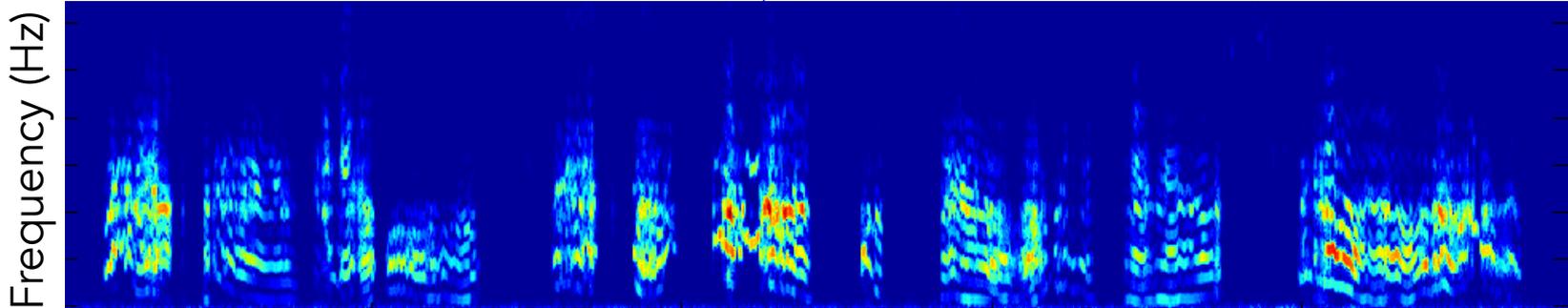
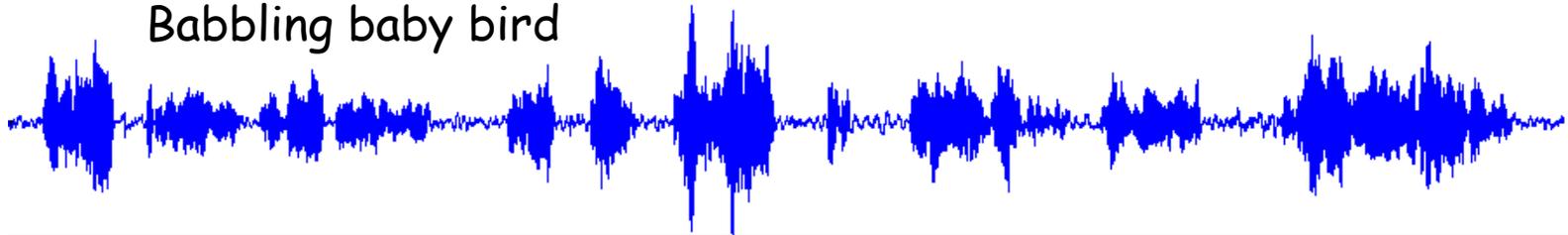
$$S(f, t)$$



