# Auditory streaming emerges from direct excitation and slow delayed inhibition 

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## Motivation - The Auditory Streaming Paradigm (AS)

The psychoacoustic perceptual experiment - pure tones $A$ and $B$



- Perception of integrated (INT) or segregated (S) rhythms
- Dependence on stimulus parameters

We explore a "minimal" firing rate model with periodic inputs driving oscillations

- Coupled neural CPG oscillators (Rubin \& Terman, 2000)
- Perceptual rivalry via adaptation or synaptic depresstion (Shpiro et al, 2009)


## Outline of the talk

- Model description
- Analyse symmetry and parameter constraints
- Analitical approach to classify dynamics (slow-fast decomposition)
- Exhaustive study of states in the space of parameters
- Interpretation of states with AS perceptions
- Show similarity with AS experiments
- Show a rich repertoire of dynamical states
- Computational analysis under smooth conditions


## Model description

Two periodically forced neural populations (A and B) coupled by fast direct excitation and slow delayed inhibition

Periodically forced system of 4 delay differential equations:


$$
\begin{aligned}
\tau \dot{u_{A}}(t) & =-u_{A}(t)+H\left(a u_{B}(t)-b s_{B}(t-D)+c i_{A}\left(t-t_{0}\right)\right) \\
\tau \dot{\dot{u}_{B}}(t) & =-u_{B}(t)+H\left(a u_{A}(t)-b s_{A}(t-D)+c i_{B}\left(t-t_{0}\right)\right) \\
\dot{s_{A}}(t) & =H\left(u_{A}(t)\right)\left(1-s_{A}(t)\right) / \tau-s_{A}(t) / \tau_{i} \\
\dot{s_{B}}(t) & =H\left(u_{B}(t)\right)\left(1-s_{B}(t)\right) / \tau-s_{B}(t) / \tau_{i}
\end{aligned}
$$

Heaviside activation $H(x)= \begin{cases}1, & \text { if } x \geq \theta \\ 0, & \text { otherwise }\end{cases}$
Slow-fast regime $\tau / \tau_{i} \ll 1$
Parameters: activity threshold $\theta \in(0,1)$, synaptic strengths $a$ and $b$, input strength $c$ and onset $t_{0}$, inhibition time scale $\tau_{i}$, activity time scale $\tau$

## Periodic square-wave inputs

$$
\begin{aligned}
& i_{A}(t)=\sum_{k=0}^{\infty} \chi_{I_{A}^{k}}(t)+\nu \sum_{k=0}^{\infty} \chi_{I_{B}^{k}}(t) \\
& i_{B}(t)=\nu \sum_{k=0}^{\infty} \chi_{I_{A}^{k}}(t)+\sum_{k=0}^{\infty} \chi_{I_{B}^{k}}(t)
\end{aligned}
$$

$\chi_{I}(t)=1$ for $t \in I$ and 0 otherwise, and scaling parameter $\nu(d=\nu c)$
$I_{A}^{k}=\left[\alpha_{k}^{A}, \beta_{k}^{A}\right]=[2 k T R, 2 k T R+T D], \quad I_{B}^{k}=\left[\alpha_{k}^{B}, \beta_{k}^{B}\right]=[(2 k+1) T R,(2 k+1) T R+T D]$
Where $T D=$ tones' duration and $P R=1 / T R=$ tone repetition rate.


- Mimic stereotyped neural responses from Macaque auditory cortex (AC)
- Populations $A$ and $B$ are assumed to be located downstream $A C$

We introduce a bit of notation:

$$
\Phi=\left\{R \subset \mathbb{R}: R=I_{k}^{A} \text { or } R=I_{k}^{B}, \exists k \in \mathbb{N}\right\}, \quad I=\bigcup_{R \in \Phi} R
$$

## $\mathbb{Z}_{2}$ equivariance - asymmetrical cycles exist in pairs

Rewrite the model as a non-autonomous dynamical system

$$
\dot{v}(t)=f\left(v(t), i_{A}(t), i_{B}(t)\right), \quad v=\left(u_{A}, u_{B}, s_{A}, s_{B}\right)
$$

