

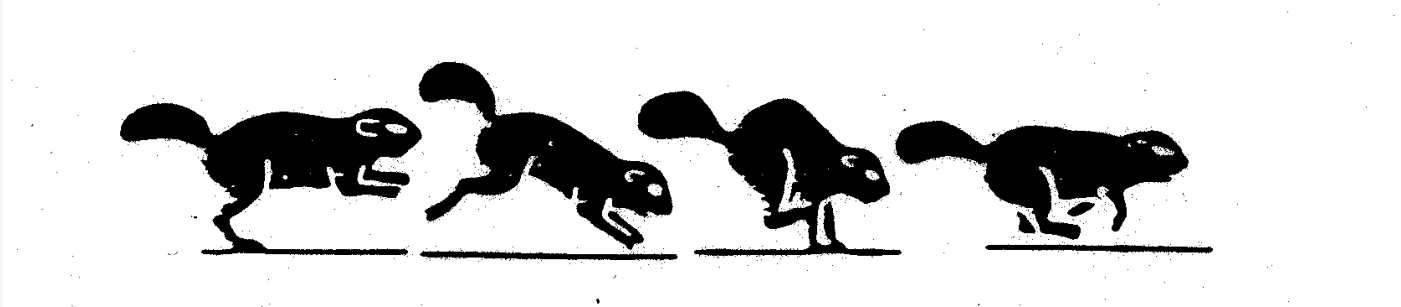
Patterns of Synchrony From Animal Gaits to Binocular Rivalry

Gateways to Emergent Behavior in Science and Society
ICAM/SFI Workshop
September 24, 2013

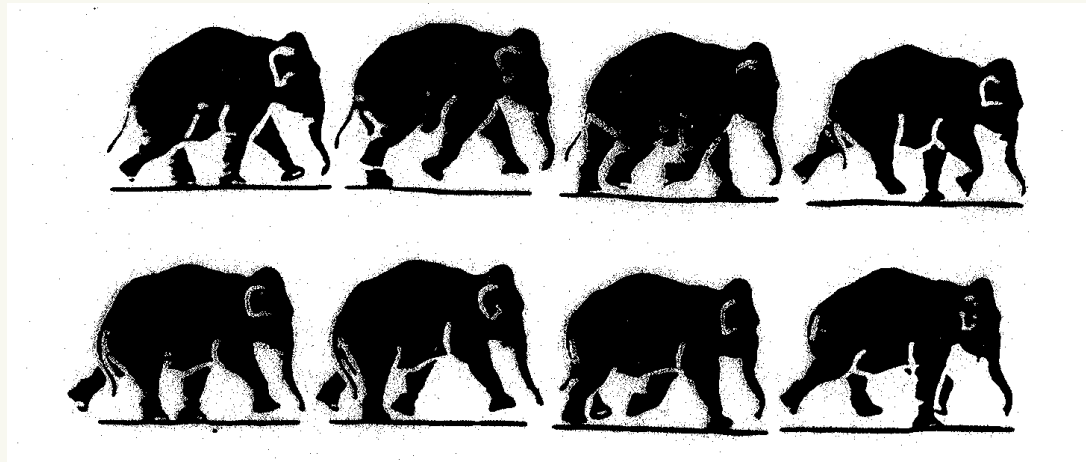
Marty Golubitsky
Mathematical Biosciences Institute
and
Department of Mathematics
Ohio State University

Quadruped Gaits

- **Bound** of the Siberian Souslik

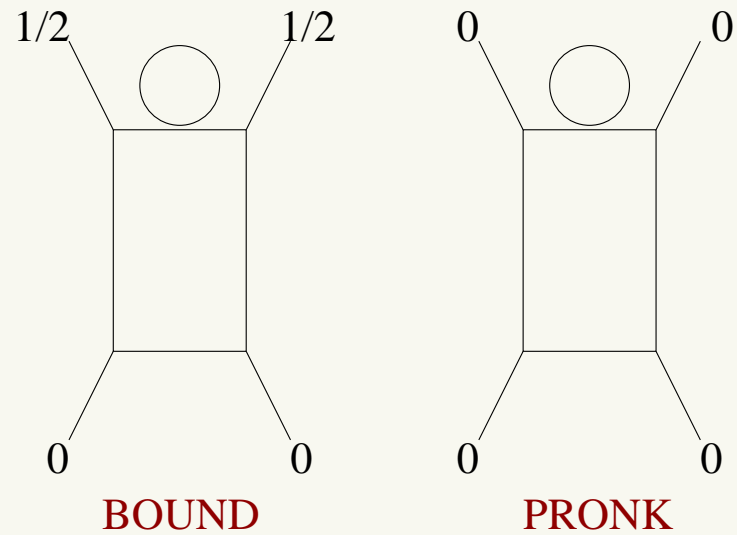
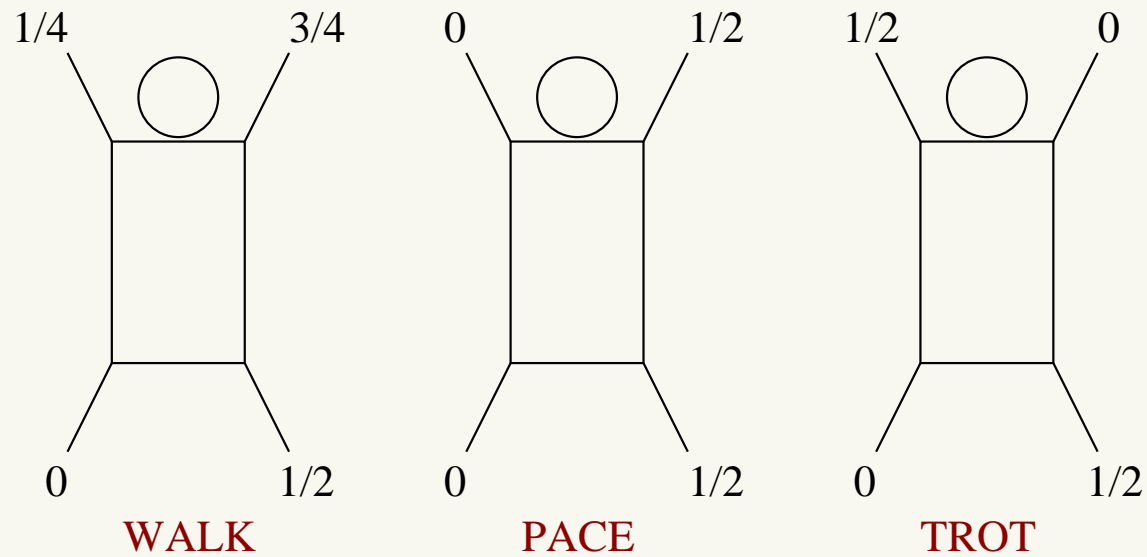


- **Amble** of the Elephant



- **Trot** of the Horse

Rigid Gait Phases for Quadruped Gaits



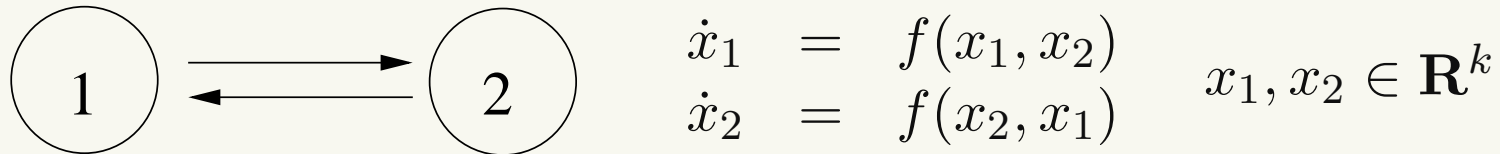
Gait Symmetries / Central Pattern Generators

Gait	Spatio-temporal symmetries
Trot	(Left/Right, $\frac{1}{2}$) and (Front/Back, $\frac{1}{2}$)
Pace	(Left/Right, $\frac{1}{2}$) and (Front/Back, 0)
Walk	(Figure Eight, $\frac{1}{4}$)

- Network of neurons (CPG) that produces gait rhythms
- Hodgkin - Huxley (1952)
Neuron modeled by system of differential equations
- Design simplest network that produces independent
walk, trot, pace

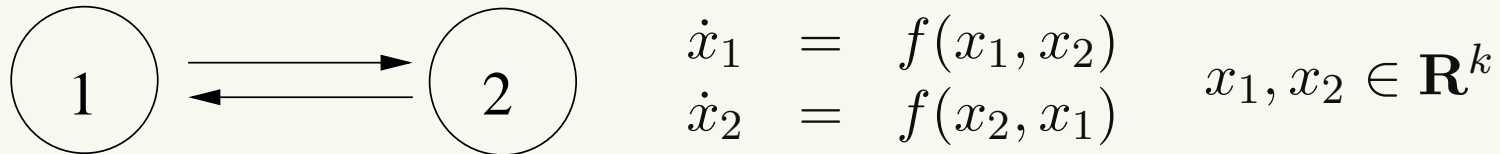
Collins and Stewart (1993); G., Stewart, Buono, and Collins (1999)