# Spectral Analysis



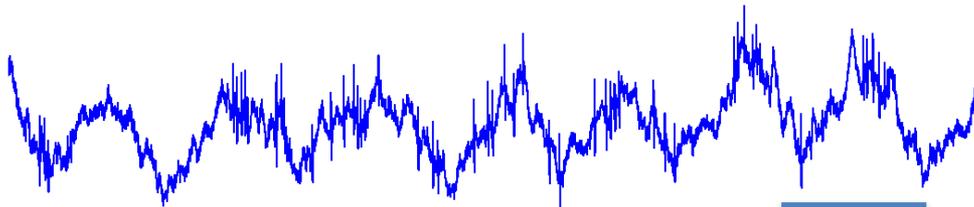
Babbling baby bird



Time

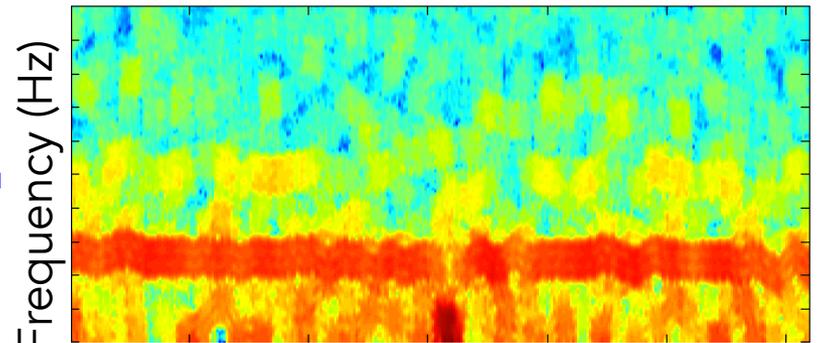
100 ms

Hippocampal theta rhythm



100 ms

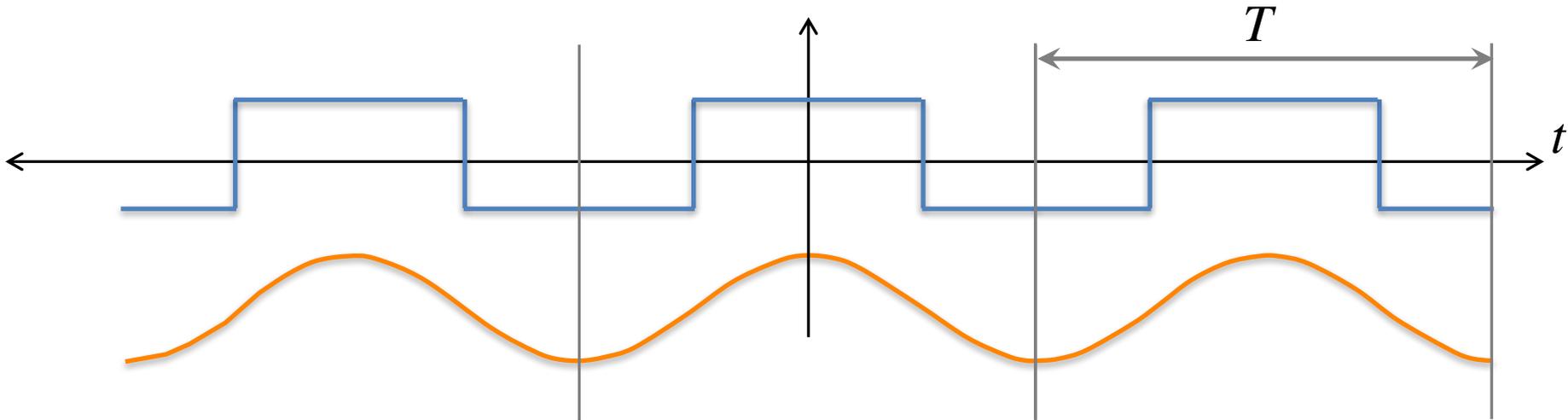
Time



Time

# 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)

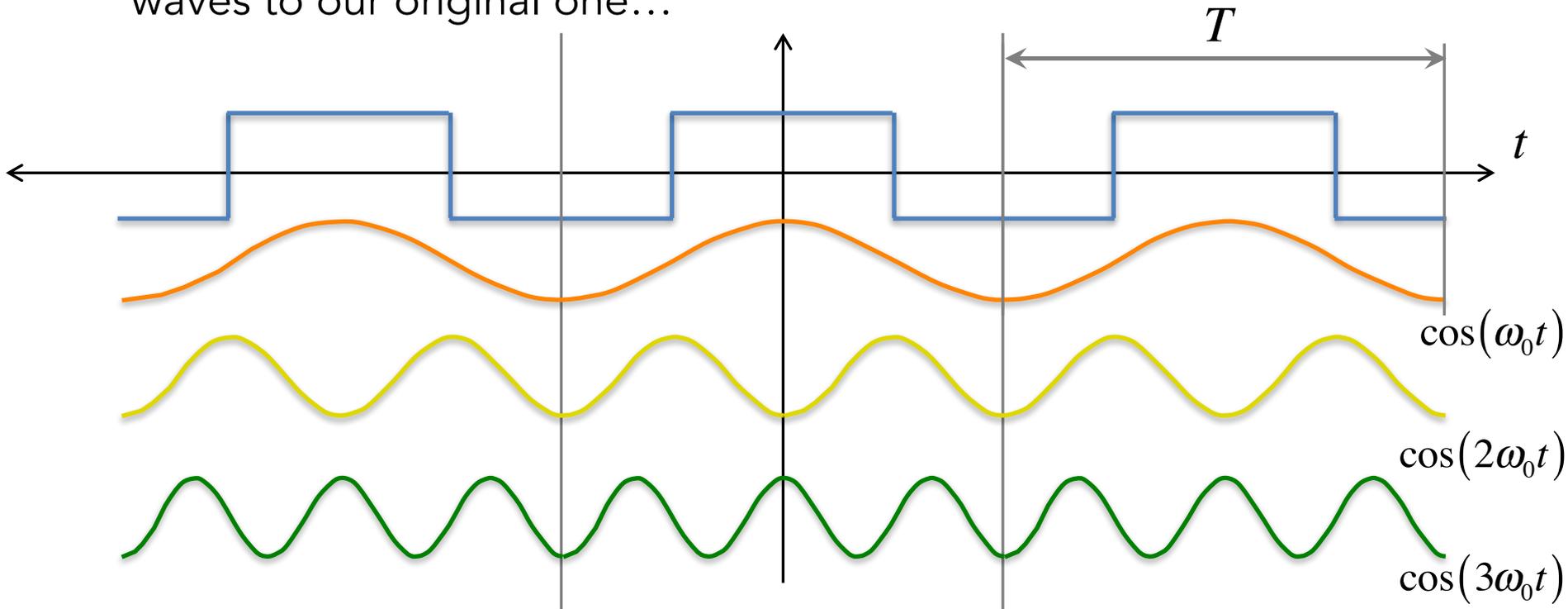
Angular frequency