Map $\kappa$ swaps $A$ and $B$ indexes in the system's variables

$$
\kappa: v=\left(u_{A}, u_{B}, s_{A}, s_{B}, i_{A}, i_{B}\right) \mapsto\left(u_{B}, u_{A}, s_{B}, s_{A}, i_{B}, i_{A}\right)
$$

Apply $T R$ time shift on the inputs

$$
i_{A}(t+T R)=i_{B}(t) \quad i_{B}(t+T R)=i_{A}(t), \quad \forall t \in \mathbb{R}
$$

We have $\mathbb{Z}_{2}$-equivariance under transformation $\kappa$ and $T R$ time shift

$$
\kappa\left(f\left(v(t), i_{A}(t), i_{B}(t)\right)\right)=f\left(\kappa\left(v(t+T R), i_{B}(t+T R), i_{A}(t+T R)\right)\right)
$$

Main conclusion: any $2 n T R$-periodic asymmetrical cycle (not in-phase nor anti-phase) has a co-existing $\kappa$-conjugate cycle $\kappa(v(t+T R))$

## Constraining model into a realistic range of parameters

With no inputs $\left(i_{A}=i_{B}=0\right)$ there are two possible equilibria: a low-activity state $P=(0,0,0,0)$ and a high-activity state $Q=(1,1,1,1)$.

If $a-b \geq \theta$ then $P$ and $Q$ co-exist, and dynamics is trivial

- If $c<\theta$ : trajectories starting in the basin of $P(Q)$ end in $P(Q)$
- $c \geq \theta$ : any trajectory converges to $Q$

To avoid this unrealistic scenario

1. $a-b<\theta \rightarrow P$ is the only equilibium without inputs (no saturation)
2. $c \geq \theta \rightarrow$ units activate in the absence of inhibition $(b=0)$

In addition, we consider input parameters contraints

- $P R \in[1,40] \mathrm{Hz}$ : physiological conditions tested in experiments
- $T R>T D:$ No active tone overlap $I_{A}^{i} \cap I_{B}^{j}=\emptyset, \forall i \neq j \in \mathbb{N}$
- $d f \in[0,1]$ defined as $\nu=\nu(d f)=\left(1-d f^{1 / m}\right)$ to model the tone pitch difference


## The fast and slow subsystem at fixed time $t \in I_{A}^{K}$

Change variables to the fast time scale $r=t / \tau, \tau \rightarrow \infty$

$$
\begin{aligned}
& u_{A}^{\prime}=-u_{A}+H\left(a u_{B}-b s_{B}(t-D)+c\right) \\
& u_{B}^{\prime}=-u_{B}+H\left(a u_{A}-b s_{A}(t-D)+d\right) \\
& s_{A}^{\prime}=H\left(u_{A}\right)\left(1-s_{A}\right) \\
& s_{B}^{\prime}=H\left(u_{B}\right)\left(1-s_{B}\right)
\end{aligned}
$$

Where ${ }^{\prime}=d / d r$. Units can be OFF $(\sim 0)$, ON $(\sim 1)$, or turning OFF or ON

- Synaptic variables may jump up or be constant (if A and B unit OFF)

Slow-dynamics

$$
\dot{s}=-s / \tau_{i}
$$

$\rightarrow s$ is decreasing (on either time scales) except when the units turn ON
Dynamics in $\mathbb{R}-I(c=d=0)$ is simple, WLOG $\tilde{s}_{B} \geq 0, \tilde{s}_{A} \geq 0$ (at steady state)

$$
\begin{aligned}
& u_{A}^{\prime}=-u_{A}+H\left(a u_{B}-b \tilde{s}_{B}\right) \\
& u_{B}^{\prime}=-u_{B}+H\left(a u_{A}-b \tilde{s}_{A}\right)
\end{aligned}
$$

$(0,0)$ is always a FP and $Q=(1,1) \mathrm{FP}$ if and only if $a-b \tilde{s}_{A} \geq \theta$ and $a-b \tilde{s}_{B} \geq \theta$

