Rhythms

A "simple" model for the organization of brain rhythms

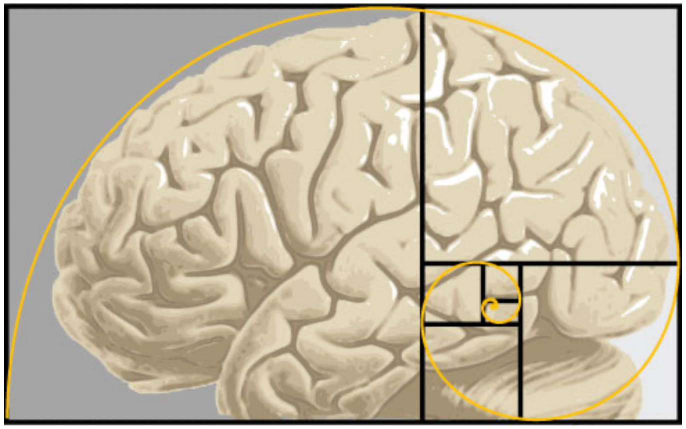
Instructor: Mark Kramer

Outline

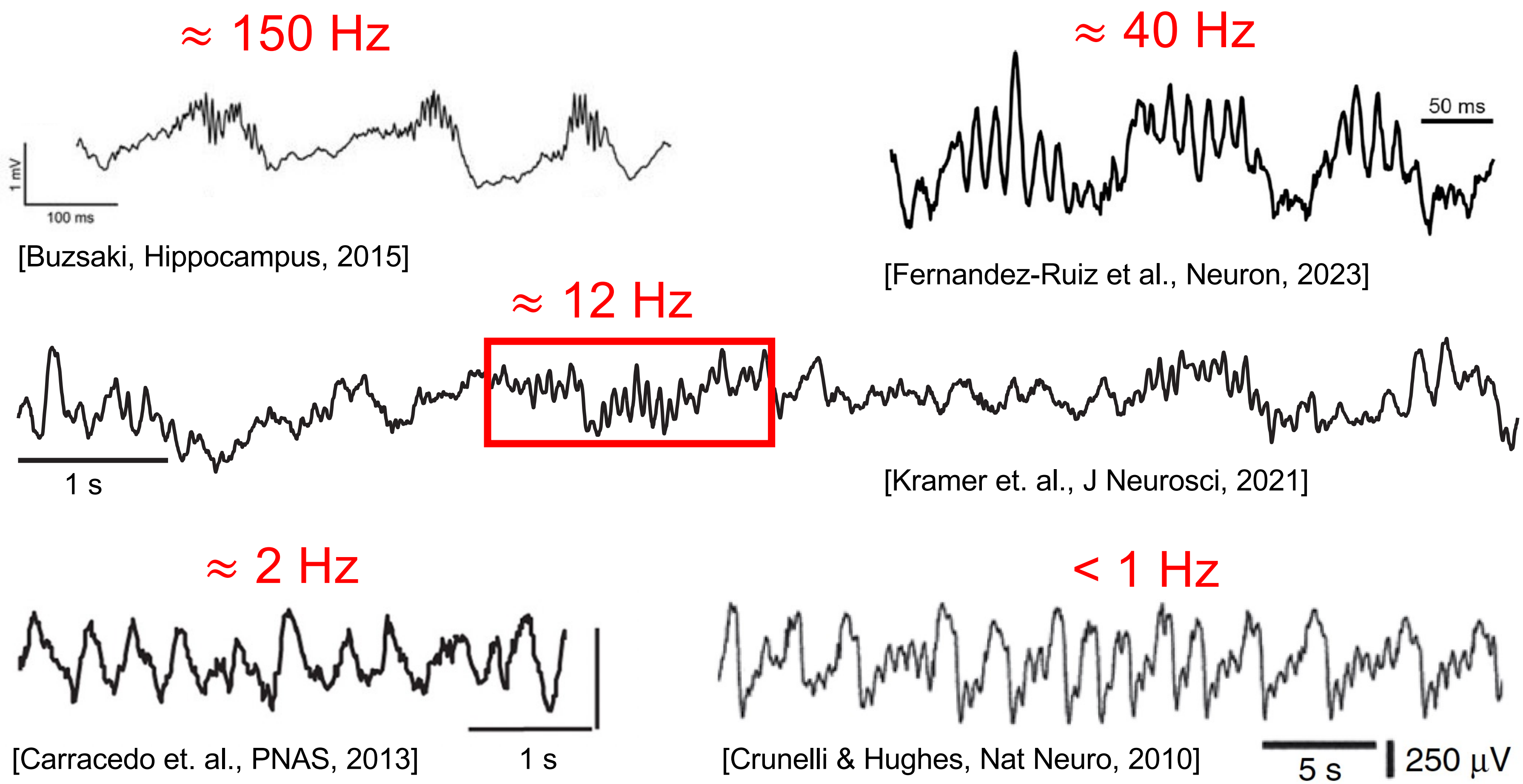
Brain rhythm facts

A big question

A proposed answer ...



1. Brain activity ... is rhythmic.



[Buzsaki, Hippocampus, 2015]

[Fernandez-Ruiz et al., Neuron, 2023]

[Kramer et. al., J Neurosci, 2021]

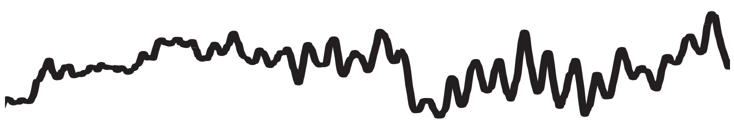
[Carracedo et. al., PNAS, 2013]

[Crunelli & Hughes, Nat Neuro, 2010]

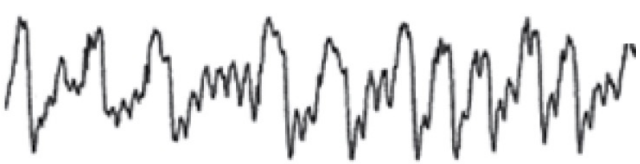
2. Brain rhythms ... appear in discrete bands.

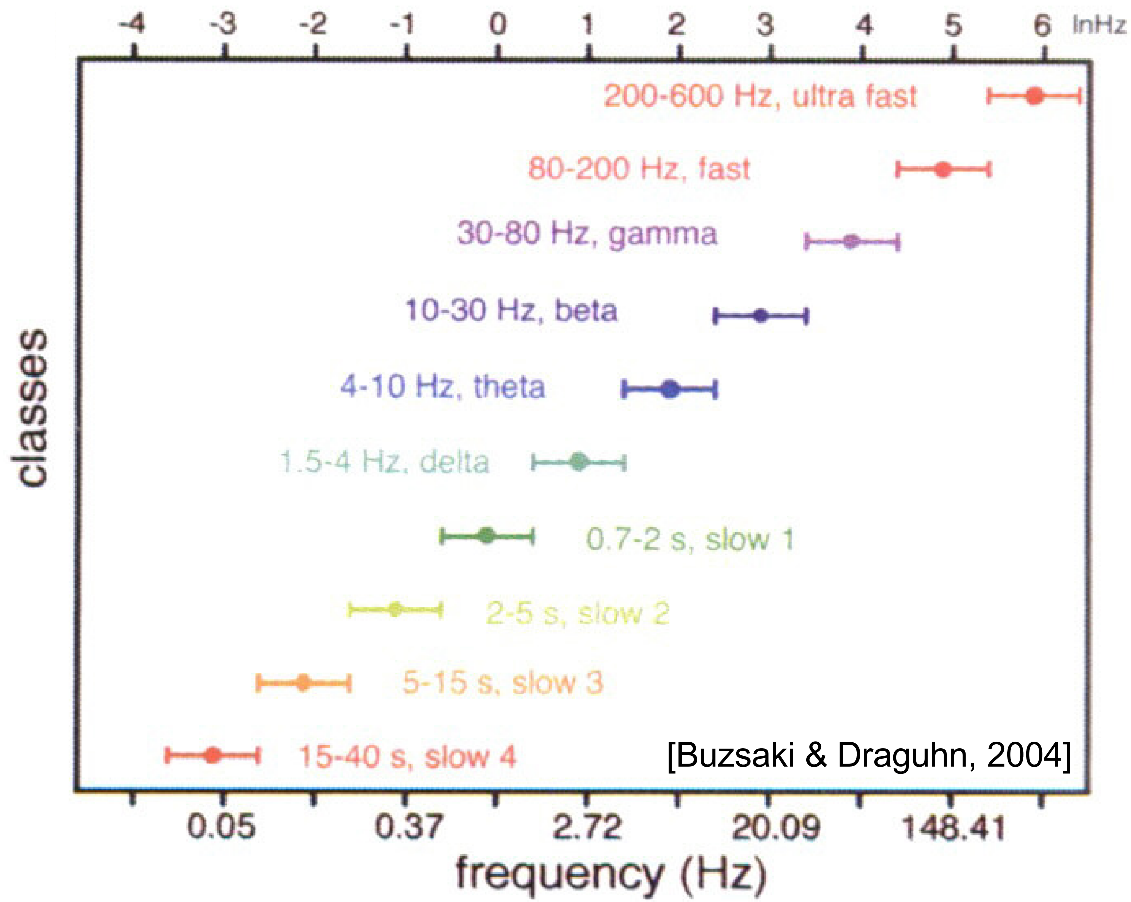
Fast

Intermediate



Slow

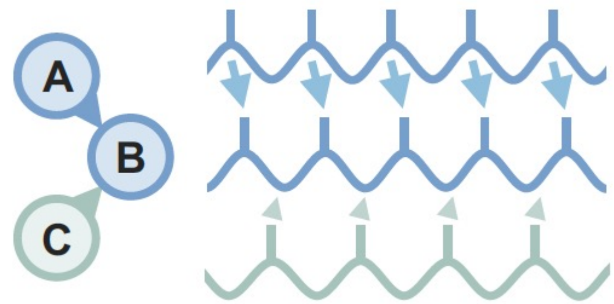




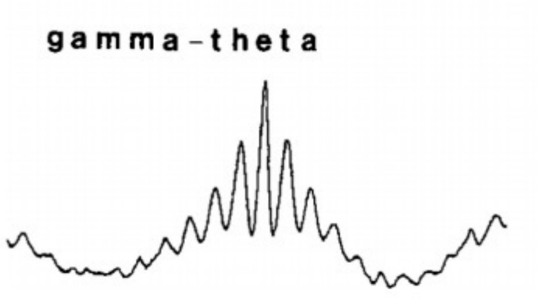
Consistent across individuals, mammalian species