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

Radians per second

# Fourier Series

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

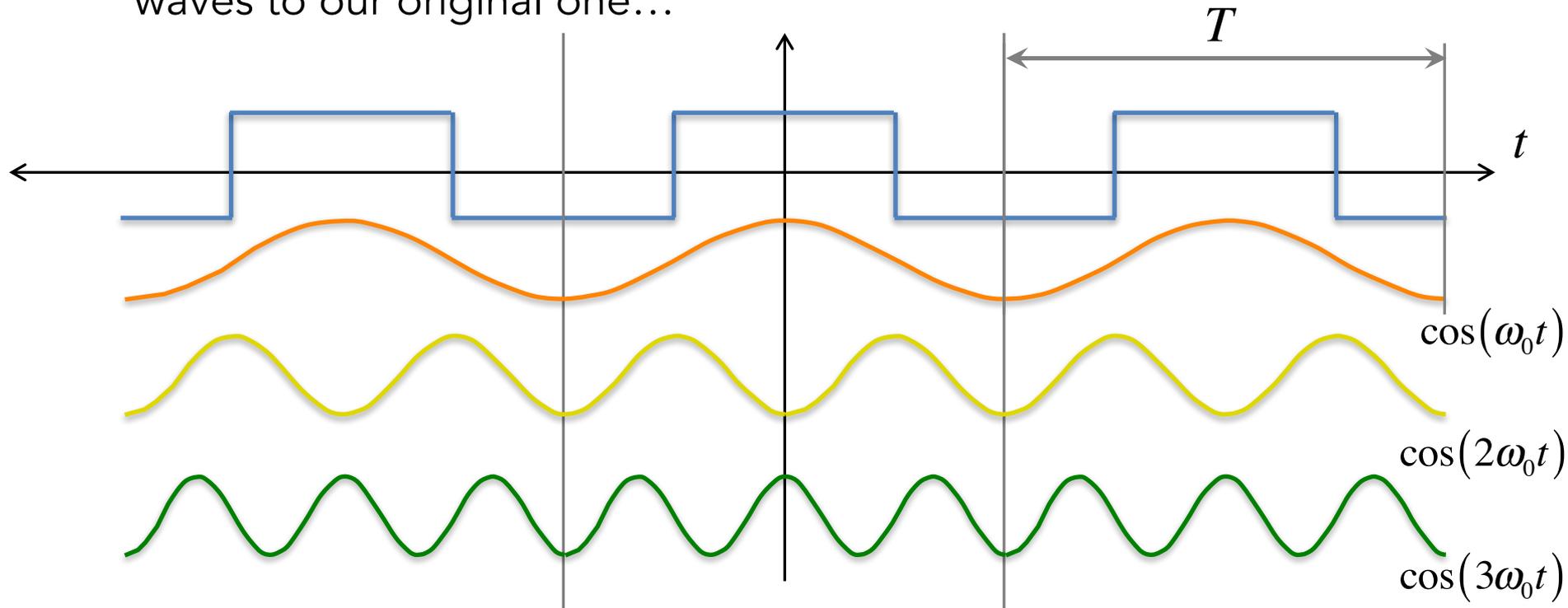


Why can we restrict ourselves to only frequencies that are integer multiples of  $\omega_0$  ?

Because only cosines that are integer multiples of  $\omega_0$  are periodic with a period  $T$ !