## Dynamics in the intervals with no inputs $(\mathbb{R}-I)$

## Theorem

For any $t \geq t_{0} \in \mathbb{R}-I$ :

1. If $A$ or $B$ is OFF at time $t$, both units are OFF in $\left(t, t^{*}\right]$, where $t^{*}$ is:

$$
t^{*}=\min _{s \in I}\{s>t\}
$$

2. If $A$ or $B$ is $O N$ at time $t$, both units are $O N$ in $\left[t_{*}, t\right)$, where $t_{*}$ is:

$$
t_{*}=\max _{s \in I}\{s<t\}
$$



Consequence: no unit can turn ON in $\mathbb{R}-l$.

## Definition (LONG and SHORT states)

- LONG - if at least one unit is ON at time $t, \exists t \geq t_{0} \in \mathbb{R}-I$
- SHORT - if both units are OFF $\forall t \geq t_{0} \in \mathbb{R}$ - I


## Synaptic decay and no saturated states if $T D+D<T R$

Lemma
Assume $T D+D<T R$. Defined $\Gamma$ as:

$$
\Gamma=\left\{L \subset \mathbb{R}: L=\left[\alpha_{k}^{A}, \alpha_{k}^{A}+D\right] \text { or } L=\left[\alpha_{k}^{B}, \alpha_{k}^{B}+D\right], \exists k \in \mathbb{N}\right\}
$$

$s_{A}(t-D)$ and $s_{B}(t-D)$ are monotonically decreasing in $L, \forall L \in \Gamma$.
Lemma
If $T D+D<T R$ both units are OFF $\forall t \in J$, where:

$$
J=\bigcup_{k \in \mathbb{N}}\left(\beta_{k}^{A}+D, \alpha_{k}^{B}\right] \cup\left(\beta_{k}^{B}+D, \alpha_{k+1}^{A}\right]
$$



## Dynamics in the the active tone intervals $/$ assuming $D \geq T D$

If $D \geq T D$ the delayed synaptic variables are constant on the fast time scale (equal to 1 or $\exp$ decaying). For $t \in I_{A}^{k}$ (A tone active phase):

$$
\begin{aligned}
& u_{A}^{\prime}=-u_{A}+H\left(a u_{B}-b \tilde{s}_{B}+c\right) \\
& u_{B}^{\prime}=-u_{B}+H\left(a u_{A}-b \tilde{s}_{A}+d\right)
\end{aligned}
$$

Where $\tilde{s}_{A}=s_{A}(t-D)$ and $\tilde{s}_{B}=s_{B}(t-D)$. Four possible FPs

1. $(0,0) \leftrightarrow c<b \tilde{s}_{B}+\theta$ and $d<b \tilde{s}_{A}+\theta$
2. $(1,0) \leftrightarrow c \geq b \tilde{s}_{B}+\theta$ and $a+d<b \tilde{s}_{A}+\theta$
3. $(0,1) \leftrightarrow a+c<b \tilde{s}_{B}+\theta$ and $d \geq b \tilde{s}_{A}+\theta$
4. $(1,1) \leftrightarrow a+c \geq b \tilde{s}_{B}+\theta$ and $a+d \geq b \tilde{s}_{A}+\theta$

## Basin of attraction of $(0,0)$ and $(1,1)$

We note that only $(0,0)$ and $(1,1)$ can coexist if $a>0$. We can rewrite system

$$
\begin{aligned}
& u_{A}^{\prime}=-u_{A}+S\left(u_{B}-s_{2}\right) \\
& u_{B}^{\prime}=-u_{B}+S\left(u_{A}-s_{1}\right)
\end{aligned}
$$


$s_{1}=\left(b \tilde{s}_{A}-c+\theta\right) / a, s_{2}=\left(b \tilde{s}_{B}-c+\theta\right) / a$
$0<s_{k} \leq 1$ for $k=1,2$

- $\left(s_{1}, s_{2}\right)$ is a degenerate saddle point where separatrices originate
- $(1,0)$ and $(0,1)$ converge to $(1,1)$