3. Brain rhythms ... do something.

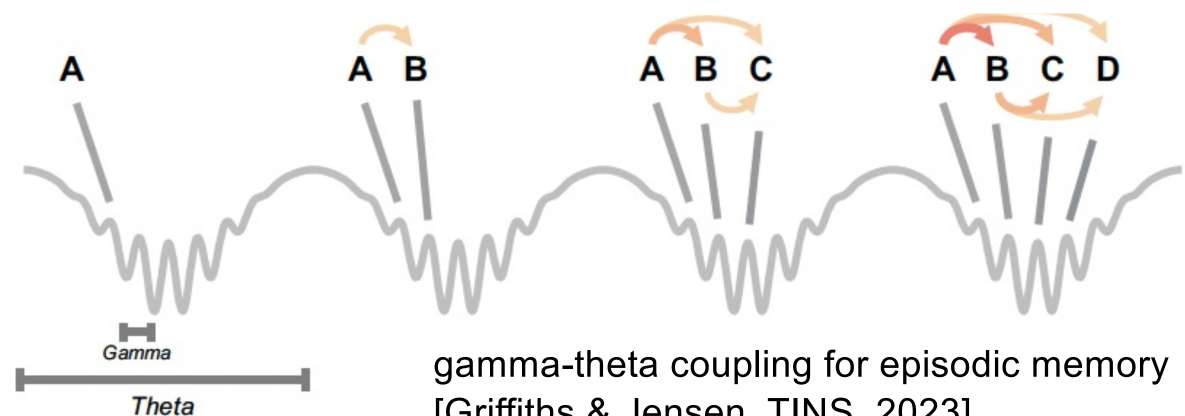
theta phase: [Buzsaki & Moser, 2013]



gamma-based communication
[Griffiths & Jensen, TINS, 2023]



[Colgin J Neurosci, 2019]



gamma-theta coupling for episodic memory
[Griffiths & Jensen, TINS, 2023]

So ...

Rhythms exist - in discrete bands - and do something.

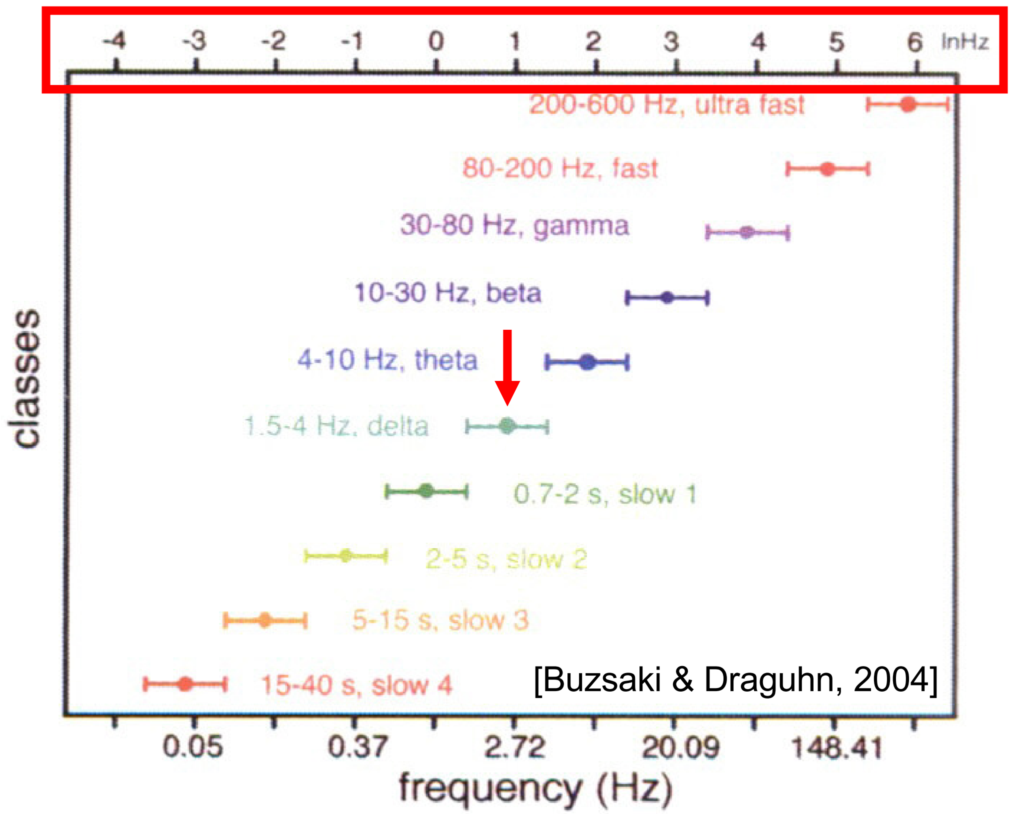
Big question: Why discrete bands? Why not a continuum of rhythms?

What's the spacing between discrete frequency bands?

Three proposed theories ...

Spacing between frequency bands

(i) Logarithmic



[Buzsaki & Draguhn, 2004]

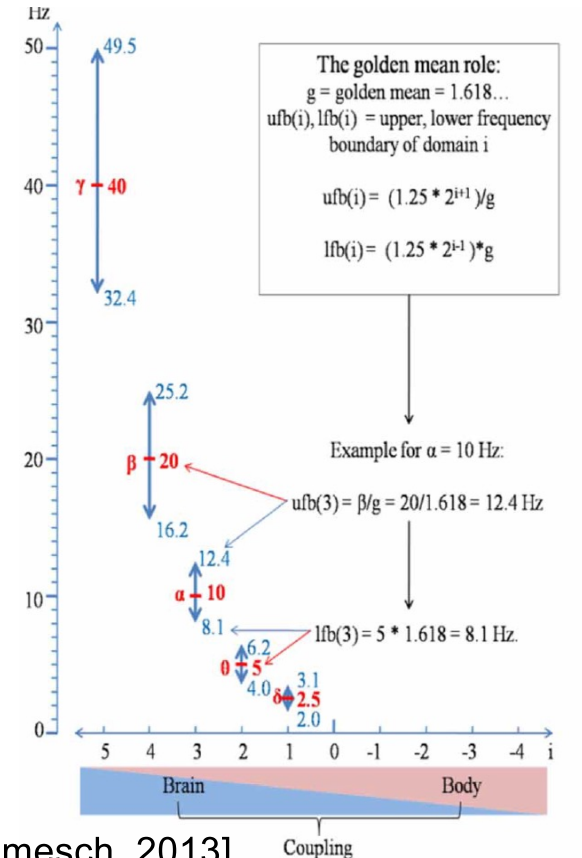
f_k = center frequency of band k

$$\frac{f_k}{f_{k-1}} = e$$

"*discrete oscillation bands form... a linear progression on a natural logarithmic scale*"
[Penttonen, Buzsaki 2003]

Spacing between frequency bands

(ii) Factor of 2



[Klimesch, 2013]

f_k = center frequency of band k

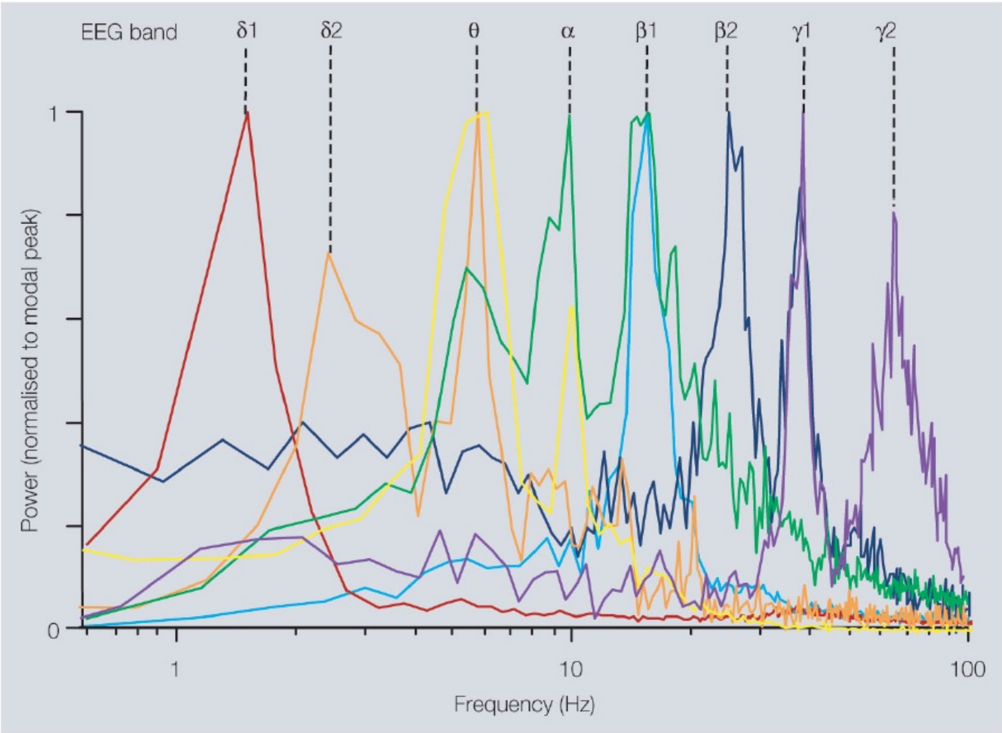
$$\frac{f_k}{f_{k-1}} = 2$$

Harmonic cross-frequency ratios (e.g., 2:1) <u>support phase synchrony</u> between different rhythms.