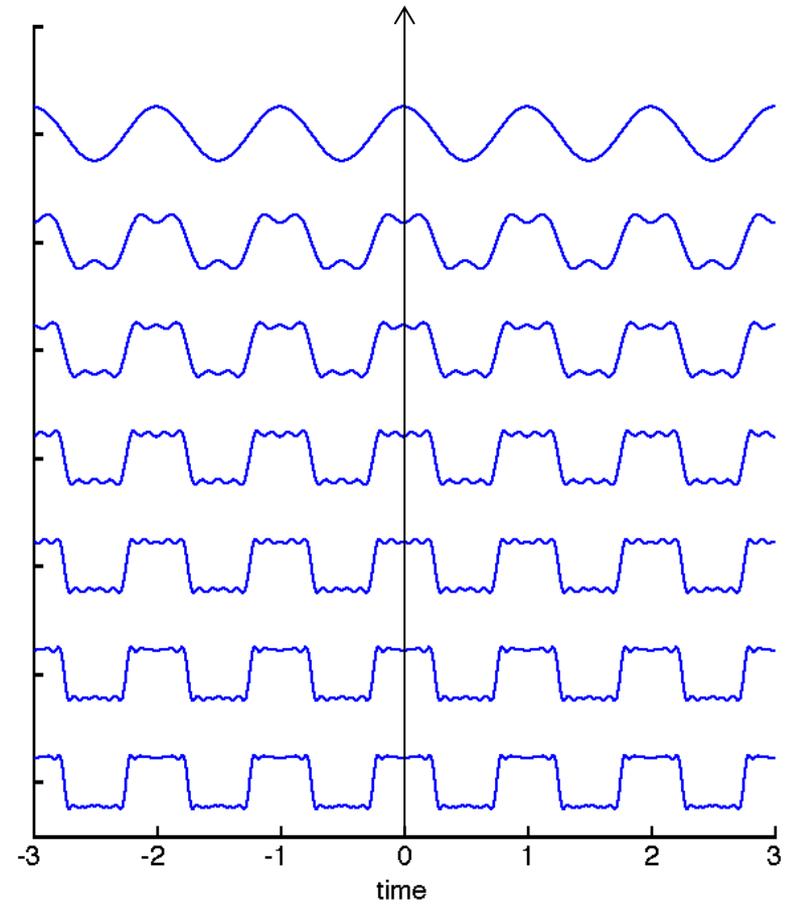
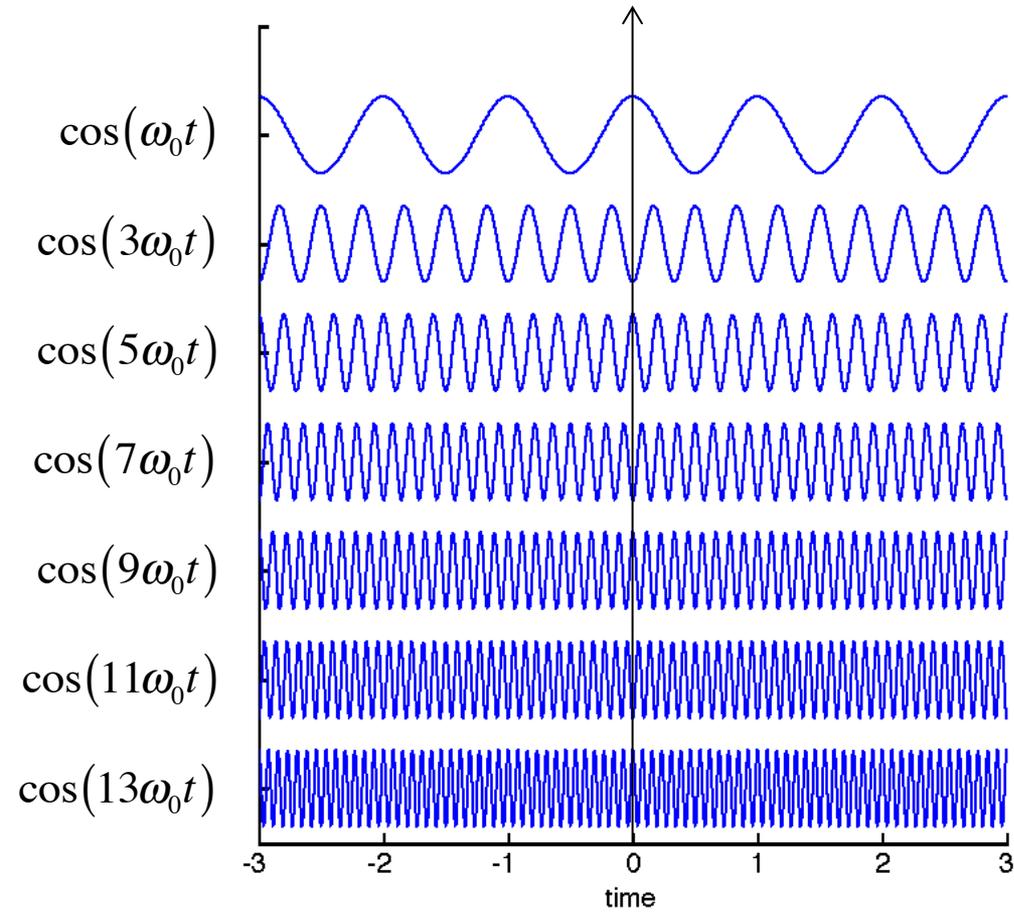
# Fourier Series