Rigid Phase-Shift Synchrony



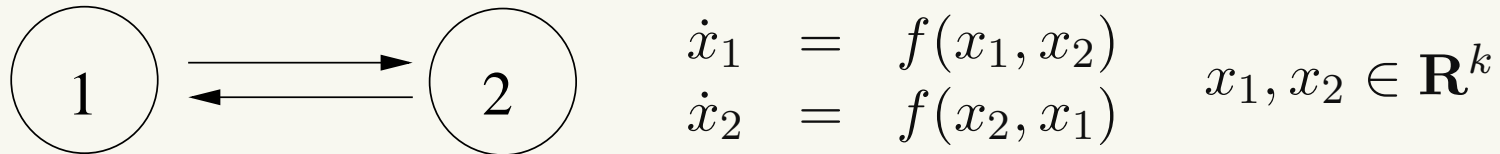
- **Symmetry**: sends solutions to solutions \mathbf{Z}_2 symmetry
- Nodes oscillate **in phase**: $x_2(t) = x_1(t)$
Nodes **half-period out of phase**: $x_2(t) = x_1(t + \frac{1}{2}T)$

Rigid Phase-Shift Synchrony



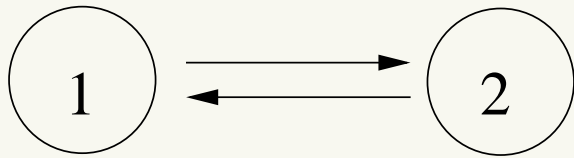
- **Symmetry**: sends solutions to solutions \mathbf{Z}_2 symmetry
- Nodes oscillate **in phase**: $x_2(t) = x_1(t)$
Nodes **half-period out of phase**: $x_2(t) = x_1(t + \frac{1}{2}T)$
- Let $x(t)$ be a hyperbolic **T -periodic** solution
 $H = \{\gamma \in \Gamma : \gamma\{x(t)\} = \{x(t)\}\}$ **spatiotemporal symmetries**
 $\gamma \in H \implies \theta \in [0, 1)$ such that $\gamma x(t) = x(t + \theta T)$

Rigid Phase-Shift Synchrony



- **Symmetry**: sends solutions to solutions \mathbf{Z}_2 symmetry
- Nodes oscillate **in phase**: $x_2(t) = x_1(t)$
Nodes **half-period out of phase**: $x_2(t) = x_1(t + \frac{1}{2}T)$
- Let $x(t)$ be a hyperbolic **T -periodic** solution
 $H = \{\gamma \in \Gamma : \gamma\{x(t)\} = \{x(t)\}\}$ **spatiotemporal symmetries**
 $\gamma \in H \implies \theta \in [0, 1)$ such that $\gamma x(t) = x(t + \theta T)$
- H is **rigid** to equivariant perturbations
- **Example**: $H = \mathbf{Z}_2(1 \ 2)$; $\theta = 0$ or $\theta = \frac{1}{2}$

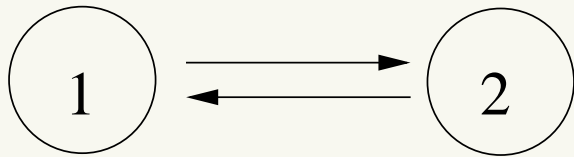
Two Identical Cells: Solutions via Hopf Bifurcation



$$\begin{aligned}\dot{x}_1 &= f(x_1, x_2, \lambda) \\ \dot{x}_2 &= f(x_2, x_1, \lambda) \\ 0 &= f(0, 0, \lambda)\end{aligned} \quad x_1, x_2 \in \mathbf{R}^k$$

- $J(\lambda) = \begin{bmatrix} \alpha(\lambda) & \beta(\lambda) \\ \beta(\lambda) & \alpha(\lambda) \end{bmatrix}$; $\begin{bmatrix} x \\ x \end{bmatrix}, \begin{bmatrix} x \\ -x \end{bmatrix}$ invariant subsp's
 α = linear internal dynamics; β = linear coupling
- eigenvalues of J are eigenvalues of $\alpha + \beta$ and $\alpha - \beta$

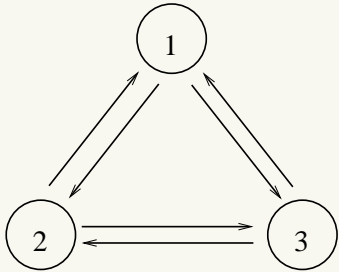
Two Identical Cells: Solutions via Hopf Bifurcation



$$\begin{aligned}\dot{x}_1 &= f(x_1, x_2, \lambda) \\ \dot{x}_2 &= f(x_2, x_1, \lambda) \\ 0 &= f(0, 0, \lambda)\end{aligned} \quad x_1, x_2 \in \mathbf{R}^k$$

- $J(\lambda) = \begin{bmatrix} \alpha(\lambda) & \beta(\lambda) \\ \beta(\lambda) & \alpha(\lambda) \end{bmatrix}$; $\begin{bmatrix} x \\ x \end{bmatrix}, \begin{bmatrix} x \\ -x \end{bmatrix}$ invariant subsp's
 α = linear internal dynamics; β = linear coupling
- eigenvalues of J are eigenvalues of $\alpha + \beta$ and $\alpha - \beta$
- $\alpha + \beta$ critical: **synchronous** periodic solutions
- $\alpha - \beta$ critical: **half-period out of phase** periodic solutions

Three-Cell Bidirectional Ring: $\Gamma = \mathbf{D}_3$



$$\begin{aligned}\dot{x}_1 &= f(x_1, x_2, x_3) \\ \dot{x}_2 &= f(x_2, x_3, x_1) & f(x_2, x_1, x_3) = f(x_2, x_3, x_1) \\ \dot{x}_3 &= f(x_3, x_1, x_2)\end{aligned}$$

- Discrete rotating waves: $H = \mathbf{Z}_3(1\ 2\ 3), \theta = \frac{1}{3}$

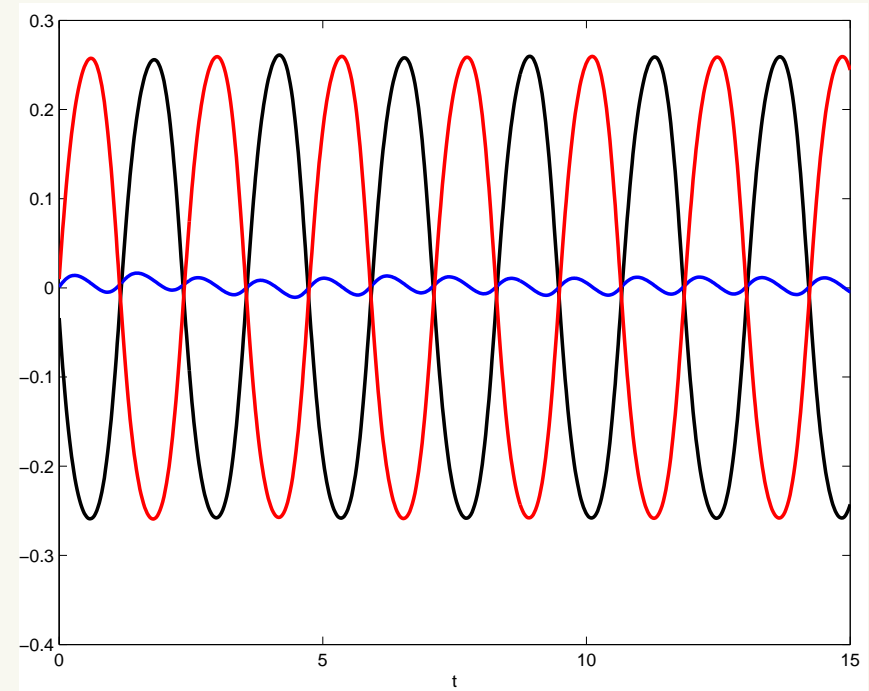
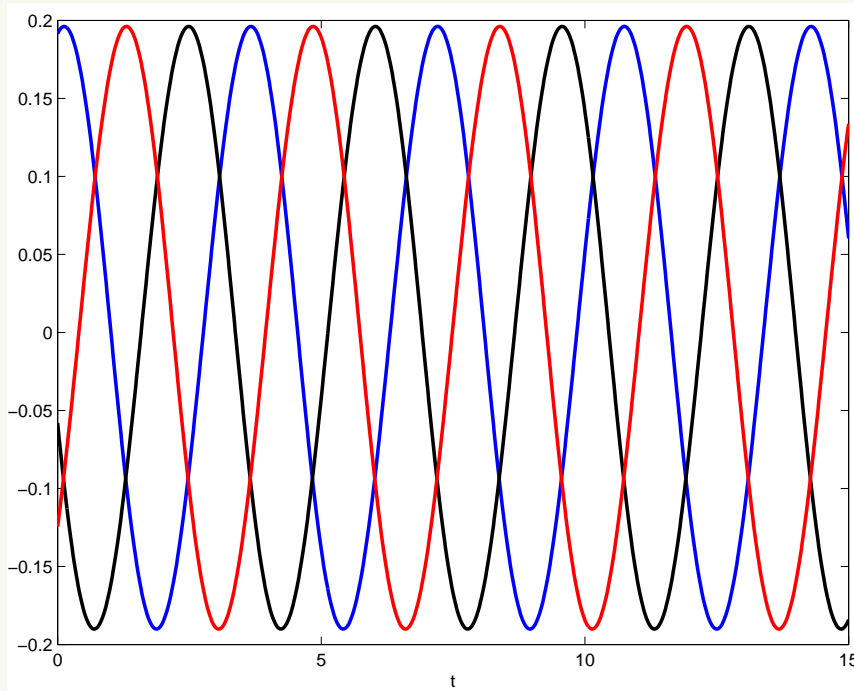
$$x_3(t) = x_2(t + \frac{1}{3}T) = x_1(t + \frac{2}{3}T)$$

- Out-of-phase periodic solutions: $H = \mathbf{Z}_2(1\ 3), \theta = \frac{1}{2}$

$$x_3(t) = x_1(t + \frac{1}{2}T) \quad \text{and} \quad x_2(t) = x_2(t + \frac{1}{2}T)$$