[Rodriguez-Larios, Alaerts, 2020]

Spacing between frequency bands

(iii) Golden ratio



[Roopun et al., 2008]

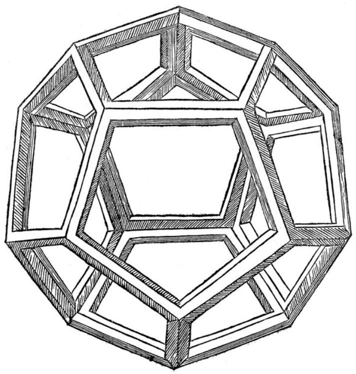
f_k = center frequency of band *k*

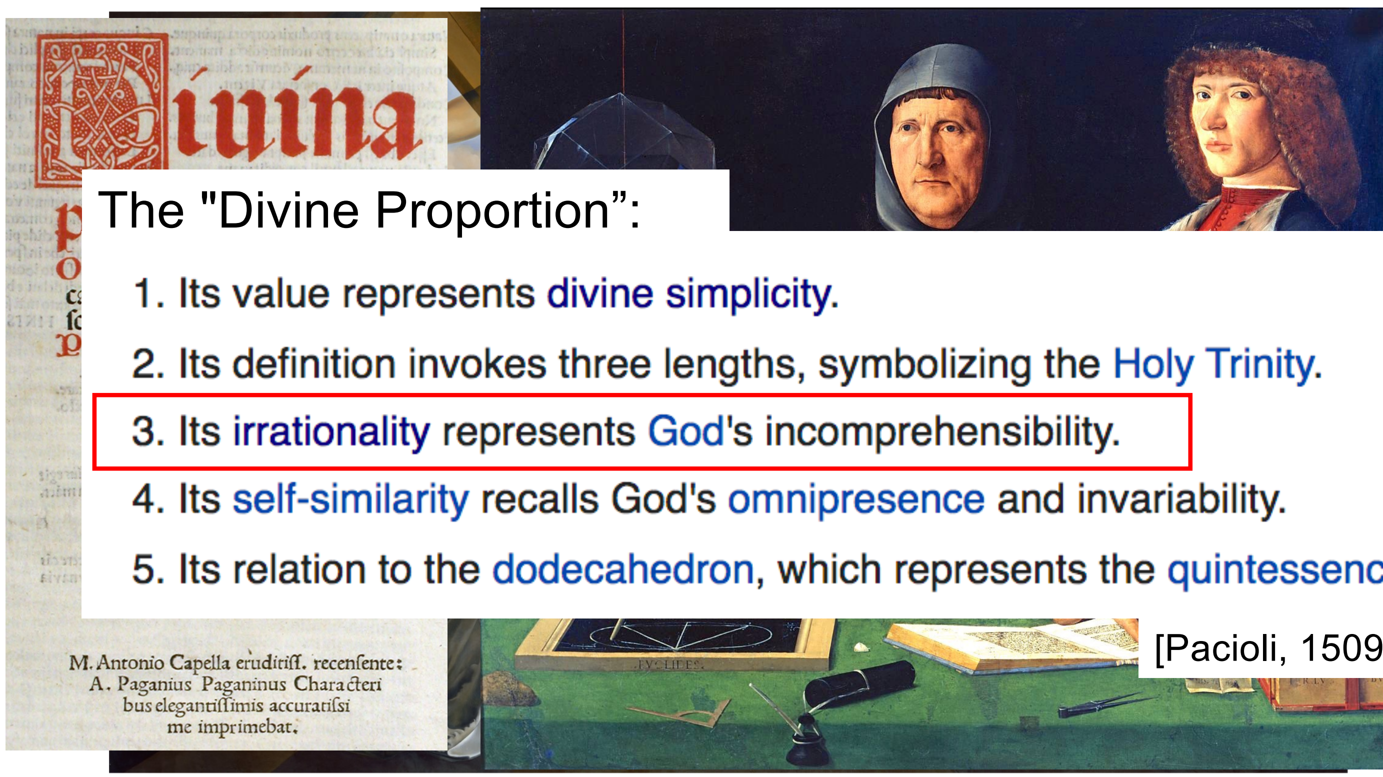
$$\frac{f_k}{f_{k-1}} = \phi$$

"... *in neocortex the ratio of adjacent frequency bands is approximately phi*"
[Roopun et al., 2004]

Golden ratio, ϕ

$$\frac{a+b}{a} = \frac{a}{b} = \phi = \frac{1+\sqrt{5}}{2} = 1.618\ldots$$





The "Divine Proportion”:

1. Its value represents divine simplicity.
2. Its definition invokes three lengths, symbolizing the Holy Trinity.
3. Its irrationality represents God's incomprehensibility.
4. Its self-similarity recalls God's omnipresence and invariability.
5. Its relation to the dodecahedron, which represents the quintessence

[Pacioli, 1509]

Golden ratio, ϕ

$$\frac{a+b}{a} = \frac{a}{b} = \phi = \frac{1+\sqrt{5}}{2} = \boxed{1.618\ \ldots}$$

Note: Related to the Fibonacci sequence

$$F_{n+1} = F_n + F_{n-1} \qquad \frac{F_n}{F_{n-1}} \approx \phi$$

F_1	F_2	F_3	F_4	F_5	F_6	F_7	F_8	F_9	F_{10}
1	1	2	3	5	8	13	21	34	55

Golden rhythms

<u>Best example</u>: beta1 (15 Hz), beta2 (25 Hz), and gamma (40 Hz)

$$\frac{40\ \text{Hz}}{25\ \text{Hz}} \approx \frac{25\ \text{Hz}}{15\ \text{Hz}} \approx 1.6 \approx \phi$$

Note: $15\ \text{Hz} + 25\ \text{Hz} = 40\ \text{Hz}$

$65\ \text{ms} = 40\ \text{ms} + 25\ \text{ms}$

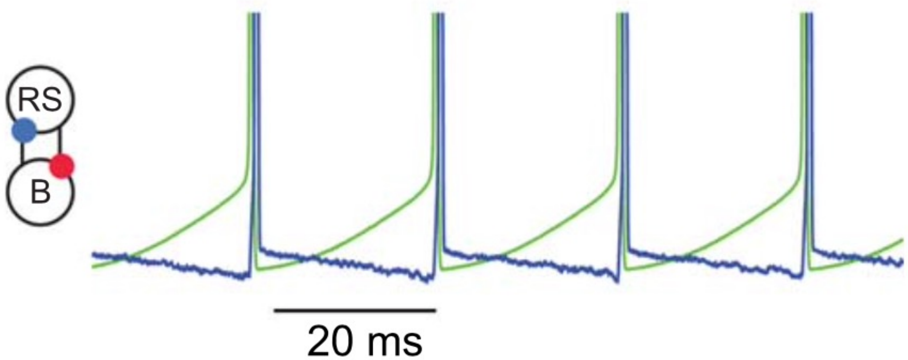
<u>Mechanism</u>:

Rhythm generation through period concatenation

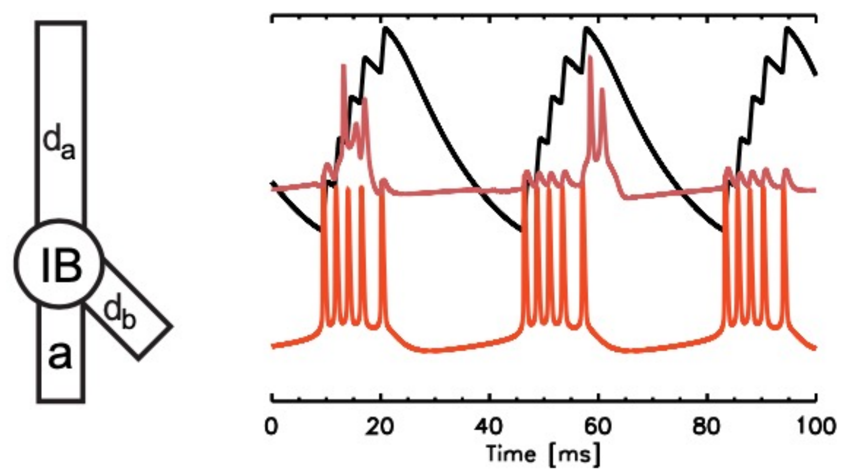
[Roopun et al., 2008a; Roopun et al., 2008b; Kramer et al., 2008]