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



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

# Fourier Series

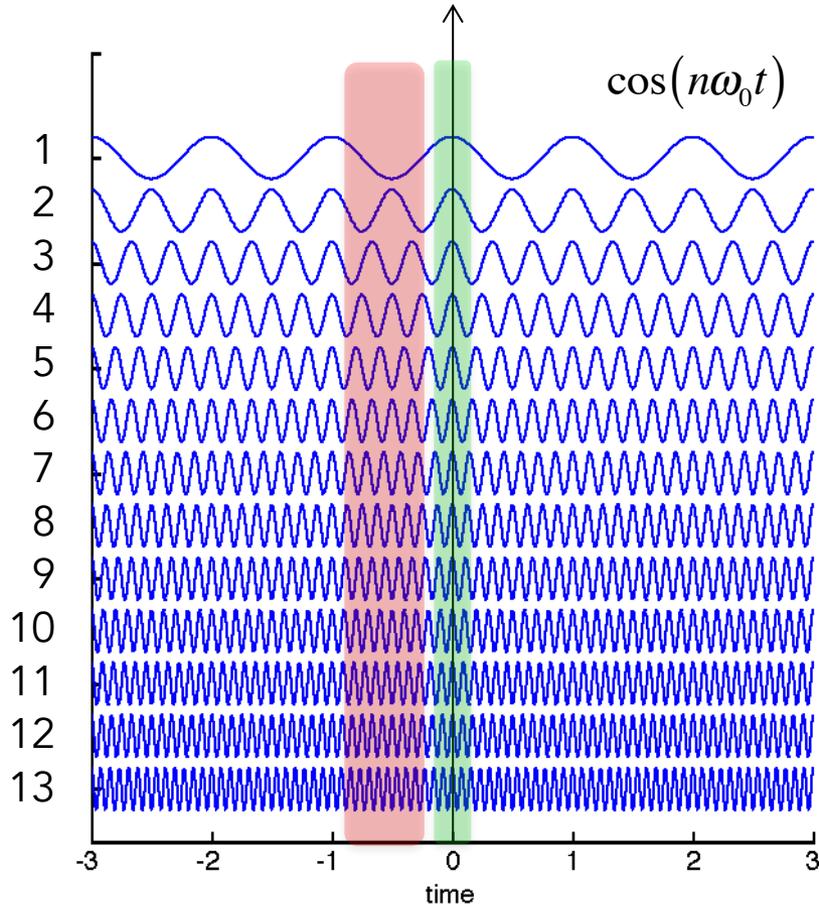


# Fourier Series

destructive  
interference

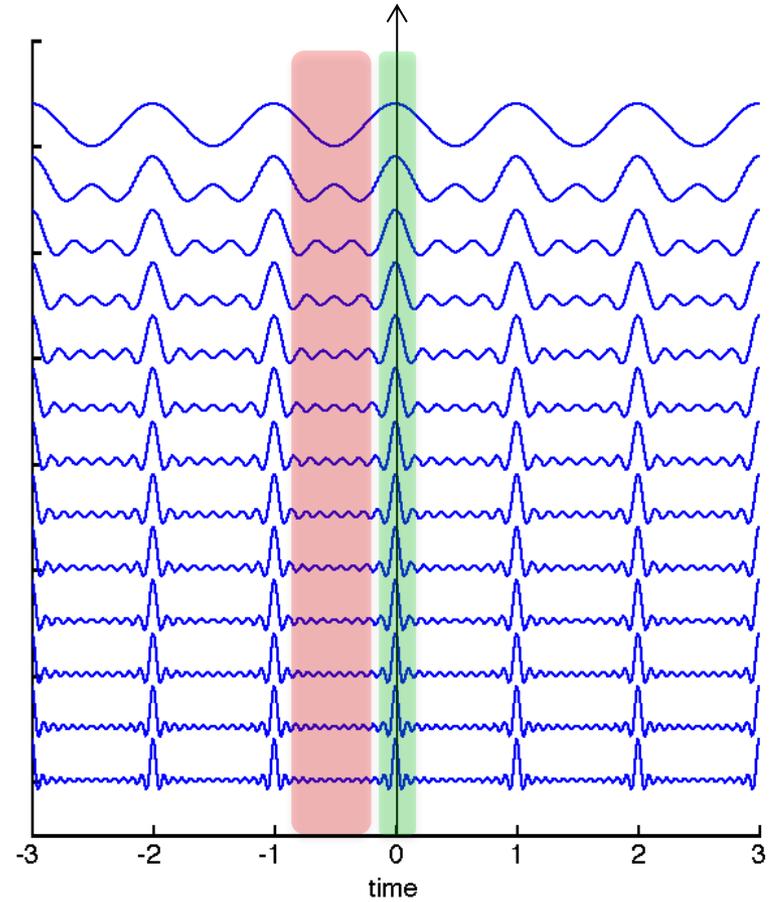
constructive  
interference

$n =$

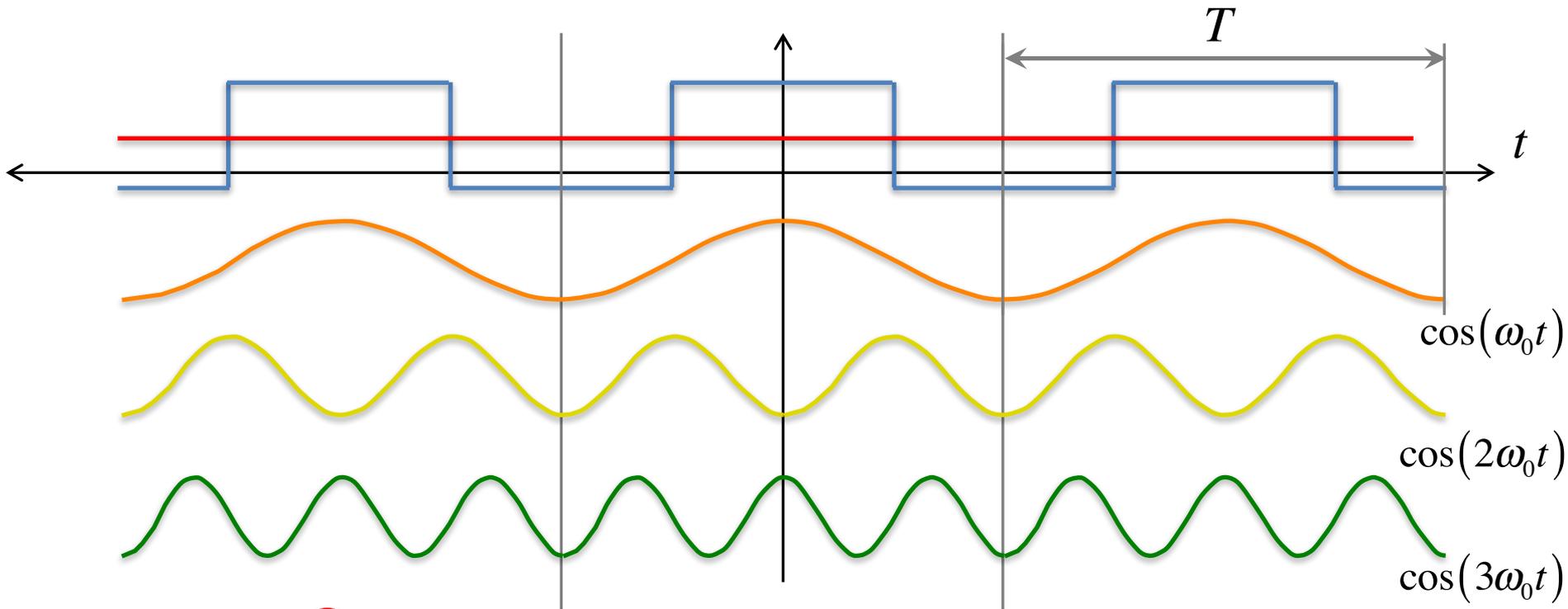


destructive  
interference

constructive  
interference



# Fourier Series



$$y(t) = \frac{a_0}{2} + a_1 \cos(\omega_0 t) + a_2 \cos(2\omega_0 t) + a_3 \cos(3\omega_0 t) + \dots$$

DC term

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

# How do we find the coefficients?

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

$$\frac{a_0}{2} = \frac{1}{T} \int_{-T/2}^{T/2} y(t) dt \quad a_0 = \frac{2}{T} \int_{-T/2}^{T/2} y(t) \cos(0\omega_0 t) dt$$

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

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

- 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?

$$a_0 = \frac{2}{T} \int_{-T/2}^{T/2} y(t) dt \quad a_1 = \frac{2}{T} \int_{-T/2}^{T/2} y(t) \cos(\omega_0 t) dt \quad a_2 = \frac{2}{T} \int_{-T/2}^{T/2} y(t) \cos(2\omega_0 t) dt$$