## Differential convergence to $(1,1)$

Consider conditions when $(1,1)$ is the only FP and an orbit starting from $(0,0)$

1. $c-b \tilde{s}_{B} \geq \theta$ and $d-b \tilde{s}_{A} \geq \theta$ both units turn ON simultaneously

$$
\begin{aligned}
& u_{A}^{\prime}=1-u_{A} \\
& u_{B}^{\prime}=1-u_{B}
\end{aligned}
$$

2. $c-b \tilde{s}_{B} \geq \theta, d-b \tilde{s}_{B}<\theta$ and $a+d-b \tilde{s}_{A} \geq \theta$ A turns $O N$ before $B$ Indeed $\exists u^{*} \in(0,1]$ for which:

$$
a u_{*}+d-b \tilde{s}_{A}=\theta
$$

From the first condition the fast subsystem reduces to:

$$
\begin{aligned}
& u_{A}^{\prime}=1-u_{A} \\
& u_{B}^{\prime}=-u_{B}+H\left(a u_{A}-b \tilde{s}_{A}+d\right)=-u_{B}+\eta\left(u_{A}\right)
\end{aligned}
$$

- $u_{A}(r) \rightarrow 1$ exponentially reaching point $u^{*}$ at time $r^{*}=\log \left[\left(1-u^{*}\right)^{-1}\right]$
- $\eta\left(u_{A}(r)\right)=0, \forall r<r^{*}$
- $\eta\left(u_{A}(r)\right)=1, \forall r \geq r^{*}$, and $u_{A}(r) \rightarrow 1$ following A dynamics at $r=0$

Back to $t=\tau r$ the B unit turns ON an infinitesimal delay $\delta=\tau r^{*}$ after A .
3. $d-b \tilde{s}_{A} \geq \theta, c-b \tilde{s}_{A}<\theta$ and $a+c-b \tilde{s}_{B} \geq \theta$ equal to 2 by swapping $A$ and $B$.

## Single OFF to ON transition during each active tone interval $R \in \Phi$

Lemma
Assume $T D+D<T R$ and $D>T D$. Let $R=[\alpha, \beta] \in \Phi$, and $A(B)$ be $O N$ at time $t \in R$, then
(1) $A(B)$ is $O N \forall s \geq t, s \in R$
(2) $\exists!t^{*} \in R$ when $A(B)$ turns $O N$
(3) $s_{A}(t-D)\left(s_{B}(t-D)\right)$ is decreasing in $\left[\alpha, t^{*}+D\right]$


Lemma

1. $A$ (B) turns $O N$ at time $\alpha \Leftrightarrow A$ (B) is $O N \forall t \in(\alpha, \beta]$
2. $A$ (B) if OFF at time $\beta \Leftrightarrow A$ (B) is OFF $\forall t \in R$

## MAIN and CONNECT states

## Definition

Assume $T D+D<T R$ and $D>T D$. A solution (state) is:

- MAIN if $\forall R \in \Phi$, if $\exists t^{*} \in R$ turning ON time for A or B , then $t^{*}=\min (R)$
- CONNECT if $\exists R \in \Phi$ and $\exists t^{*} \in R, t^{*}>\min (R)$ turning ON time for the A or the $B$ unit




## Classification of MAIN states

From the FP conditions of the fast system - dynamics in $R=[\alpha, \beta] \in \Phi$

- Both units turn ON at time $\alpha-(1,1)$ is the only FP at time $\alpha$.