Golden rhythms: HH-type model

Gamma rhythm model



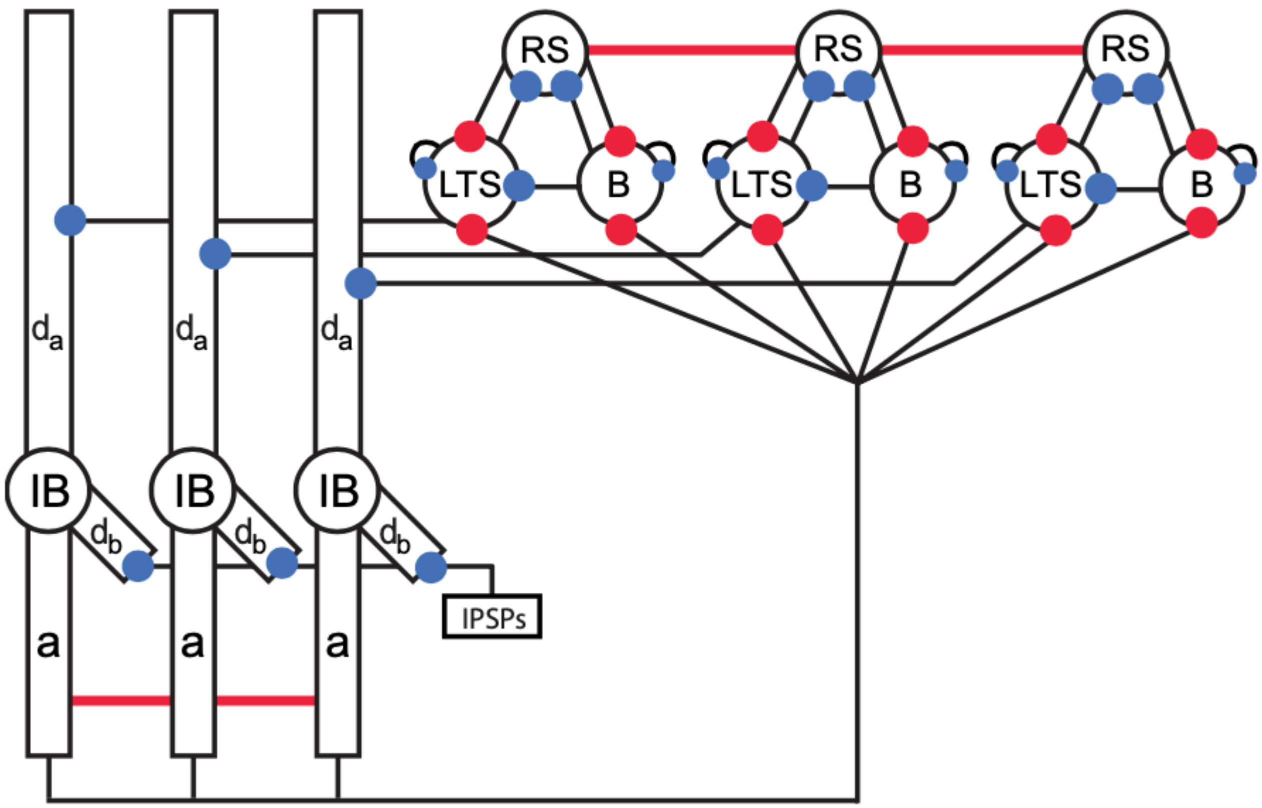
Beta rhythm model



[Kramer et al., PLOS Comp Bio, 2008]

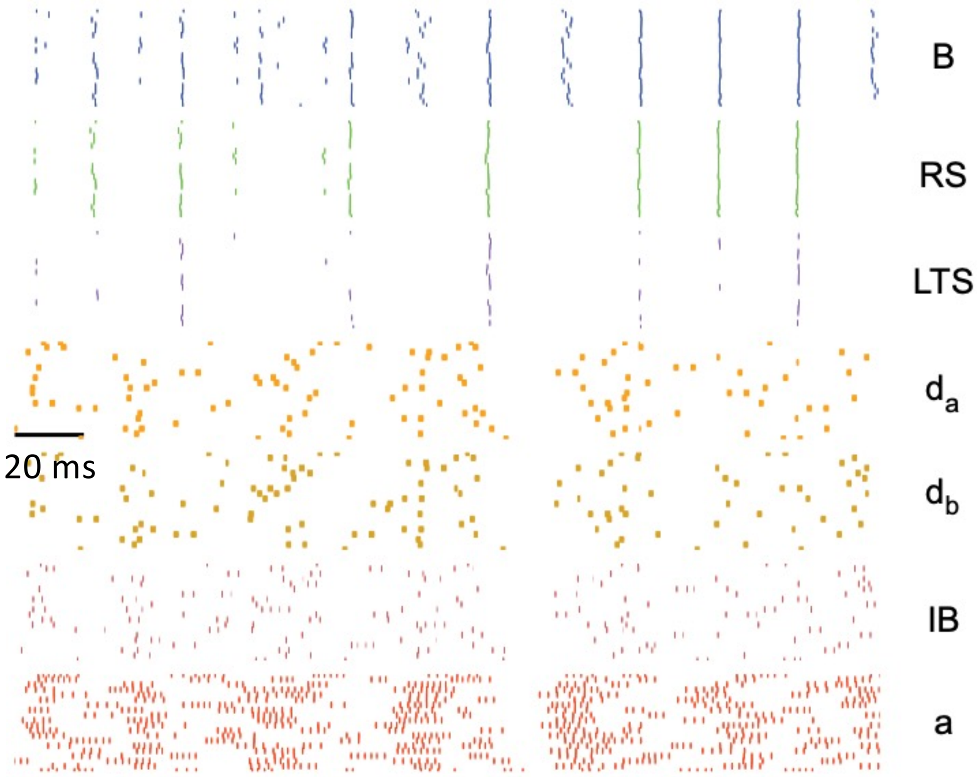
Combine them ...