G. and Stewart (1986); van Gils and Valkering (1986)

Time Series and Phase Shifts



- Discrete Rotating Wave: $x_3(t) = x_2(t + \frac{1}{3}T) = x_1(t + \frac{2}{3}T)$
- Out-of-phase: $x_3(t) = x_1(t + \frac{1}{2}T)$ and $x_2(t) = x_2(t + \frac{1}{2}T)$

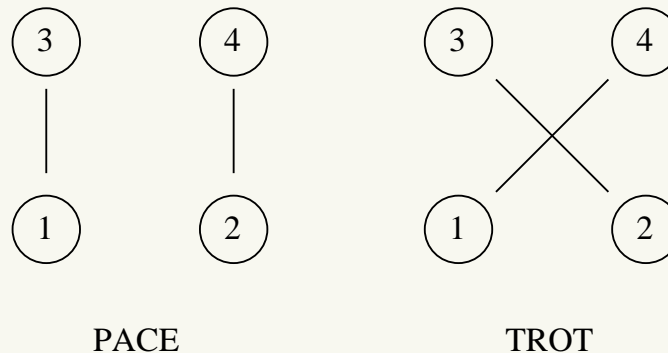
G. and Stewart (1986); van Gils and Valkering (1986)

Four Cells Do Not Suffice

- Network produces **walk**. There is a four-cycle symmetry

$$(1\ 3\ 2\ 4)$$

- Four-cycle **permutes** **pace** to **trot**

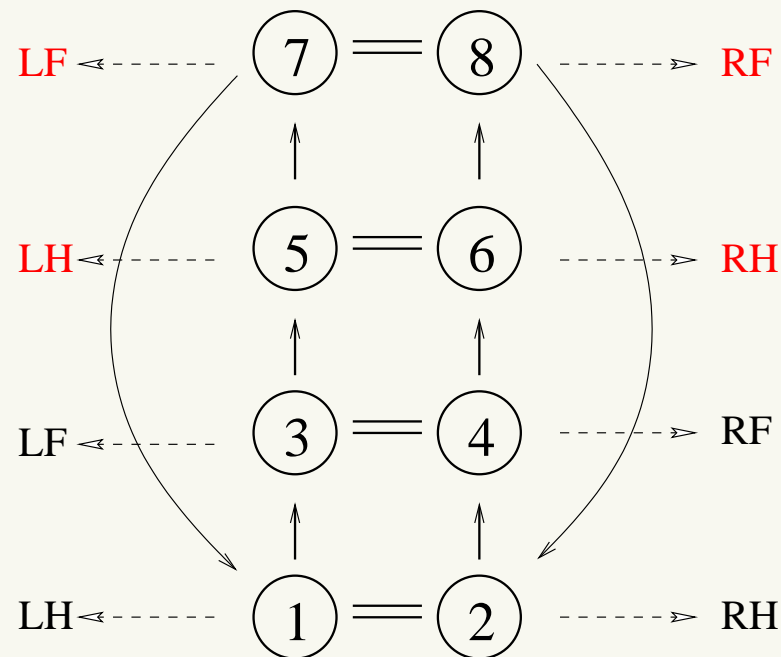


- CPG **cannot** be modeled by **four-cell** network where each cell gives rhythmic pulsing to one leg

G., Stewart, Buono, and Collins (1999)

Central Pattern Generators (CPG)

- Use gait symmetries to construct network and rhythms
 - 1) **walk** \implies four-cycle ω in symmetry group
 - 2) **pace** or **trot** \implies transposition κ in symmetry group
- **Simplest** network has $\mathbf{Z}_4(\omega) \times \mathbf{Z}_2(\kappa)$ symmetry



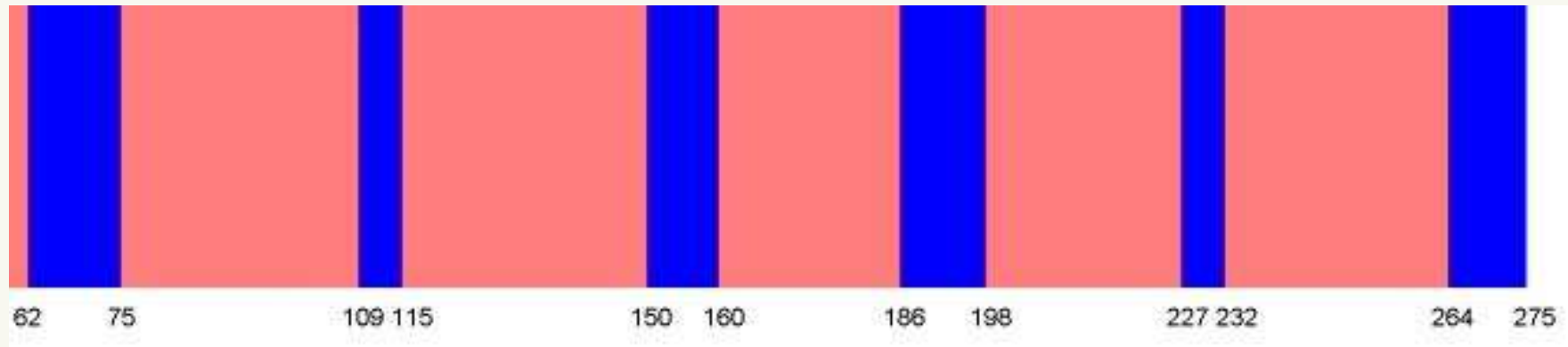
G., Stewart, Buono, and Collins (1999); Buono and G. (2001)

Primary Gaits or Hopf Bifurcation from Stand: $H = \mathbf{Z}_4(\omega) \times \mathbf{Z}_2(\kappa)$

Kernel of H	Phase Diagram	Gait
$\mathbf{Z}_4(\omega) \times \mathbf{Z}_2(\kappa)$	$\begin{array}{cc} 0 & 0 \\ 0 & 0 \end{array}$	pronk
$\mathbf{Z}_4(\omega)$	$\begin{array}{cc} 0 & \frac{1}{2} \\ 0 & \frac{1}{2} \end{array}$	pace
$\mathbf{Z}_4(\kappa\omega)$	$\begin{array}{cc} \frac{1}{2} & 0 \\ 0 & \frac{1}{2} \end{array}$	trot
$\mathbf{Z}_2(\kappa) \times \mathbf{Z}_2(\omega^2)$	$\begin{array}{cc} \frac{1}{2} & \frac{1}{2} \\ 0 & 0 \end{array}$	bound
$\mathbf{Z}_2(\kappa\omega^2)$	$\begin{array}{cc} \frac{1}{4} & \frac{3}{4} \\ 0 & \frac{1}{2} \end{array}$	walk
$\mathbf{Z}_2(\kappa)$	$\begin{array}{cc} 0 & 0 \\ \frac{1}{4} & \frac{1}{4} \end{array}$	jump

G., Stewart, Buono, and Collins (2000)

The Jump

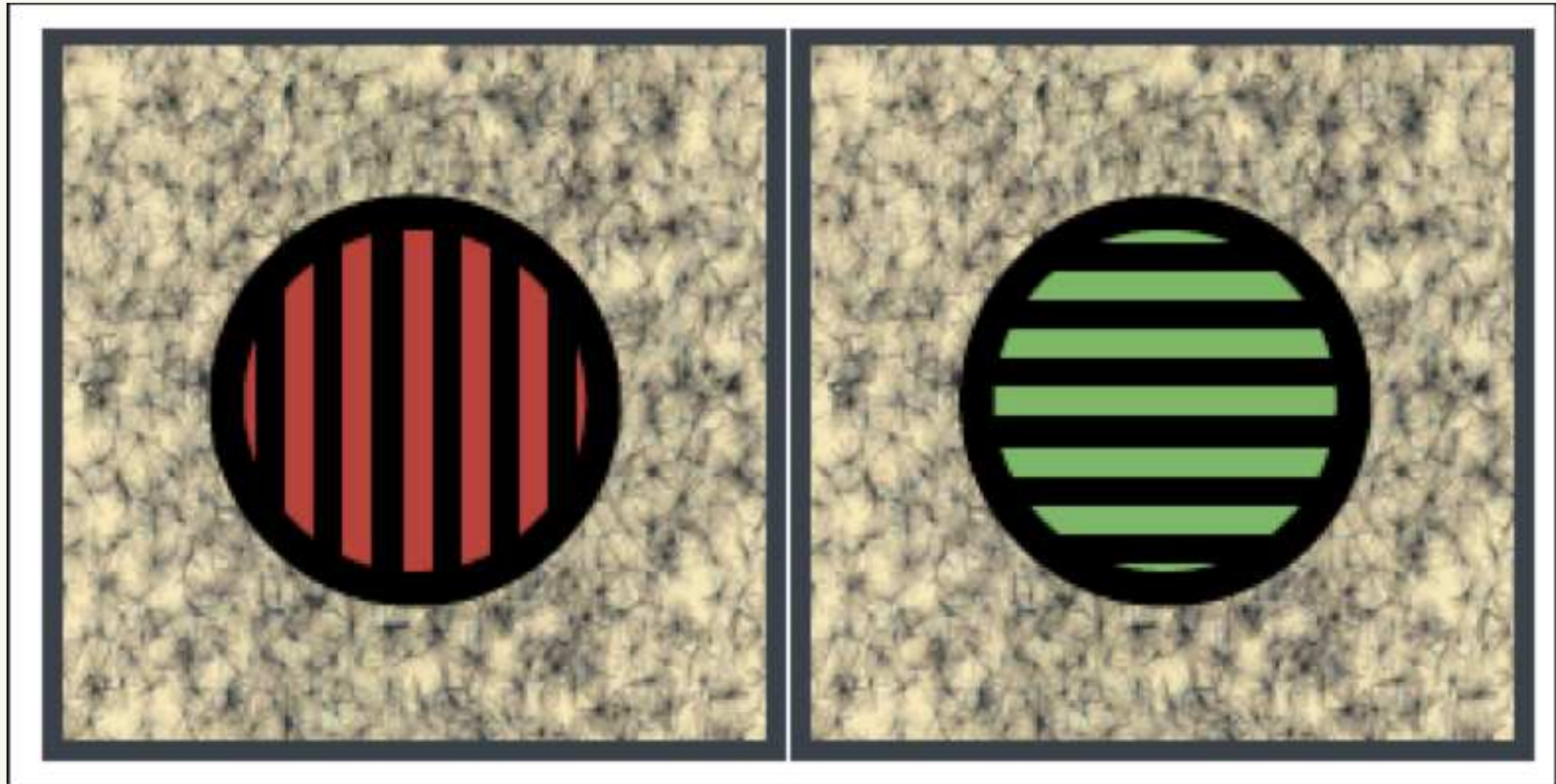


- Average Right Rear to Right Front = 31.2 frames
- Average Right Front to Right Rear = 11.4 frames
- $\frac{31.2}{11.4} = 2.74$