1. $f\left(\underline{s}_{B}\right) \geq \theta, g\left(\underline{s}_{A}\right) \geq \theta \rightarrow$ both units instantaneously turn ON
2. $g\left(\underline{s}_{A}\right)<\theta, f\left(\underline{s}_{B}\right) \geq \theta$ and $a+g\left(\underline{s}_{A}\right) \geq \theta \rightarrow B$ turns $O N$ after $A$
3. $f\left(\underline{s}_{B}\right)<\theta, g\left(\underline{s}_{A}\right) \geq \theta$ and $a+f\left(\underline{s}_{B}\right) \geq \theta \rightarrow \mathrm{A}$ turns ON after B

$M=\{$ MAIN states $\}=\{s=s(t)$ states satisfying one of $1-6, \forall R \in \Phi\}$

## Matricial form of MAIN states

## Theorem

Let $R \in \Phi$. There is an injective map $\rho$

$$
\begin{array}{rlrl}
\rho: M & \rightarrow B(2,2) & x_{A}=H\left(f\left(\underline{s}_{B}\right)\right), & y_{A}=\left\{\begin{array}{ll}
1 & \text { if } a x_{B}+f\left(\underline{s}_{B}\right) \geq \theta \\
0 & \text { if } a x_{B}+f\left(\bar{s}_{B}\right)<\theta
\end{array},\right. \\
s & \mapsto V=\left[\begin{array}{ll}
x_{A} & y_{A} \\
x_{B} & y_{B}
\end{array}\right] & x_{B}=H\left(g\left(\underline{s}_{A}\right)\right), \quad y_{B}= \begin{cases}1 & \text { if } a x_{A}+g\left(\underline{s}_{A}\right) \geq \theta \\
0 & \text { if } a x_{A}+g\left(\bar{s}_{A}\right)<\theta\end{cases}
\end{array}
$$

Moreover:

$$
\operatorname{Im}(\rho)=\left\{V=\rho(s): x_{A} \leq y_{A}, x_{B} \leq y_{B}, x_{A}=x_{B}=0 \Rightarrow y_{A}=y_{B}=0\right\}
$$

Element $s \in M$ satisfying condition $1-6$ have one of the following images $\rho(s)$ :
(1) $\left[\begin{array}{ll}1 & 1 \\ 1 & 1\end{array}\right]$
(2) $\left[\begin{array}{ll}1 & 1 \\ 0 & 1\end{array}\right]$
(3) $\left[\begin{array}{ll}0 & 1 \\ 1 & 1\end{array}\right]$
(4) $\left[\begin{array}{ll}1 & 1 \\ 0 & 0\end{array}\right]$
(5) $\left[\begin{array}{ll}0 & 0 \\ 1 & 1\end{array}\right]$
(6) $\left[\begin{array}{ll}0 & 0 \\ 0 & 0\end{array}\right]$

## Classification of CONNECT states and matricial form

For the classification we consider the following cases:

- (1-2) $\mathbf{A}(\mathbf{B})$ and $\mathbf{B}(\mathbf{A})$ turn ON at $\alpha$ and $t^{*} \in(\alpha, \beta]$ respectively
-(3-4) $\mathbf{A}(\mathbf{B})$ is OFF at $\beta$ and $\mathbf{B}(\mathbf{A})$ turns $\mathbf{O N}$ at $t^{*}, \exists t^{*} \in(\alpha, \beta]$
- (5) $\mathbf{A}$ and $\mathbf{B}$ turn $\mathbf{O N}$ at $t^{*}, s^{*} \in(\alpha, \beta]$
$C=\{$ CONNECT states $\}=\{s=s(t)$ states satisfying one of $1-5, \exists R \in \Phi\}$


## Theorem

Let $R \in \Phi$. There is an injective map $\rho$

$$
\begin{aligned}
\rho: C & \rightarrow B(2,3) & x_{A}=H\left(f\left(\underline{s}_{B}\right)\right), & x_{B}
\end{aligned}=H\left(g\left(\underline{s}_{A}\right)\right), ~\left(\begin{array}{lll}
x_{A} & y_{A} & x_{A} \\
x_{B} & y_{B} & z_{B}
\end{array}\right] \quad \begin{aligned}
y_{A} & \left.=H\left(a x_{B}+f\left(\underline{s}_{B}\right)\right)\right), \\
y_{B} & \left.=H\left(a x_{A}+g\left(\underline{s}_{A}\right)\right)\right), \\
z_{A} & \left.=H\left(a y_{B}+f\left(\bar{s}_{B}\right)\right)\right), \\
z_{B} & \left.=H\left(a y_{A}+g\left(\bar{s}_{A}\right)\right)\right)
\end{aligned}
$$

$$
\operatorname{Im}(\rho)=\left\{W: x_{A} \leq y_{A} \leq z_{A}, x_{B} \leq y_{B} \leq z_{B}, x_{A}=x_{B}=0 \Rightarrow y_{A}=y_{B}=0, y_{A}<z_{A} \text { or } y_{B}<z_{B}\right\}
$$