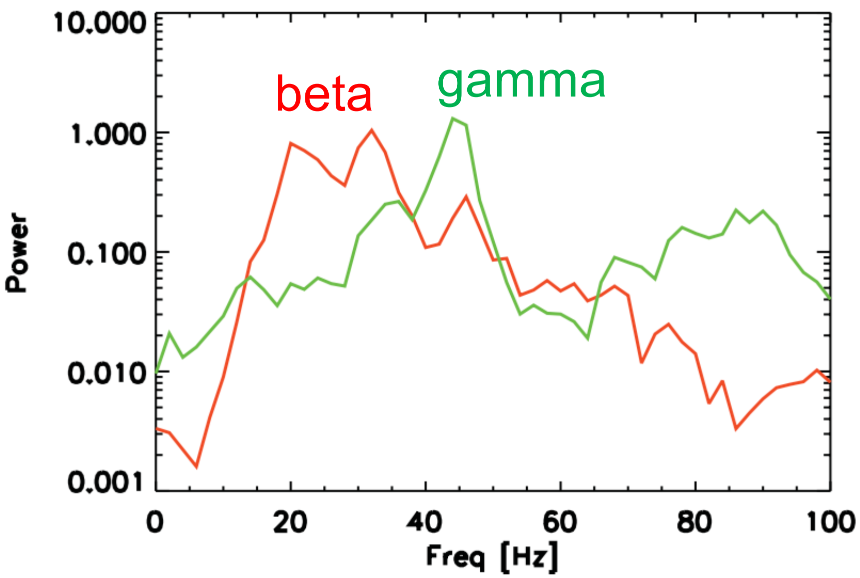
Golden rhythms: HH-type model



Golden rhythms: HH-type model

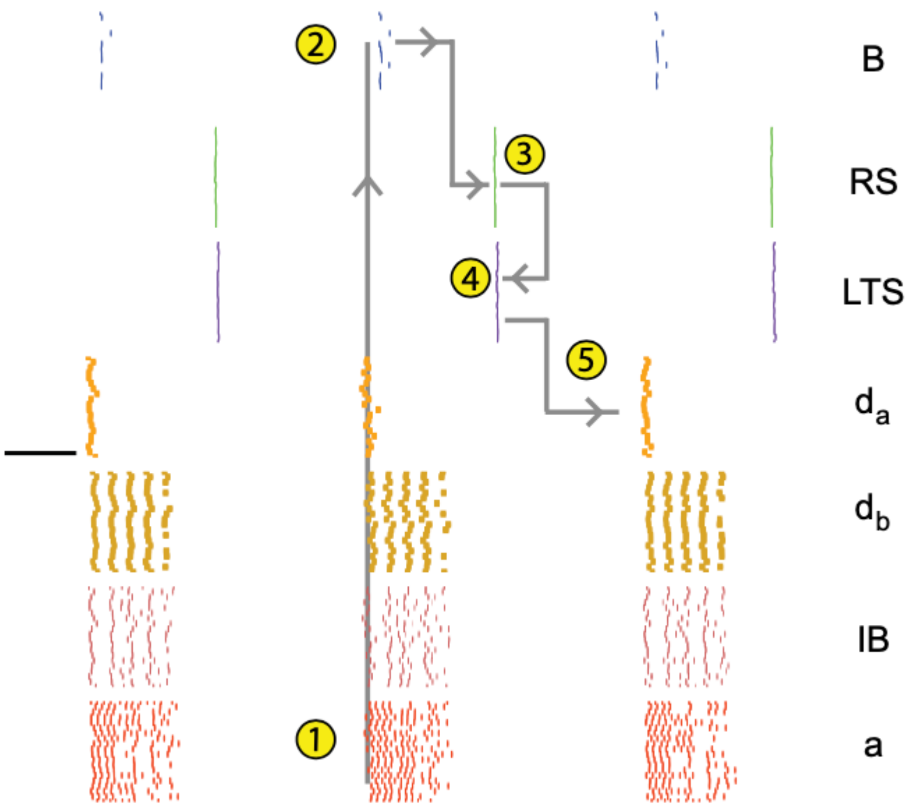
High excitability

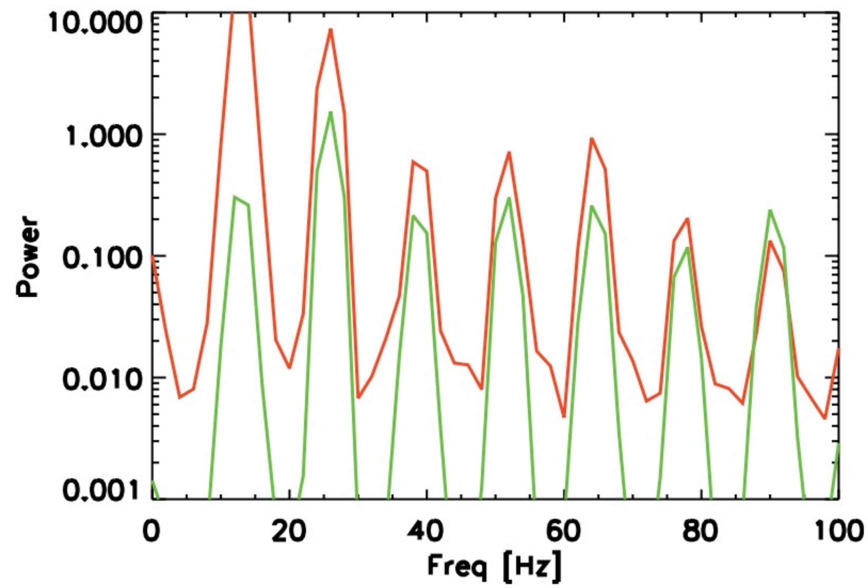




Golden rhythms: HH-type model

Low excitability

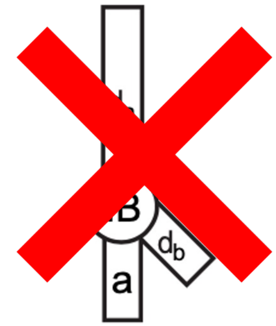




“rhythm generation through period concatenation”

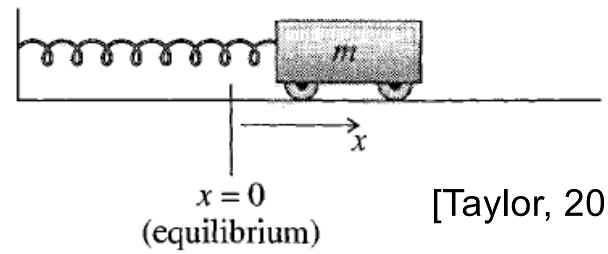
Neural model

Can be complicated:



Simple model of neural population activity

... a damped, driven oscillator



[Taylor, 2005]

Why?

spring: restorative mechanisms about a stable equilibrium

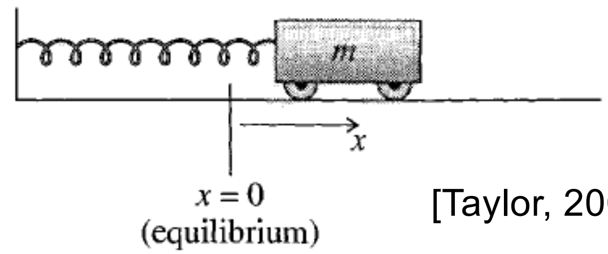
damping: produces transient oscillations

equivalent to an AR(2), reasonable model of brain rhythms (gamma)

[Spyropoulos et al, Nat Comm, 2022]

Damped-driven oscillator

Equations



[Taylor, 2005]

$$\ddot{x} + 2\beta\dot{x} + \omega^2 x = F$$

damping or friction   spring   forcing

$$\omega = 2\pi f$$

f = natural frequency of the spring

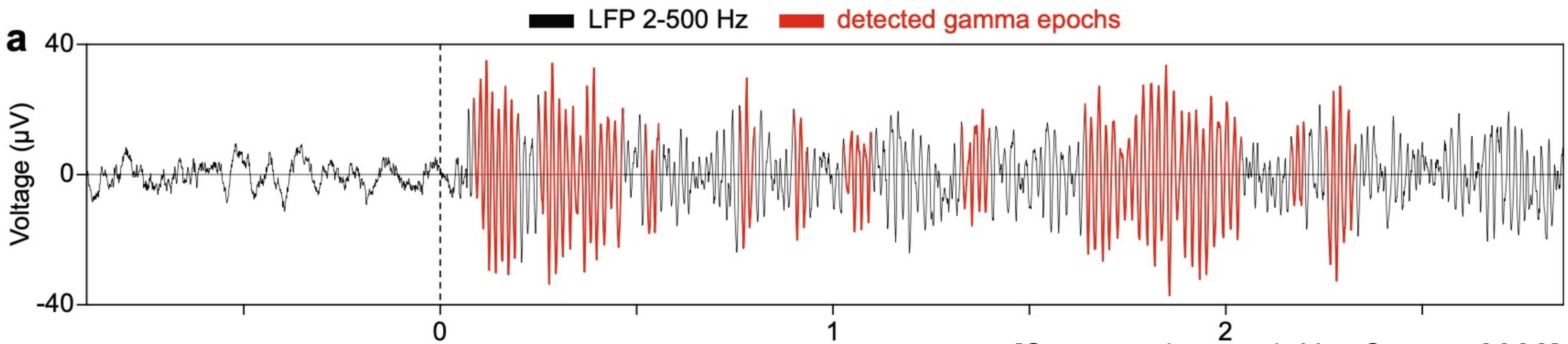
<u>Note</u>: Can be expressed as an autoregressive model of order 2 or AR(2)

Damped-driven oscillator

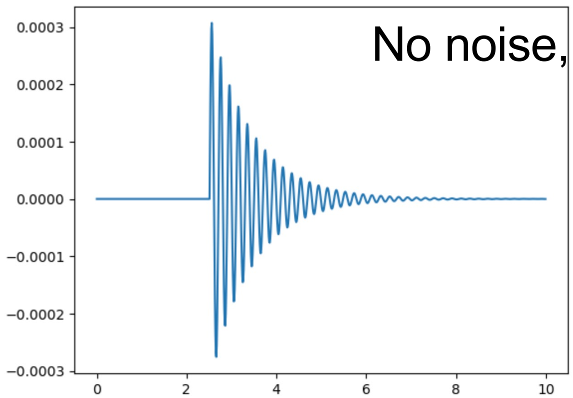
Simulate it

Python

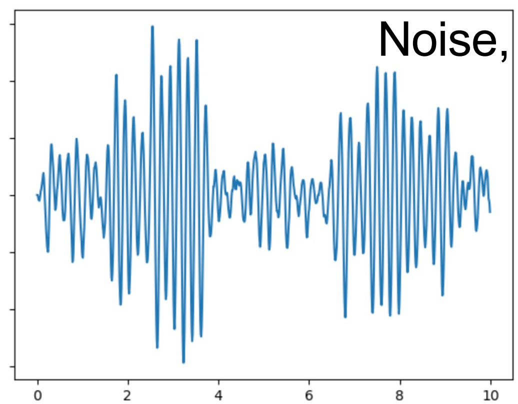
Damped-driven oscillator



[Spyropoulos et al, Nat Comm, 2022]