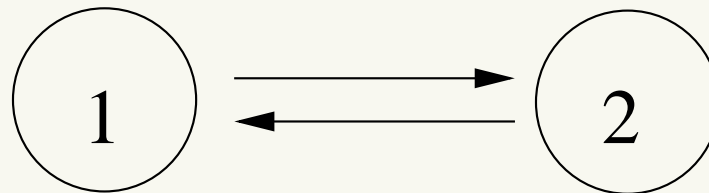
G., Stewart, Buono, and Collins (2000)

Binocular Rivalry: Different Images Presented to Two Eyes

How does the brain deal with CONTRADICTORY information



- Often modeled by two units



Simplest Rivalry Equations for Two Units

- Units a and b consist of an **activity variable** $*^E$ (firing rate) and a **fatigue variable** $*^H$ (reduces activity on long time scale)

$$\begin{aligned}\varepsilon \dot{a}^E &= -a^E + \mathcal{G}(I - \beta b^E - g a^H) \\ \dot{a}^H &= a^E - a^H \\ \varepsilon \dot{b}^E &= -b^E + \mathcal{G}(I - \beta a^E - g b^H) \\ \dot{b}^H &= b^E - b^H\end{aligned}$$

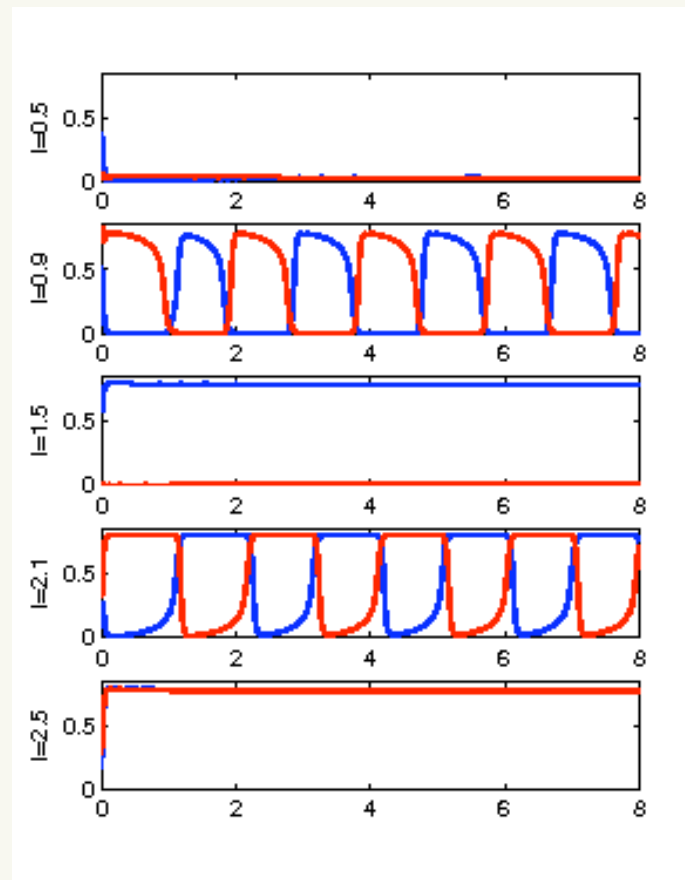
- \mathcal{G} = **gain function**
 β = **reciprocal inhibition**
 I = **external signal strength**
 g = **strength** of reduction of $*^E$ by $*^H$
 $\varepsilon \ll 1$ is **ratio of time scales** on which $*^E$ and $*^H$ evolve

Laing and Chow (2002), Curtu, Shpiro, Rubin, and Rinzel (2008); Wilson (2009);
Curtu (2010); Diekmann, G., McMillen, and Wang (2012)

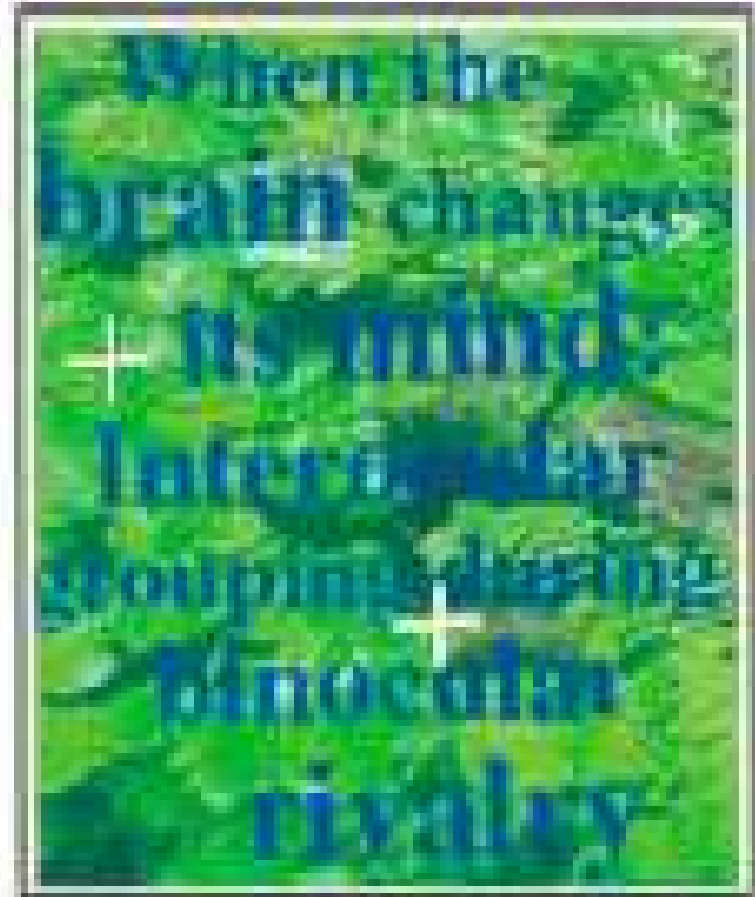
Two Unit Model Solution Types

Three types of states:

- **Fusion** = equilibria in which units have equal values
Rigid fused states forced by symmetry
- **Winner-Take-All** = equilibria with different activity levels
- **Rivalry** = two units oscillate in periods of dominance
Rigid rivalry forced by symmetry



Kovács First Experiment: Conventional Monkey and Text



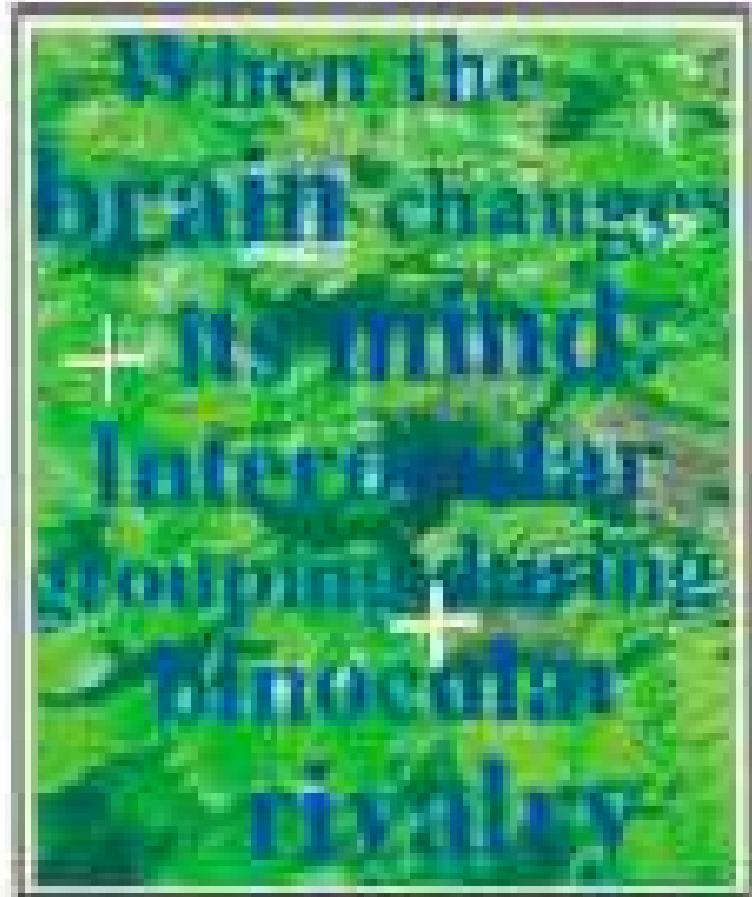
Kovács, Papathomas, Yang, and Fehér (1996)