Dynamics visualisation via the Matricial form $V$

The units' dynamics in $R$ is given by 1 st and 2 nd rows of $V$


## LONG states

Lemma (LONG equivalence)
If $D \geq T D$ and $T D+D<T R$. A state is LONG if and only if $\exists R=[\alpha, \beta] \in \Phi$

1. $A$ and $B$ turn $O N$ at times $t_{A}^{*}$ and $t_{B}^{*} \in R$, respectively.
2. $a-b s_{A}(\beta) \geq \theta$ and $a-b s_{B}(\beta) \geq \theta$, with $\beta=\max (R)$

Moreover, both units are ON for $t \in\left[\beta, t^{*}+D\right]$, turn OFF at time $t^{*}+D$, and are $O F F \forall t \in\left(t^{*}+D, t_{u p}\right]$, where $t^{*}=\min \left\{t_{A}^{*}, t_{B}^{*}\right\}$ and $t_{u p}=\min _{s \in I}\{s>t\}$.


## $2 k T R$-periodic MAIN and CONNECT states

Theorem
Any periodic state $\psi=\psi(t)$ must be $2 k T R$-periodic, $\exists k \in \mathbb{N}$

$$
\psi(t+2 k T R)=\psi(t), \quad \forall t \geq t_{0}, t \in \mathbb{R}
$$

## Definition

- $M_{k}^{S}$ and $M_{k}^{L}$ - sets of SHORT and LONG $2 k T R$-periodic MAIN states
- $C_{k}^{S}$ and $C_{k}^{L}$ - sets of SHORT and LONG $2 k T R$-periodic CONNECT states

Case $k=1$


- Activity of A and B during $I_{i}$ can be represented by matrices $V_{i}, i=1,2$
- $V_{i}$ depend on the delayed synaptic variables at $\alpha_{i}$ and $\beta_{i}$

$$
\begin{gathered}
s_{A}^{i-}=s_{A}\left(\alpha_{i}-D\right), \quad s_{B}^{i-}=s_{B}\left(\alpha_{i}-D\right), \quad s_{A}^{i+}=s_{A}\left(\beta_{i}-D\right), \quad s_{B}^{i+}=s_{B}\left(\beta_{i}-D\right) \\
\alpha_{i}=(i-1) T R, \quad \beta_{i}=(i-1) T R+T D
\end{gathered}
$$

## Matricial form for $2 T R$-periodic MAIN states

For $2 T R$-periodic SHORT states these delayed synaptic values depend on

$$
N^{-}=e^{-(T R-T D-D) / \tau_{i}}, N^{+}=e^{-(T R-D) / \tau_{i}}, M^{-}=e^{-(2 T R-T D-D) / \tau_{i}}, M^{+}=e^{-(2 T R-D) / \tau_{i}}
$$

## Theorem

There is an injective map:

$$
\begin{aligned}
\rho: M_{1}^{S} & \rightarrow B(2,4) \\
\psi & \mapsto V=\left[\begin{array}{l|l}
V_{1} & V_{2}
\end{array}\right]=\left[\begin{array}{ll|ll}
x_{A}^{1} & y_{A}^{1} & x_{A}^{2} & y_{A}^{2} \\
x_{B}^{1} & y_{B}^{1} & x_{B}^{2} & y_{B}^{2}
\end{array}\right]
\end{aligned}
$$