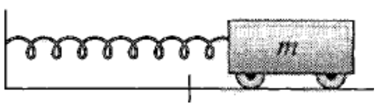


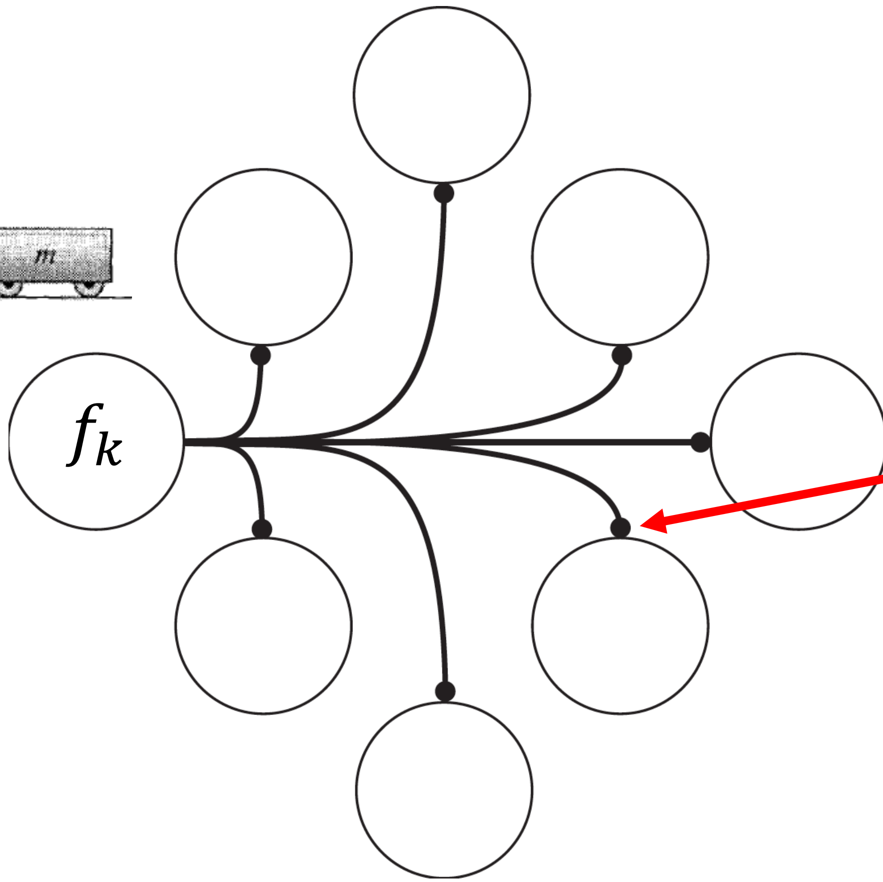
No noise, strong kick



Noise, strong kick

Network of damped, driven oscillators





Coupling is all-to-all

Connection strength is **modulated**

Connectivity

Gain modulation

Connection strength $(\bar{g}_C + \boxed{\bar{g}_S \cos \omega_S t})$

Constant $\bar{g}_C$

Modulated $\bar{g}_S \cos \omega_S t$

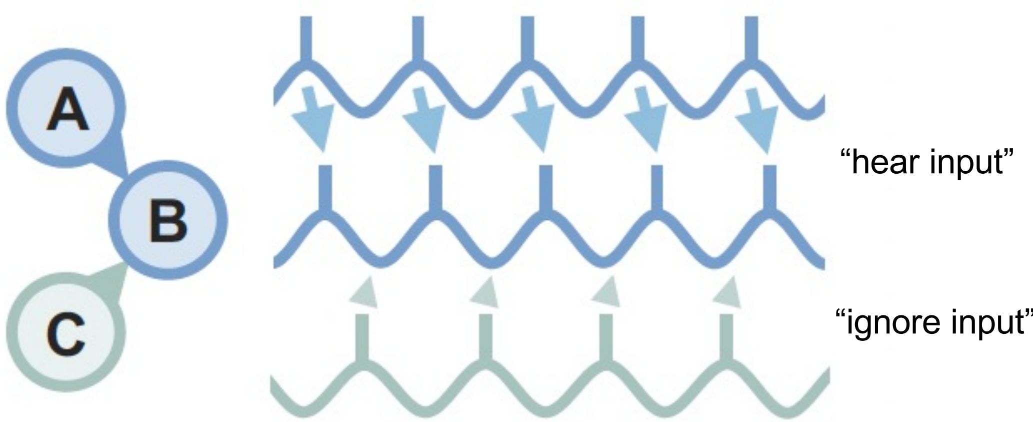
Modulate connection strength at frequency $\omega_S = 2\pi f_S$

Gain modulation

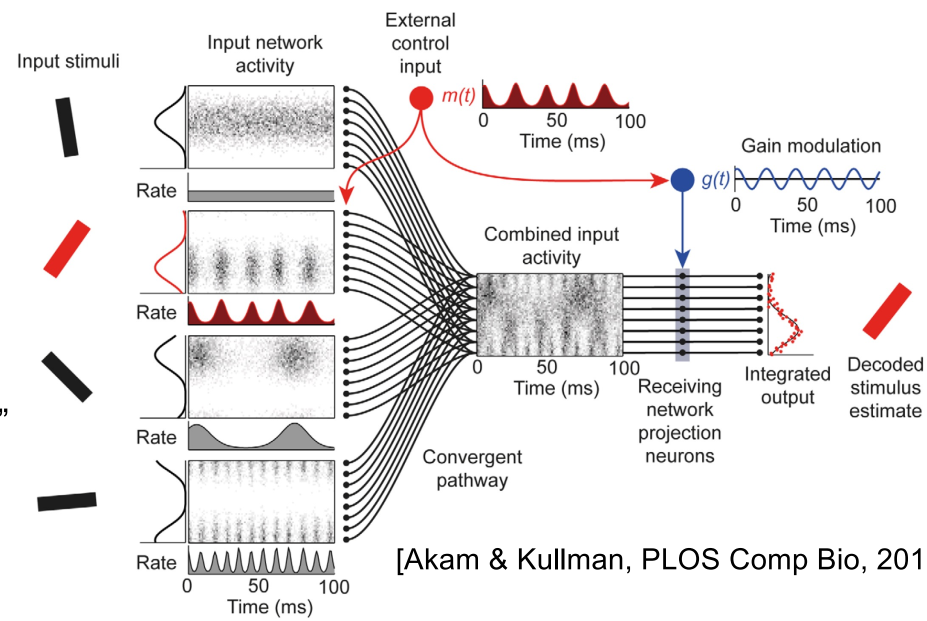
“A phenomenon whereby the gain or sensitivity of a neuron to inputs ... is altered.”

[Ferguson & Cardin, Nat Review Neuro, 2020]

activity is rhythmic



[Griffiths & Jensen, TINS, 2023]



[Akam & Kullman, PLOS Comp Bio, 2012]

Sensitivity of target node modulates in time

The model

Equations (damped, driven oscillator)

$$\ddot{x}_k + 2\beta\dot{x}_k + \omega_k^2 x_k = (\bar{g}_C + \bar{g}_S \cos\omega_S t) \sum_{j \neq k} x_j$$

Damped oscillator *k* ... driven by other nodes
... without and with gain modulation

Analytic results

$$\ddot{x}_k + 2\beta\dot{x}_k + \omega_k^2 x_k = (\bar{g}_C + \bar{g}_S \cos\omega_S t) \sum_{j\neq k} x_j$$

Assume input *j* at natural frequency with constant amplitude

$$x_j \approx A_j \cos(\omega_j t)$$

$$\ddot{x}_k + 2\beta\dot{x}_k + \omega_k^2 x_k = \bar{g}_C \sum_{j\neq k} \boxed{A_j \cos(\omega_j t)} + \bar{g}_S \cos(\omega_S t) \sum_{j\neq k} \boxed{A_j \cos(\omega_j t)}$$

Analytic results (<u>first term</u>)

$$\ddot{x}_k + 2\beta\dot{x}_k + \omega_k^2 x_k = \boxed{\bar{g}_C \sum_{j \neq k} A_j \cos(\omega_j t)} + \bar{g}_S \cos(\omega_S t) \sum_{j \neq k} A_j \cos(\omega_j t)$$

Focus on input from j^th oscillator

$$\ddot{x}_k + 2\beta\dot{x}_k + \omega_k^2 x_k = \bar{g}_C A_j \cos(\omega_j t)$$

Solve it ... for amplitude of k^th oscillator

$$A_k^2 = \frac{\bar{g}_C^2 A_j^2}{\boxed{(\omega_k^2 - \omega_j^2)^2} + 4\beta^2\omega_j^2}$$

for large amplitude response $\omega_j = \omega_k$

... input frequency matches target frequency

Analytic results (second term)

$$\ddot{x}_k + 2\beta\dot{x}_k + \omega_k^2 x_k = \bar{g}_C \sum_{j\neq k} A_j \cos(\omega_j t) + \boxed{\bar{g}_S \cos(\omega_S t) \sum_{j\neq k} A_j \cos(\omega_j t)}$$

Focus on input from jth oscillator

$$\ddot{x}_k + 2\beta\dot{x}_k + \omega_k^2 x_k = \quad \bar{g}_S A_j \cos(\omega_j t) \cos(\omega_S t)$$

Solve it ... for amplitude of kth oscillator

$$B_k^2 = \frac{\bar{g}_C^2 A_j^2 / 4}{\boxed{\left(\omega_k^2 - (\omega_j \pm \omega_S)^2\right)^2} + 4\beta^2 (\omega_j \pm \omega_S)^2}$$

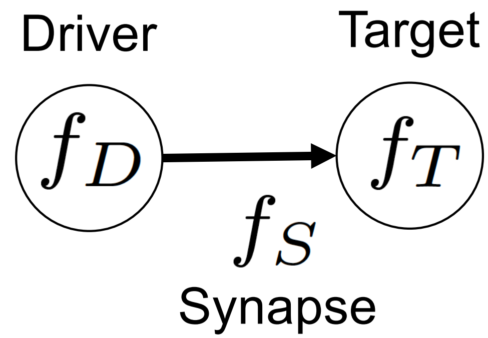
for large amplitude response

$$\omega_S = \omega_k - \omega_j$$

$$\omega_S = \omega_j - \omega_k$$

$$\omega_S = \omega_k + \omega_j$$

Analytic results (summary)



Evoked response when ...

No gain modulation $\quad f_D = f_T \quad$ Drive target at its natural frequency

Sinusoidal gain modulation

$$f_S = f_T - f_D$$

Choose gain modulation frequency (f_S) as sum or difference of driver and target frequencies

$$f_S = f_D - f_T$$

$$\boxed{f_S = f_D + f_T}$$

Restrict rhythms

Motivated by observations

$$\frac{f_k}{f_{k-1}} = e \qquad \frac{f_k}{f_{k-1}} = 2 \qquad \frac{f_k}{f_{k-1}} = \phi$$

Require rhythms in the model spaced by a constant factor:

$$f_k = f_0\, c^k \quad \text{so} \quad \frac{f_k}{f_{k-1}} = c$$

where c = unspecified (could be *golden ratio, e, 2*, ...)

Restrict rhythms

Motivated by observations $\boxed{f_k = f_0\, c^k}$

Consider $f_S = f_D + f_T$ Relationship derived for coupled oscillator model

Neighbors $(f_S, f_D, f_T) = (f_{k+2}, f_{k+1}, f_k)$

Then $f_{k+2} = f_{k+1} + f_k$

So $c^2 - c - 1 = 0$ $c = \dfrac{1+\sqrt{5}}{2} = \phi$

Analytic results (summary)

Model $$\ddot{x}_k + 2\beta \dot{x}_k + \omega_k^2 x_k = (\bar{g}_C + \bar{g}_S \cos \omega_S t) \sum_{j \neq k} x_j$$

$$f_D \xrightarrow{f_S} f_T$$

Resonance

$$f_S = f_T - f_D$$

$$f_S = f_D - f_T$$

$$f_S = f_D + f_T$$

For large amplitude response at target, choose gain frequency (f_S) as the sum or difference of the target & driver frequencies.