Kovács Second Experiment: Scrambled Monkey and Text



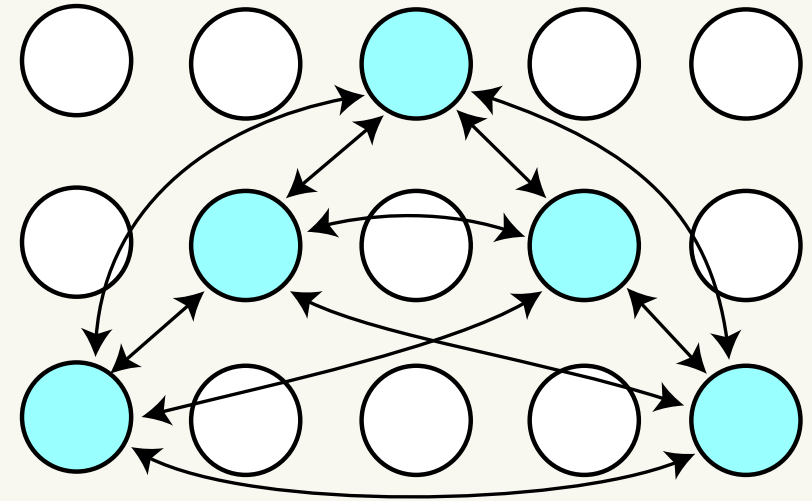
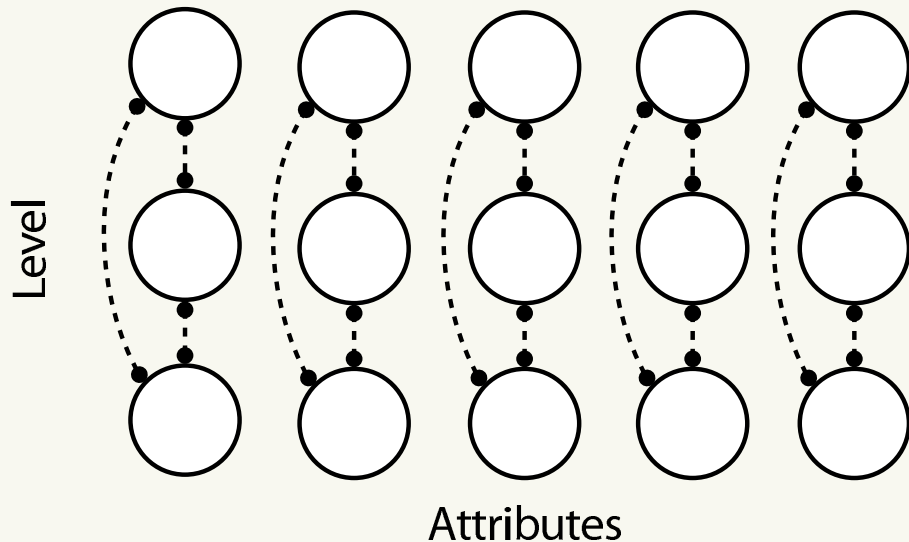
Kovács, Papathomas, Yang, and Fehér (1996)

Scrambled Monkey and Text: Interocular Groupings



Kovács, Papathomas, Yang, and Fehér (1996)

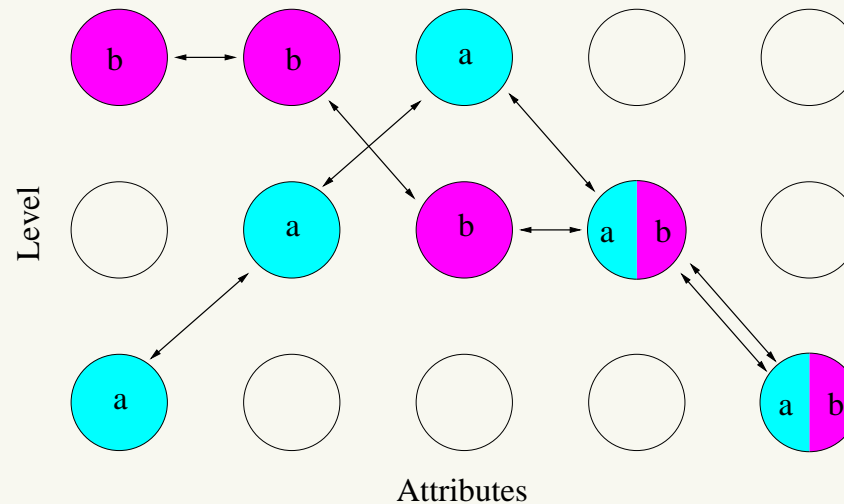
Wilson's Model for Generalized Rivalry



- Columns represent **attributes**; rows represent **level** of attribute
- (L) **Inhibition** between nodes in column (dashed lines)
- (R) **Excitation** between nodes in **learned** pattern (solid lines)

Wilson (2008, 2009)

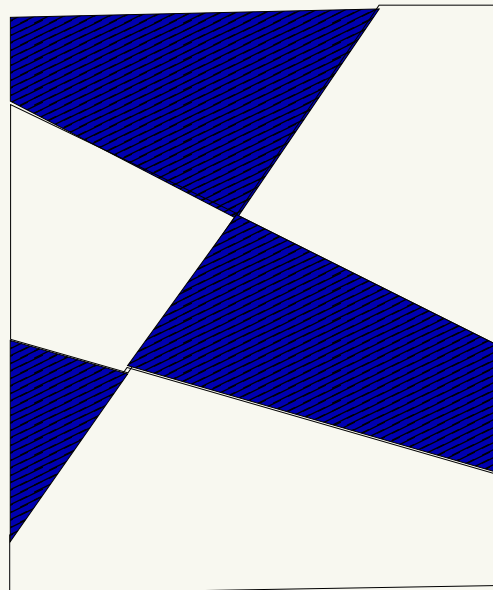
Two Learned Patterns a and b



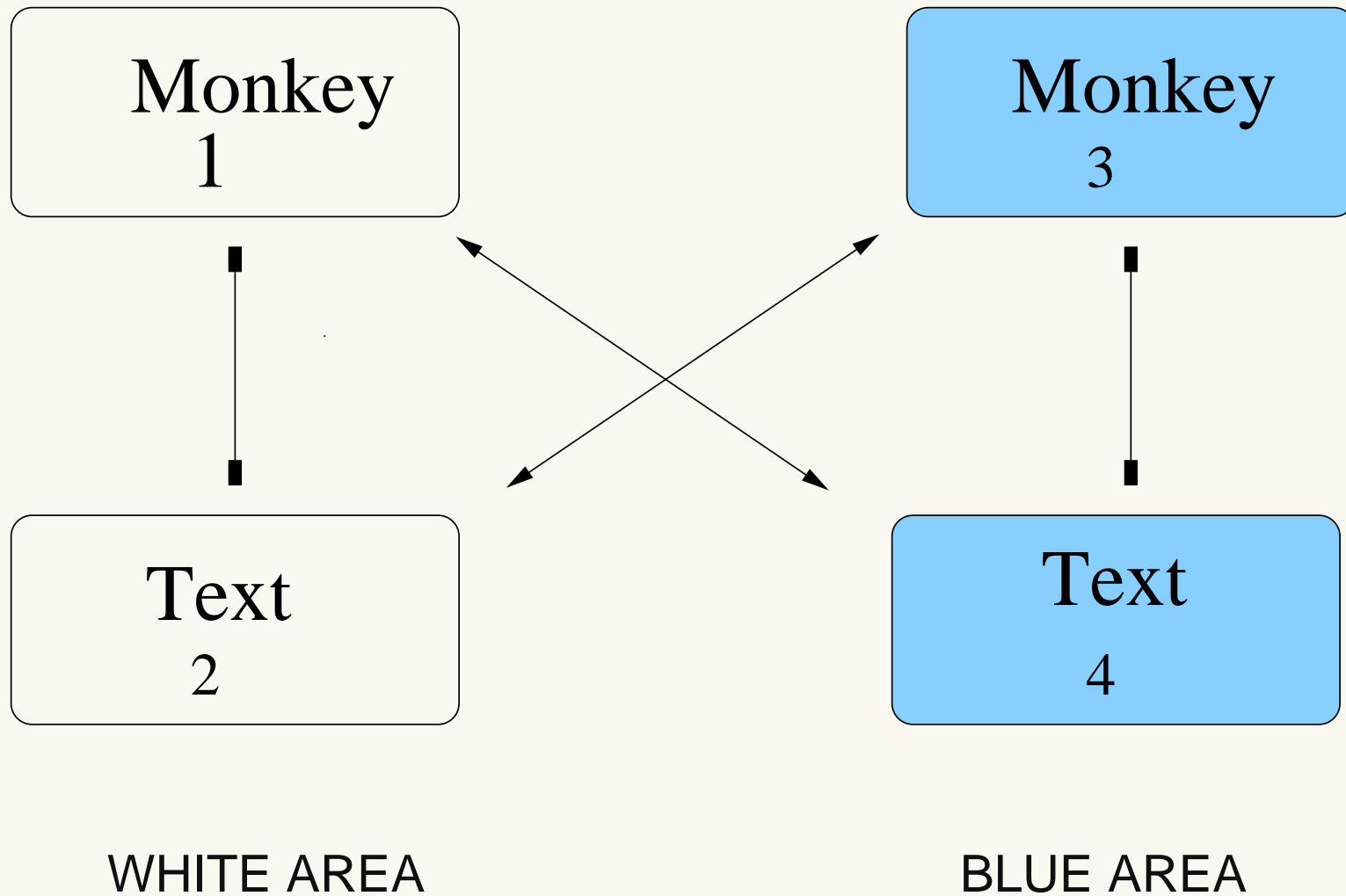
- **Learned pattern:** one node from each attribute column
Excitation between nodes in learned pattern
- **Derived Patterns:** Patterns that are not learned