Where, for $i=1,2, V_{i}$ is the matricial forms of $\psi$ during the interval $I_{i}$ :

$$
\begin{aligned}
& s_{B}^{i \pm}=N^{ \pm} y_{B}^{j}+M^{ \pm}\left(1-y_{B}^{j}\right) y_{B}^{i}, \quad \text { and } s_{A}^{i \pm}=N^{ \pm} y_{A}^{j}+M^{ \pm}\left(1-y_{A}^{j}\right) y_{A}^{i}, \quad \forall i, j=1,2, i \neq j \\
& \operatorname{Im}(\rho)=\left\{V=\left[V_{1} \mid V_{2}\right]: V_{1} \in \operatorname{Im}\left(\rho^{\prime 1}\right), V_{2} \in \operatorname{Im}\left(\rho^{\prime 1}\right) \text { satisfying 1-4 below }\right\} \\
& \text { 1. } y_{A}^{1}=y_{B}^{2}=1 \Rightarrow x_{A}^{1}=x_{B}^{2} \text { and } y_{A}^{2}=y_{B}^{1}=1 \Rightarrow x_{A}^{2}=x_{B}^{1} \\
& \text { 2. } y_{B}^{1}=y_{B}^{2} \Rightarrow x_{A}^{1} \geq x_{A}^{2} \text { and } y_{A}^{1}=y_{A}^{2} \Rightarrow x_{B}^{1} \geq x_{B}^{2} \\
& \text { 3. } y_{A}^{2}=1 \Rightarrow x_{B}^{1} \leq r \text { and } y_{B}^{1}=1 \Rightarrow x_{A}^{2} \leq r, \text { for any entry } r \text { in } V \\
& \text { 4. } y_{A}^{2}=y_{B}^{2}, y_{A}^{1}=y_{B}^{1} \Rightarrow x_{A}^{1} \geq x_{B}^{1} \text { and } x_{B}^{2} \geq x_{A}^{2}
\end{aligned}
$$

## Matricial form and conditions for all $2 T R$-periodic SHORT MAIN states

- Using the conditions over $V$ we find 13 possible states (algorithmically)
- Conditions for the well-definiteness of all $V \mathrm{~s}$ and simplification
- Add conditions contained in the LONG equivalence theorem

$$
\begin{aligned}
& C_{1}=d, \quad C_{2}^{ \pm}=a-b M^{ \pm}+d, \quad C_{3}^{ \pm}=c-b N^{ \pm}, \quad C_{4}^{ \pm}=c-b M^{ \pm}, \quad C_{5}^{ \pm}=a-b N^{ \pm}+d, \\
& C_{6}^{ \pm}=a-b N^{ \pm}+c, \quad C_{7}^{ \pm}=d-b N^{ \pm}, \quad C_{8}^{ \pm}=d-b M^{ \pm}, \quad C_{9}=a-b M^{+} \quad C_{10}=a-b N^{+}
\end{aligned}
$$

| $S_{1}$ | $S A B_{1}$ | $S D_{1}$ | $A P$ | $A S_{1}$ | $A S D_{2}$ | $I N T_{1}$ | $I N T D$ | $I N T$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1100 | 1100 | 1100 | 1100 | 1111 | 1101 | 1111 | 1101 | 1111 |
| 0000 | 1100 | 0100 | 0011 | 0011 | 0011 | 0000 | 0111 | 1111 |
|  |  | $C_{4}^{-} \geq \theta$ |  | $C_{3}^{-} \geq \theta$ | $C_{2}^{-} \geq \theta$ |  | $C_{3}^{-} \geq \theta$ |  |
| $C_{1}<\theta$ | $C_{3}^{+}<\theta$ | $C_{2}^{-} \geq \theta$ |  | $C_{2}^{+}<\theta$ | $C_{5}^{+}<\theta$ | $C_{3}^{-} \geq \theta$ |  | $C_{1} \geq \theta$ |
| $C_{2}^{+}<\theta$ | $C_{8}^{-} \geq \theta$ | $C_{3}^{+}<\theta$ | $C_{3}^{-} \geq \theta$ | $C_{8}^{-} \geq \theta$ | $C_{5}^{+}<\theta$ | $C_{6}^{+}<\theta$ | $C_{7}^{-}<\theta$ | $C_{7}^{-} \geq \theta$ |
| $C_{3}^{+}<\theta$ | $C_{9}<\theta$ | $C_{8}^{-}<\theta$ |  | $C_{10}<\theta$ | $C_{8}^{-}<\theta$ |  | $C_{10}<\theta$ |  |
|  |  | $C_{9}<\theta$ |  |  | $C_{10}<\theta$ |  |  |  |