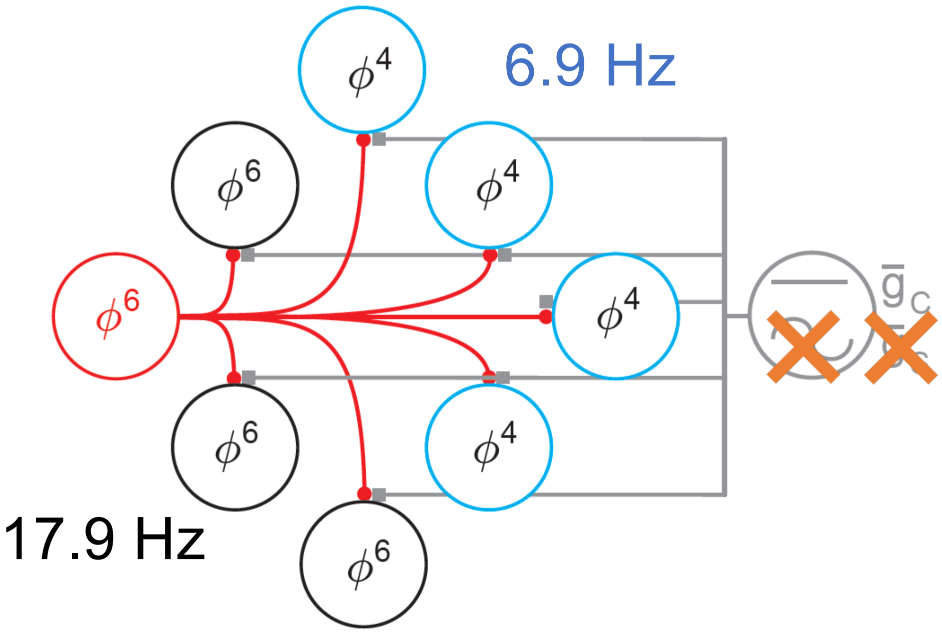
If $f_k = f_0 \, c^k$ to satisfy resonance between neighboring bands $c = \dfrac{1 + \sqrt{5}}{2} = \phi$

(from data)

For communication between brain rhythms → golden ratio spacing

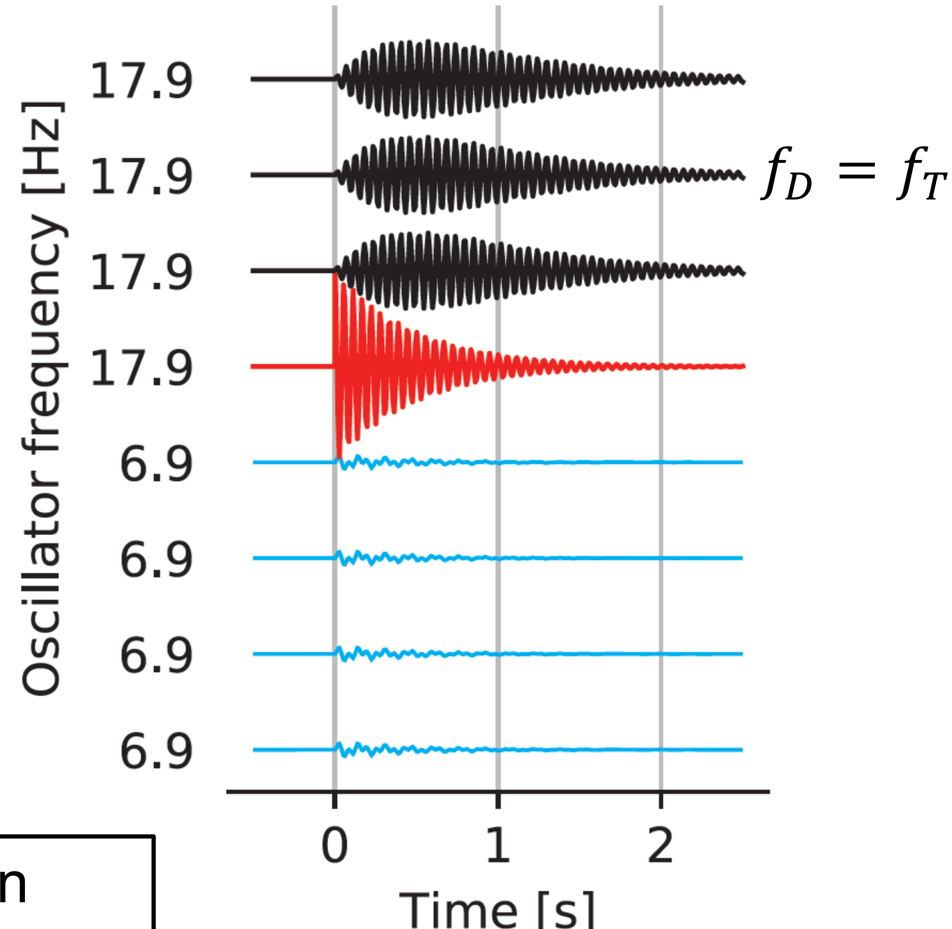
Simulations

Two populations,
natural frequencies: $f_k = \phi^k$



* Establish isolated communication channel at 17.9 Hz.