Diekman, G., McMillen, and Wang (2012, 2013)

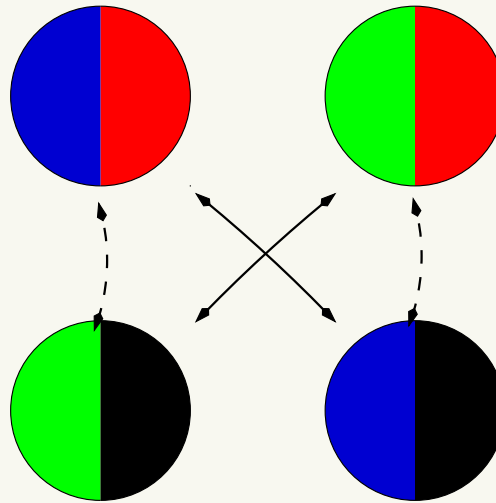
Rivalry in Monkey and Text



Wilson Network for Second Kovacs Experiment

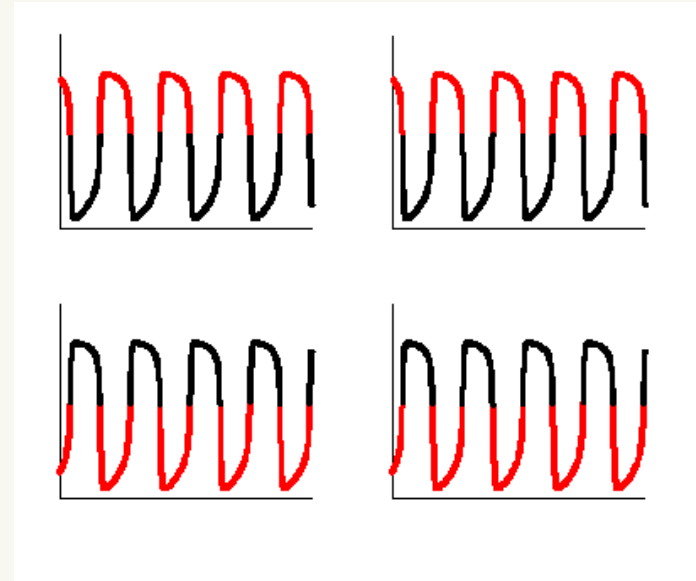
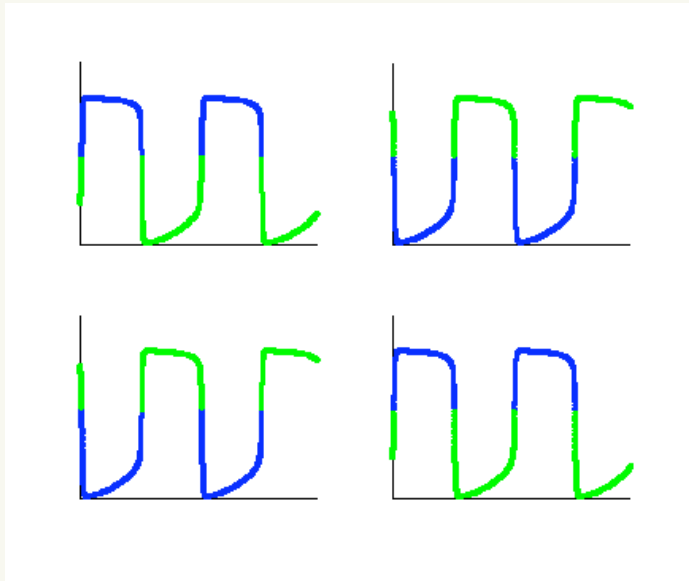


2 Attributes; 2 Levels; 2 Learned Patterns; 2 Derived Patterns



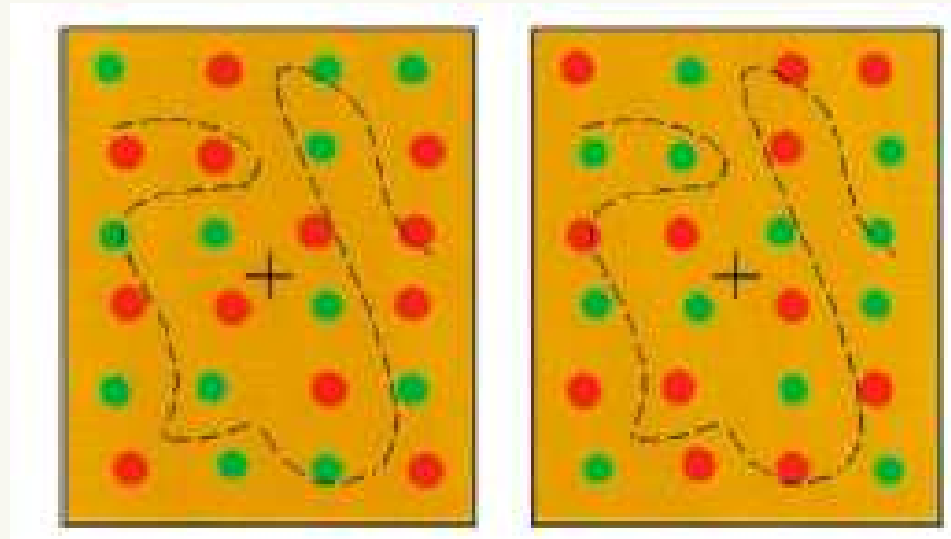
- $x_1^E > x_2^E$ and $x_3^E > x_4^E$ (whole monkey; derived, RED)
- $x_1^E > x_2^E$ and $x_4^E > x_3^E$ (mixed image; learned, BLUE)
- $x_2^E > x_1^E$ and $x_3^E > x_4^E$ (mixed image; learned, GREEN)
- $x_2^E > x_1^E$ and $x_4^E > x_3^E$ (all text; derived, BLACK)

Patterns in Wilson Model of Kovacs Second Experiment

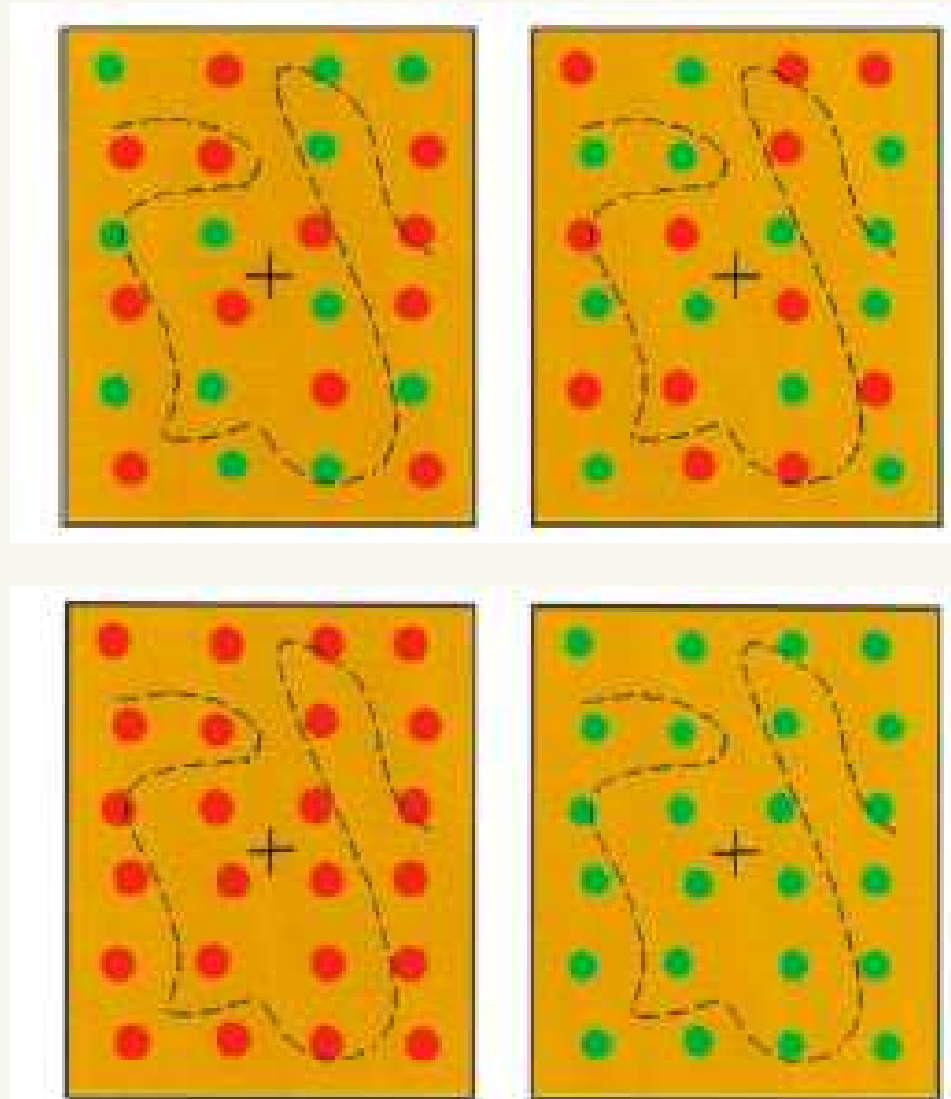


- 2 **learned** patterns: **BLUE** and **GREEN**
2 **derived** patterns: **RED** and **BLACK**
- Rivalry: **BLUE-GREEN** (**learned**); **BLACK-RED** (**derived**)