Consider the following functions  $y(t)$ :

$$y(t) = 1$$

$$a_0 = 2$$

$$a_1 = 0$$

$$a_2 = 0$$

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

$$a_0 = 0$$

$$a_1 = 1$$

$$a_2 = 0$$

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

$$a_0 = 0$$

$$a_1 = 0$$

$$a_2 = 1$$

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

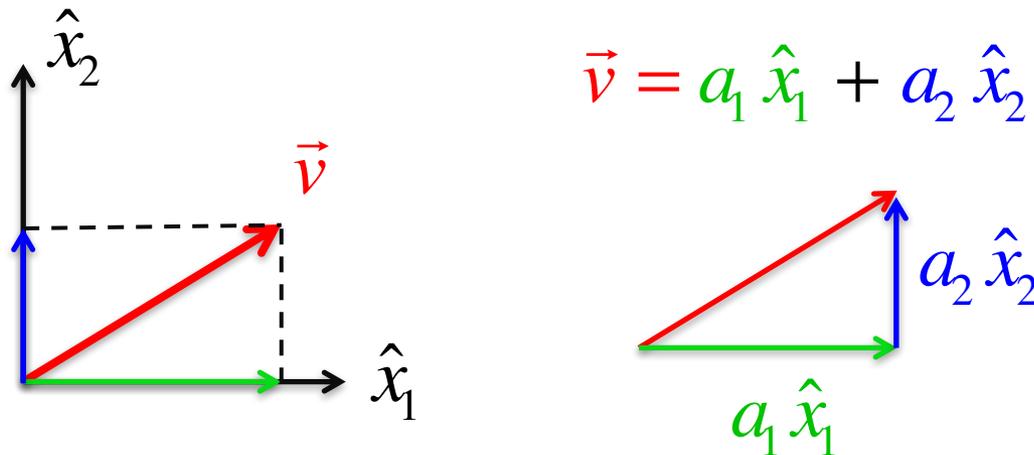
$$\int_{-T/2}^{T/2} \cos(\omega_0 t) \cos(2\omega_0 t) dt = 0$$

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

# 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...

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



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

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

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

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

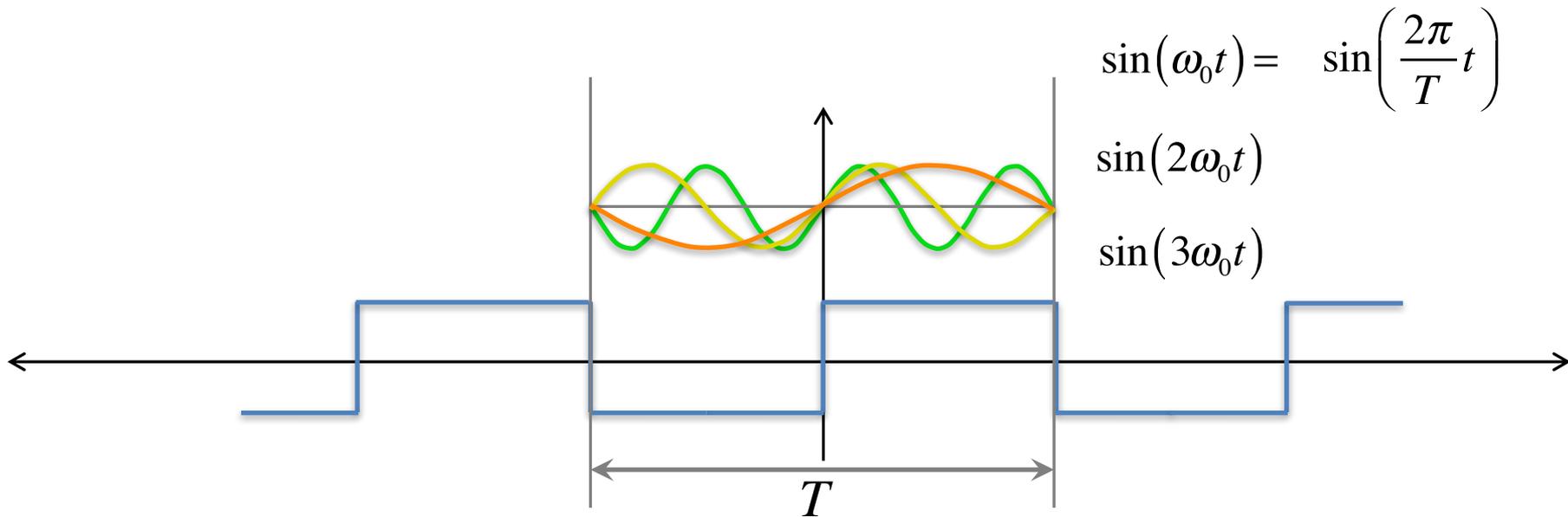
How do we find the coefficients  $a_1$  and  $a_2$ ?