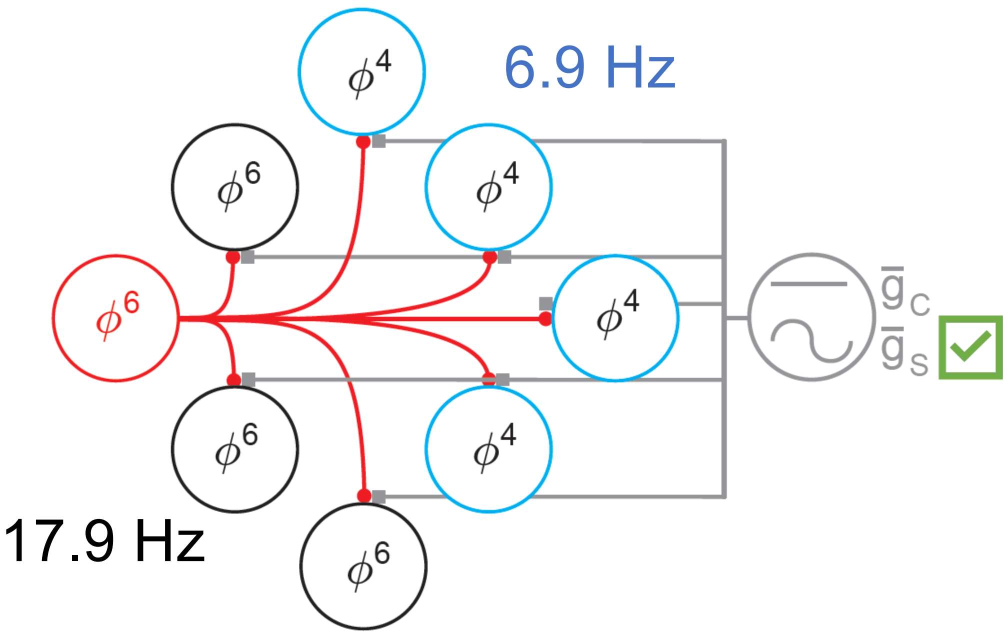
No gain modulation: $\bar{g}_S = 0$

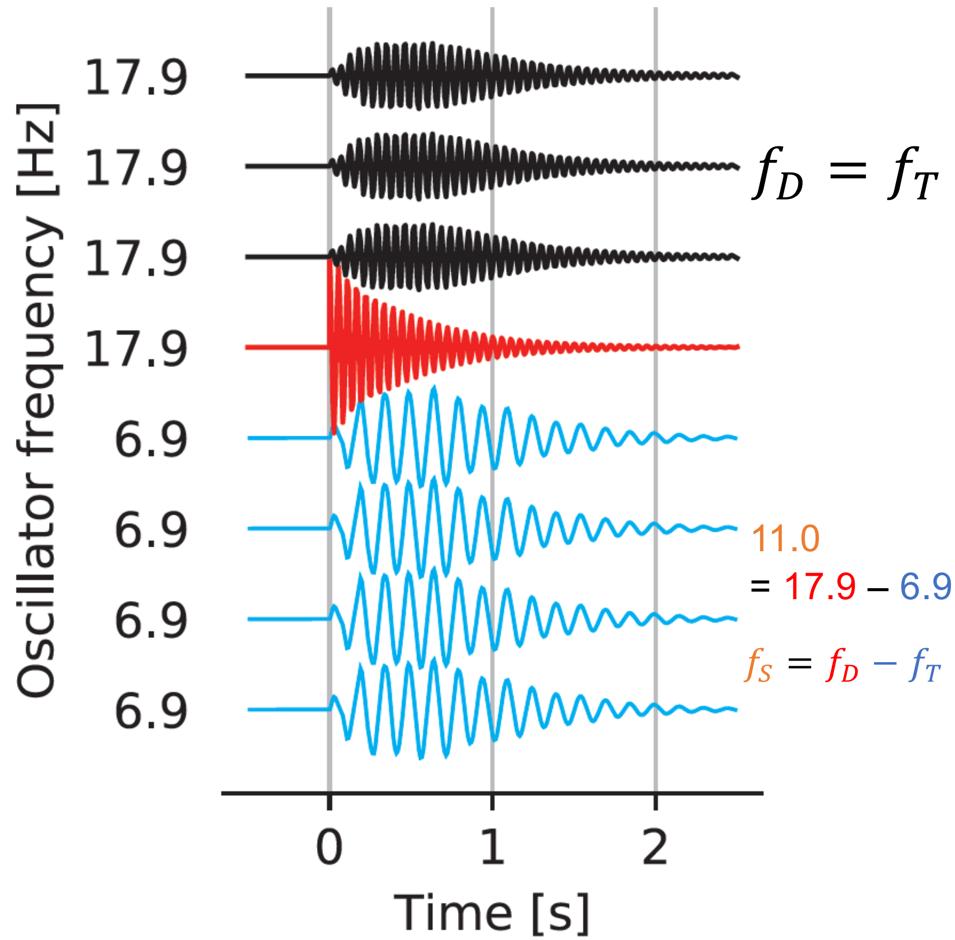


Simulations

Two populations,
natural frequencies: $f_k = \phi^k$

Gain modulation: $\bar{g}_S = 50$ $f_S \approx \boxed{11.0\ \text{Hz}} = \phi^5$

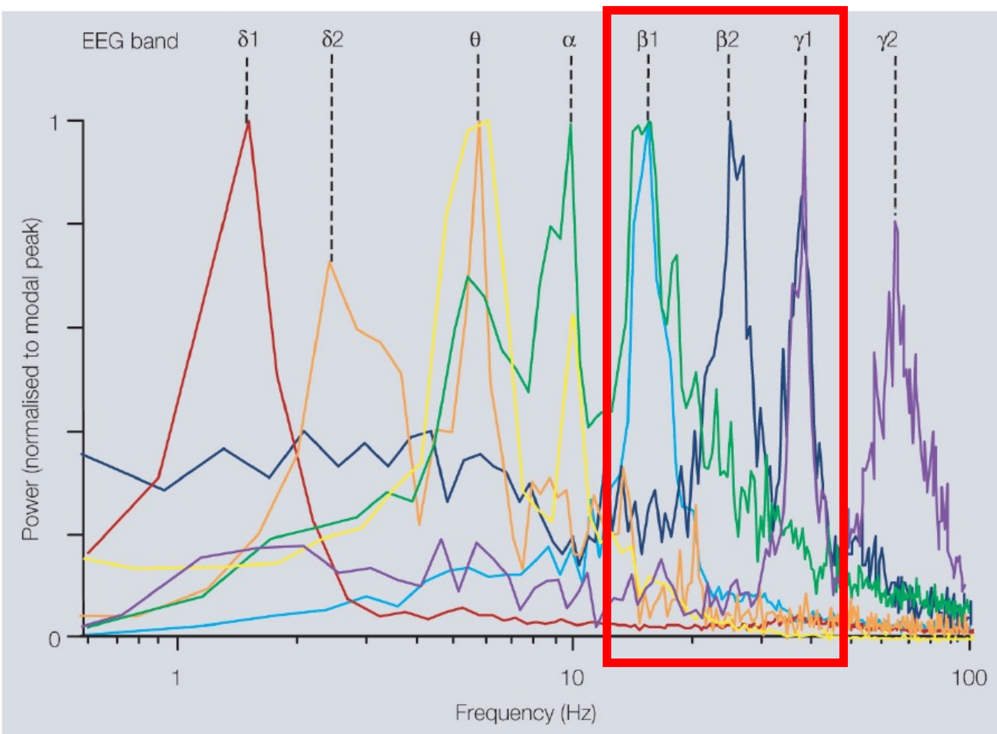




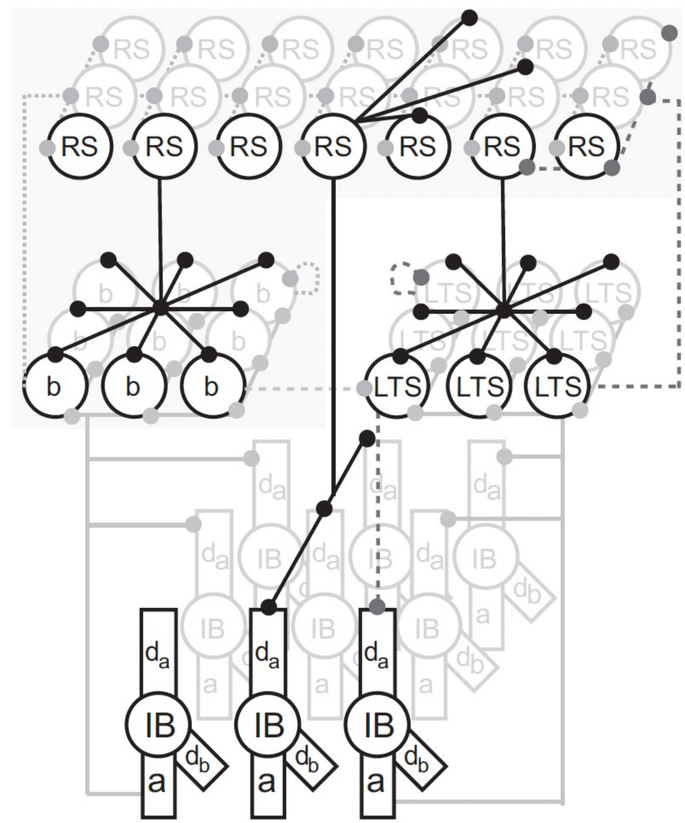
* Bind two rhythmic populations with a 3rd rhythm.

Evidence?

$$\frac{f_k}{f_{k-1}} = \phi$$

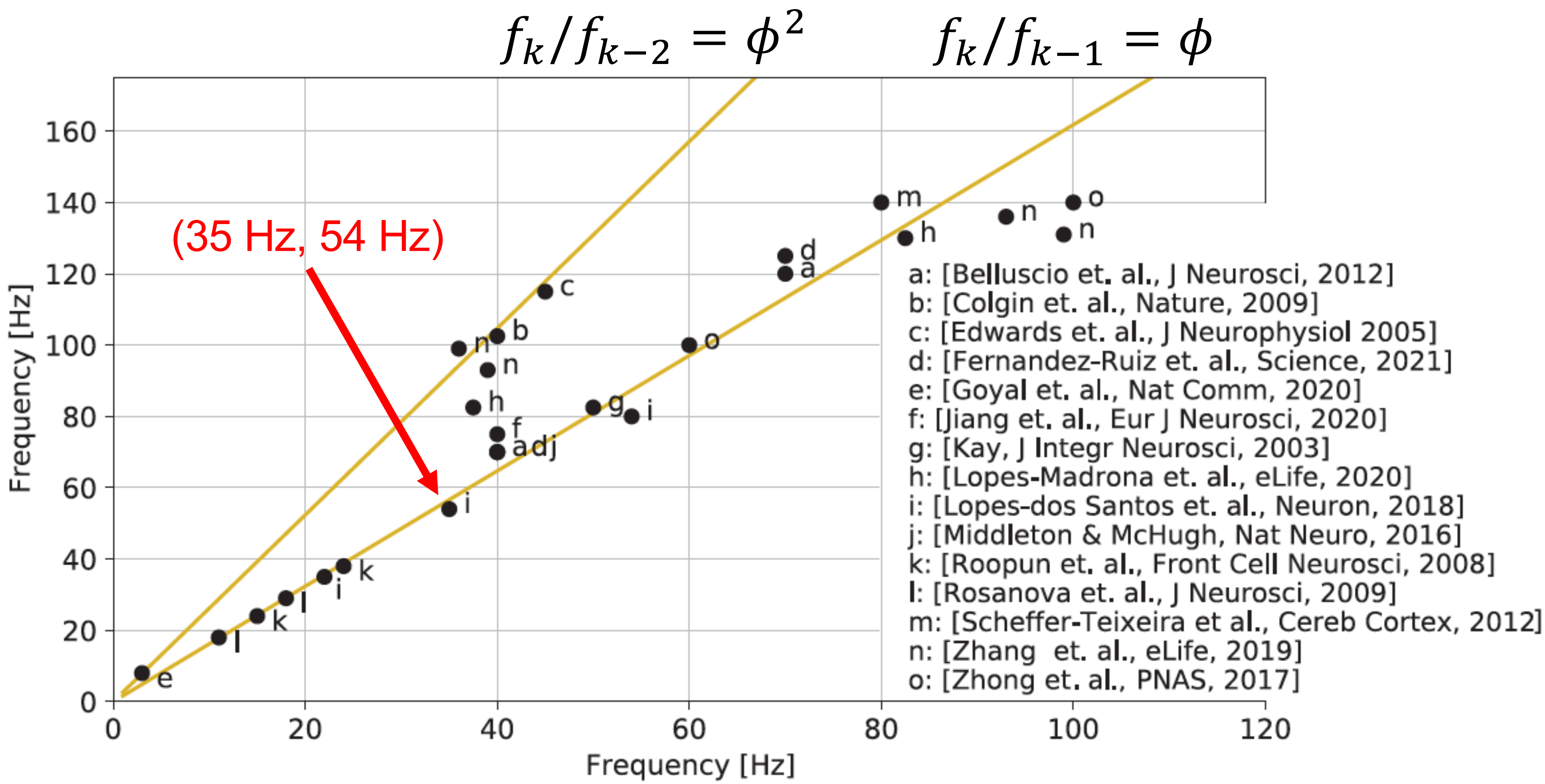


[Roopun et al., 2008]



[Kopell et al., 2011]

Evidence? Consider rhythms reported together in the literature ...



Conclusions

- <u>Claim</u>: Brain rhythms are organized by the golden ratio.
- <u>Claim</u>: Cross-frequency interactions via 3 rhythms.
- It’s “simple”

  damped harmonic oscillators

  ... prove things

  ... make experimental predictions

Try it

https://github.com/Mark-Kramer/Golden-Framework

This repository contains code to perform the simulations and generate the figures in:

Golden rhythms as a theoretical framework for cross-frequency organization

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Notebook	Run It
Figure 2	Open in Colab
Figure 3	Open in Colab
Figure 4	Open in Colab
Figure 5	Open in Colab
Figure 6	Open in Colab
Figure 7	Open in Colab