Third Kovacs Experiment: Scrambled Disc Patterns

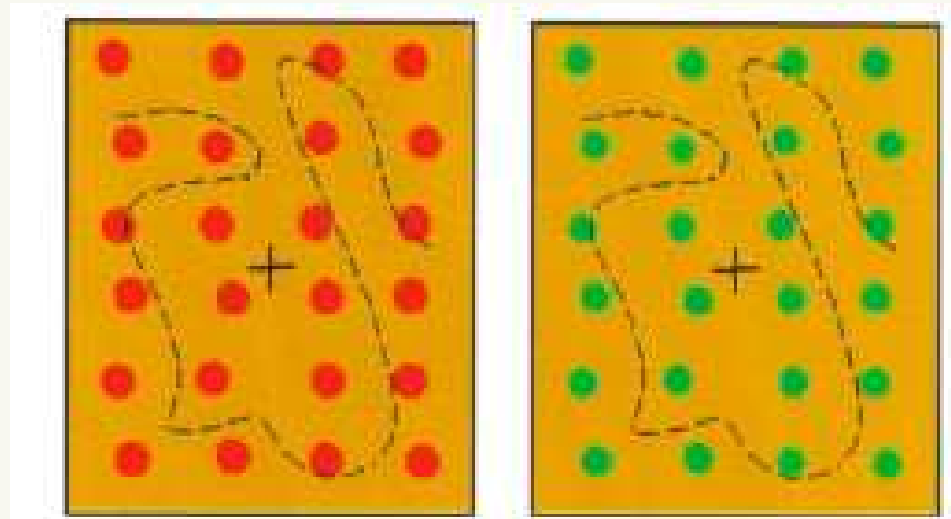


Third Kovacs Experiment: Scrambled Disc Patterns

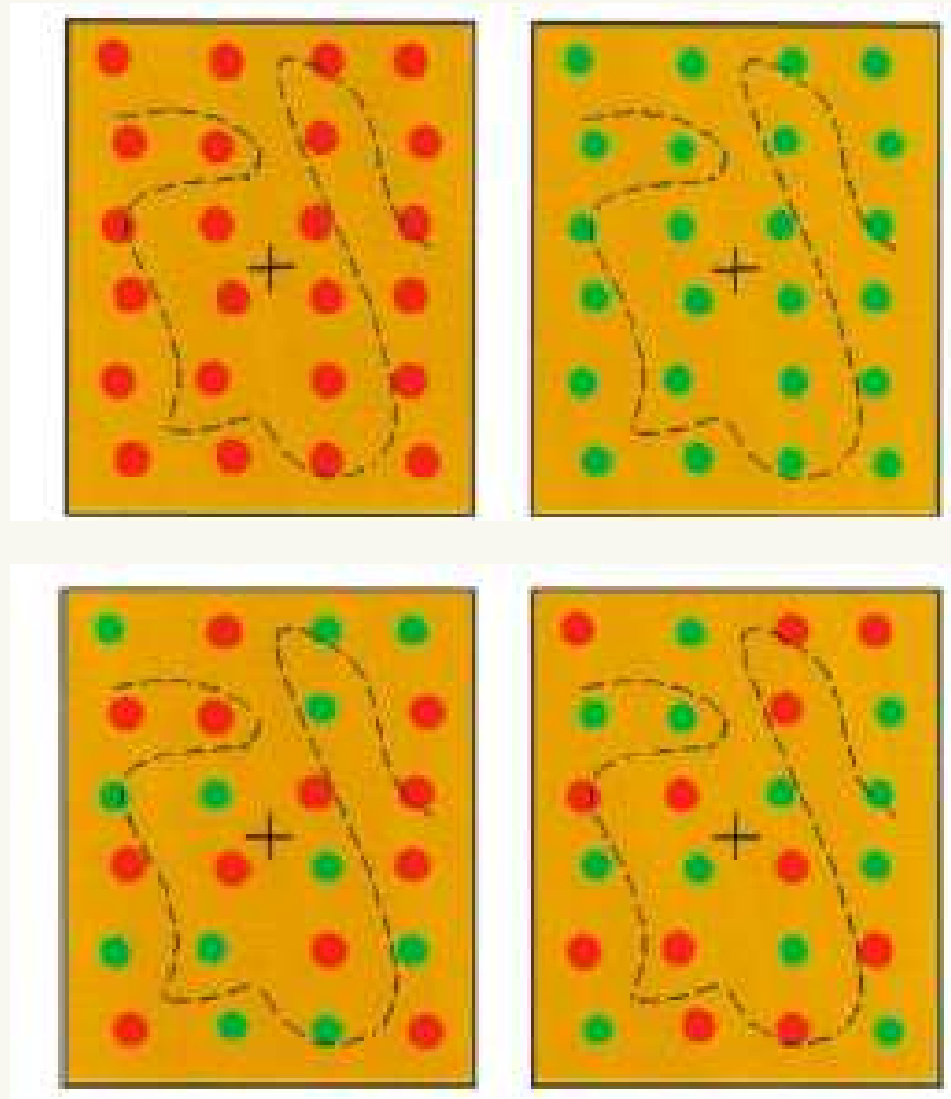


Kovács, Papathomas, Yang, and Fehér (1996)

Fourth Kovacs Experiment: Conventional Disc Patterns



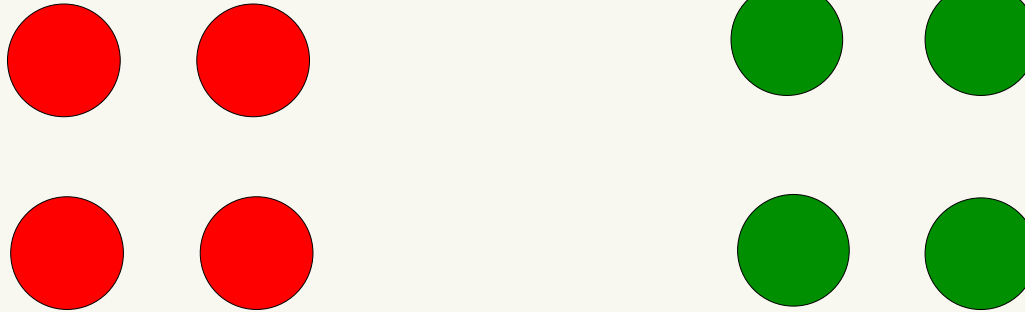
Fourth Kovacs Experiment: Conventional Disc Patterns



Kovács, Papathomas, Yang, and Fehér (1996)

Tong's Simplified Rivalry Between Disc Patterns

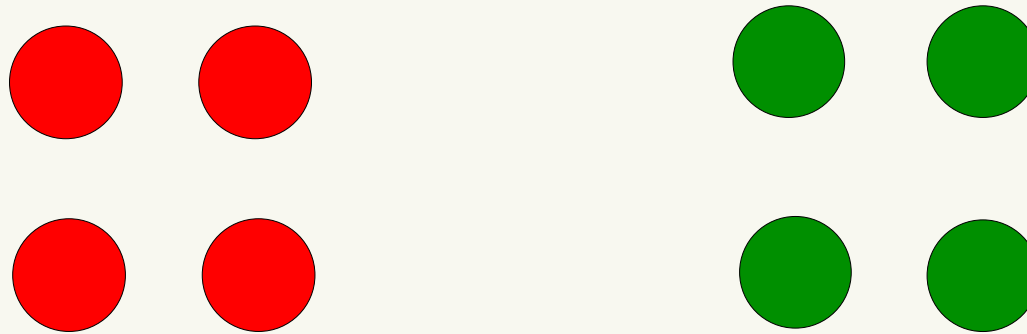
- Rivalry between two **learned patterns**



Tong, Meng, and Blake (2006)

Tong's Simplified Rivalry Between Disc Patterns

- Rivalry between two **learned patterns**



Tong, Meng, and Blake (2006)

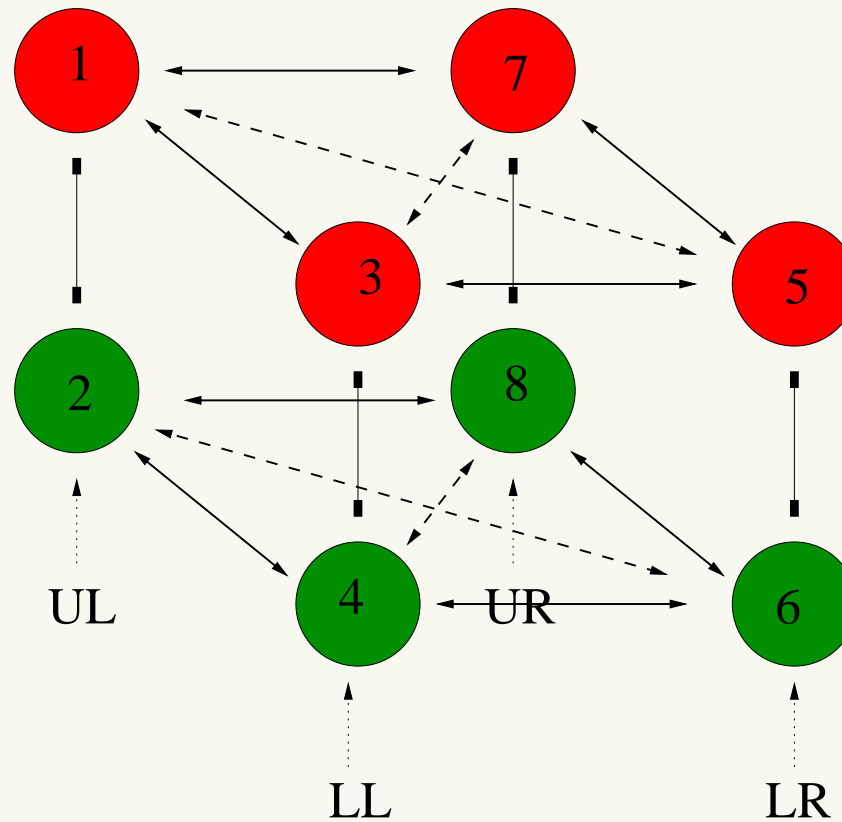
- Rivalry between two **derived patterns** should also be observed