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

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

# 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.

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

# Complex Fourier Series

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

Euler's formula

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

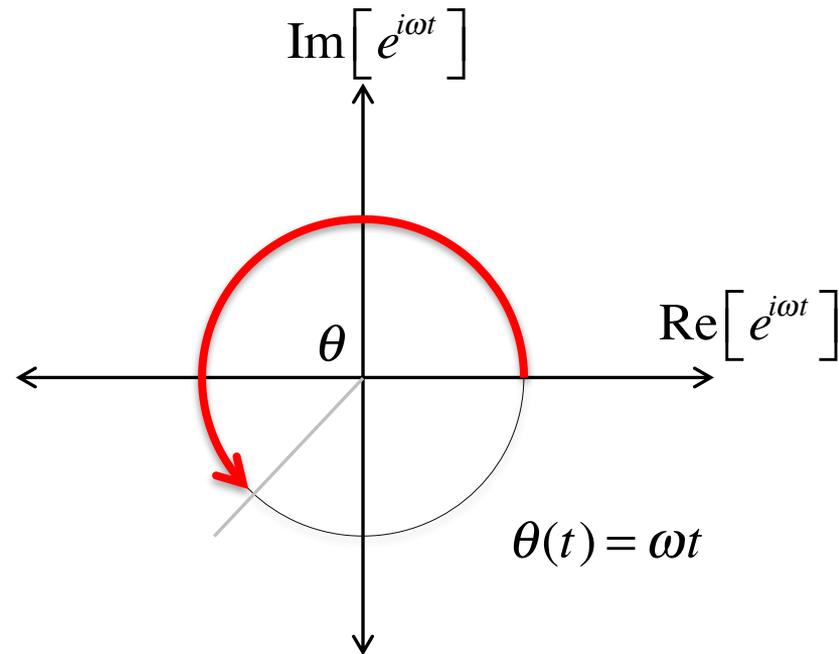
$$e^{-i\omega t} = \cos \omega t - i \sin \omega t$$

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

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

$$y(t) = \frac{a_0}{2} + \sum_{n=1}^{\infty} \frac{a_n}{2} (e^{in\omega_0 t} + e^{-in\omega_0 t}) + \sum_{n=1}^{\infty} \frac{-ib_n}{2} (e^{in\omega_0 t} - e^{-in\omega_0 t})$$

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

'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  $n = 0$ ,

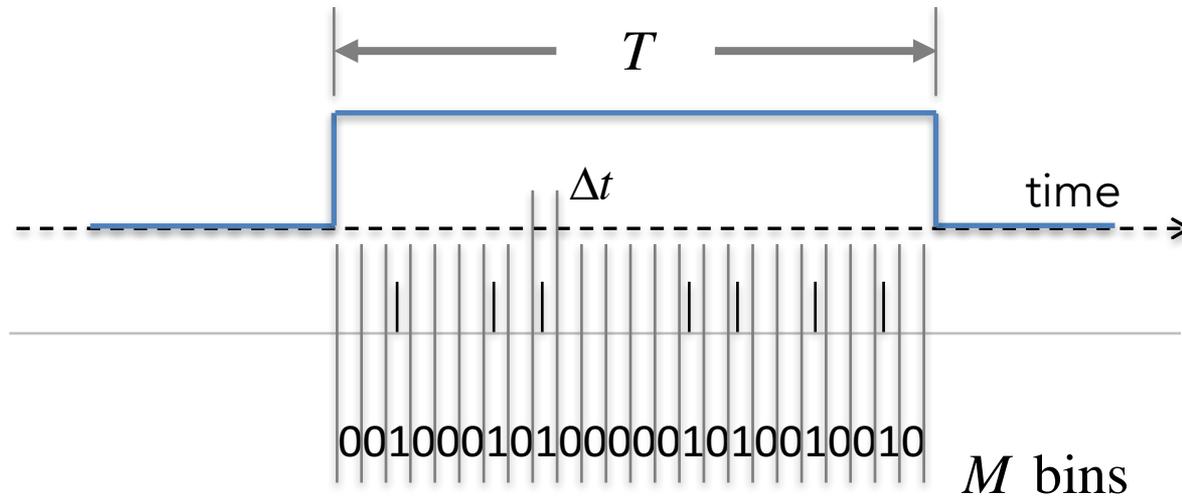
$$e^{in\omega_0 t} = e^0 = 1$$

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

# 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  $\Delta t \rightarrow 0$ :  $M = \frac{T}{\Delta t} \rightarrow \infty$        $M - n \simeq M$

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

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

# 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  $M \rightarrow \infty$ :

$n$  terms

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

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

Poisson distribution!

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

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9.40 Introduction to Neural Computation  
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