## The next slides...

- Time histories and 2D regions of existence of $2 T R$-periodic SHORT MAIN STATES
- Examples of $2 T R$-periodic SHORT CONNECT and LONG MAIN states
- Cycles with higher periods and cascades
- Period doubling of SHORT MAIN states
- Segrated switching SHORT MAIN and CONNECT states
- MAIN states under the case $D<T D$ and comparisons with experiments
- Numerical study with smooth inputs and gain function, and non slow-fast regime


## $2 T R$-periodic SHORT MAIN states time histories and regions of existence



- Integration - at least one unit responds to both tones
- Segregation - no unit responds to both tones

Theorem (Multistability)
No 2TR-periodic SHORT MAIN states can be bistable except for INTA and SAB (not shown)

## $2 T R$-periodic SHORT CONNECT and LONG MAIN states

A similar analysis can be carried out for all combinations of SHORT/LONG and MAIN/CONNECT states

STABILITY REGIONS OF MAIN-CONNECT STATES


STABILITY REGIONS OF MAIN-LONG STATES


APcAS



## Period doubling MAIN and CONNECT states

Extension to conditions for period doubling cascade using quantities

$$
\begin{aligned}
& L_{k}^{-}=e^{-(k T R-T D-D) / \tau_{i}}, \quad L_{k}^{+}=e^{-(k T R-D) / \tau_{i}}, \quad L_{0}^{ \pm}=+\infty
\end{aligned}
$$

$S_{k}=S A B_{k}, S A_{k}$ and $I_{k}=I N T D_{k}, I N T_{k} \quad$ PERIOD: $T_{S_{k}}=2 k T R$ and $T_{l_{k}}=2(2 k-1) T R$
Theorem
Period doubling solutions of the other MAIN states cannot occur: AP, AS, SA, INTA
$\rightarrow$ similar condiderations can be made with CONNECT states

Period doubling MAIN and CONNECT states


Segregated switching MAIN and CONNECT states $K_{k}^{m}$ and $W_{k}^{m}$
$m=\#$ of skipped tone and $k=\#$ of segregated cycles



Theorem
$W_{m}^{k}$ may exist for $m$ even. $K_{m}^{k}$ may exist for $m$ odd

## Cascades of $W_{k}^{m}$ and $K_{k}^{m}$ in 2D




Extension to CONNECT states $c, d, g, c d, c g, d g$ and $c d g$

The case $D<T D$ under $c-b \geq \theta$
Theorem
If $c-b \geq \theta$ these are the all possible stable states (LONG states cannot exist)


Computational analysis under smooth gain and inputs, non slow-fast scales Sidmoid $H(x)=[1+\exp (\lambda(x-\theta))]^{-1}$ with fixed $\lambda=30$ and $\tau / \tau_{i}$ up to $\sim 10^{-1}$


Provide insights on the case $T D+D>T R$

## RECAP AND MORE...

- Detailed analytical study of a rich repertoire of model states
- All possible $2 T R$-periodic states
- Cascades of period doubling and segregated switching
- Computational analysis under smooth conditions
- Link $2 T R$-periodic states with AS perceptions
- States occupying larger region of existence
- Quantitative agreement when varying parameters influencing AS perception
- Neuro-inspired model of AS with biophysical parameters
- Slow inhibition masks the perception of subsequent tones during segregation
- Fast excitation enables integration for large tones' pitch differences
- More... (not shown in this presentation)
- Bistability via inhibitory feedback from a third, intrinsically oscillating unit
- Study of other exotic states (cycle skipping)

Thank you!!