Rivalry Network for Conventional Tong Experiment

- Two learned patterns: RED and GREEN

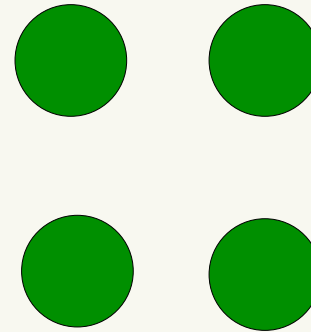
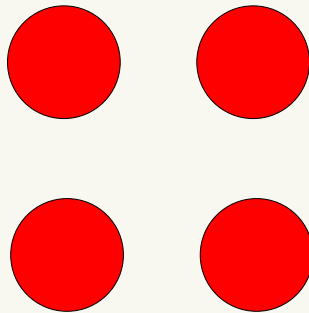
Symmetry group $\Gamma = \mathbf{D}_4 \times \mathbf{Z}_2(\rho)$



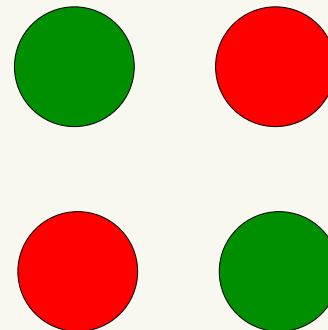
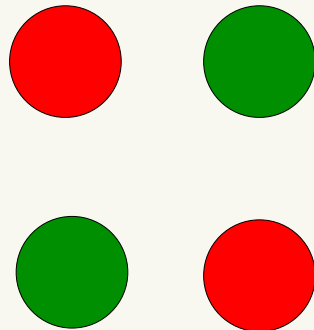
Diekman, G., and Wang (2013)

Patterns in Conventional Tong Experiment (1)

-
- Rivalry between **learned patterns**

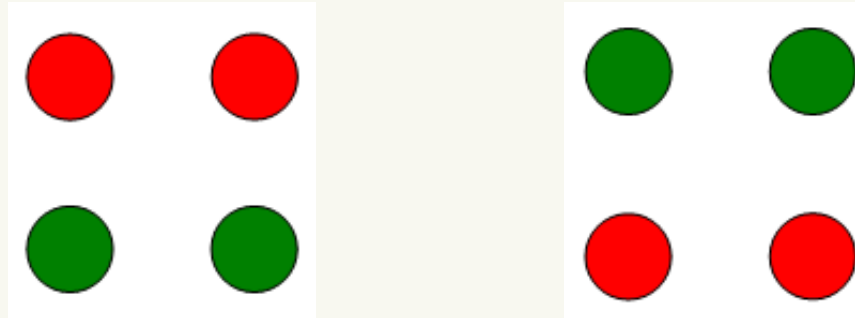


- Rivalry between **derived patterns**

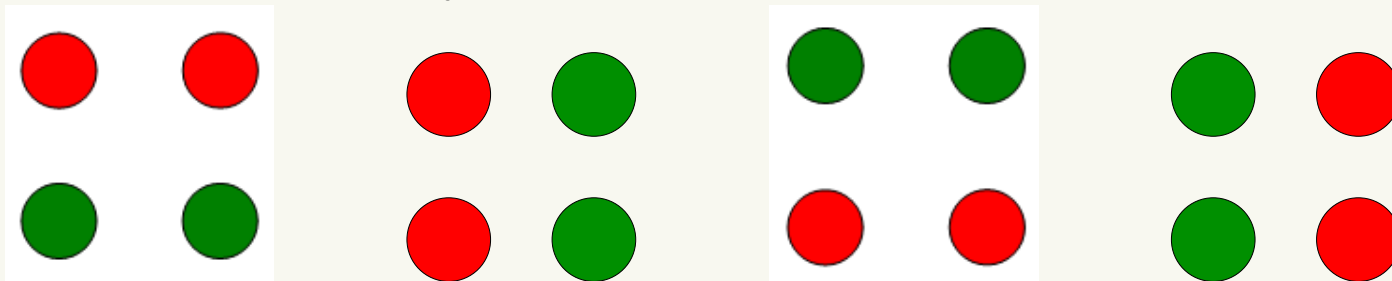


Patterns in Conventional Tong Experiment (2)

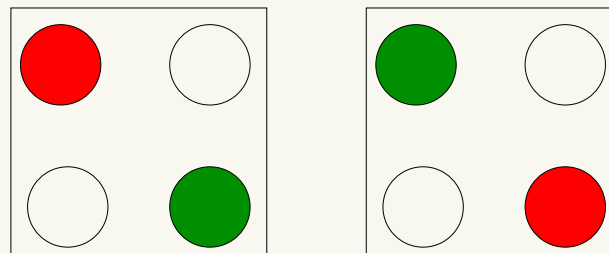
- Adjacent colors



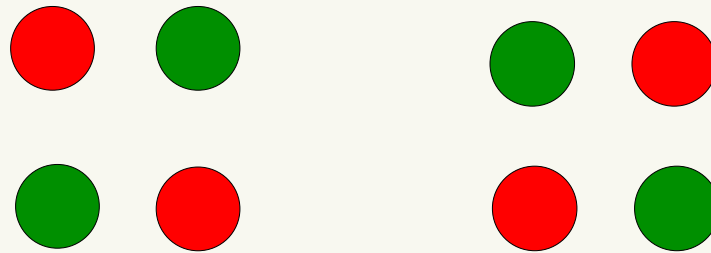
- Adjacent colors rotate by 90° in quarter period



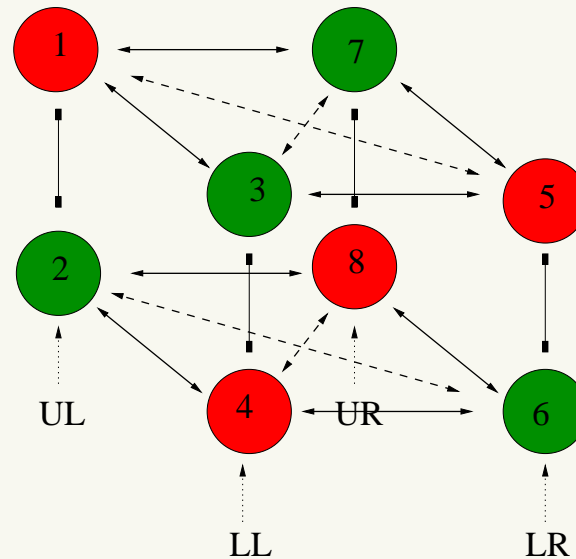
- Two dots on diagonal alternate between; other two dots are fused



Wilson Network for Scrambled Tong Experiment

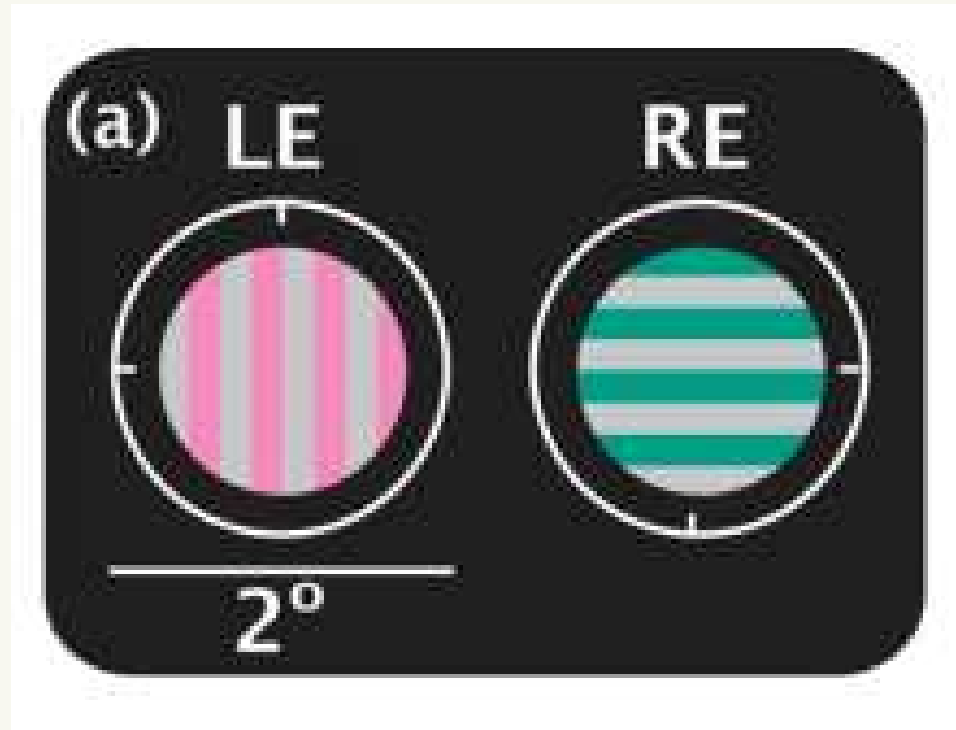


Learned Images in simplification of scrambled *colored dot* experiment

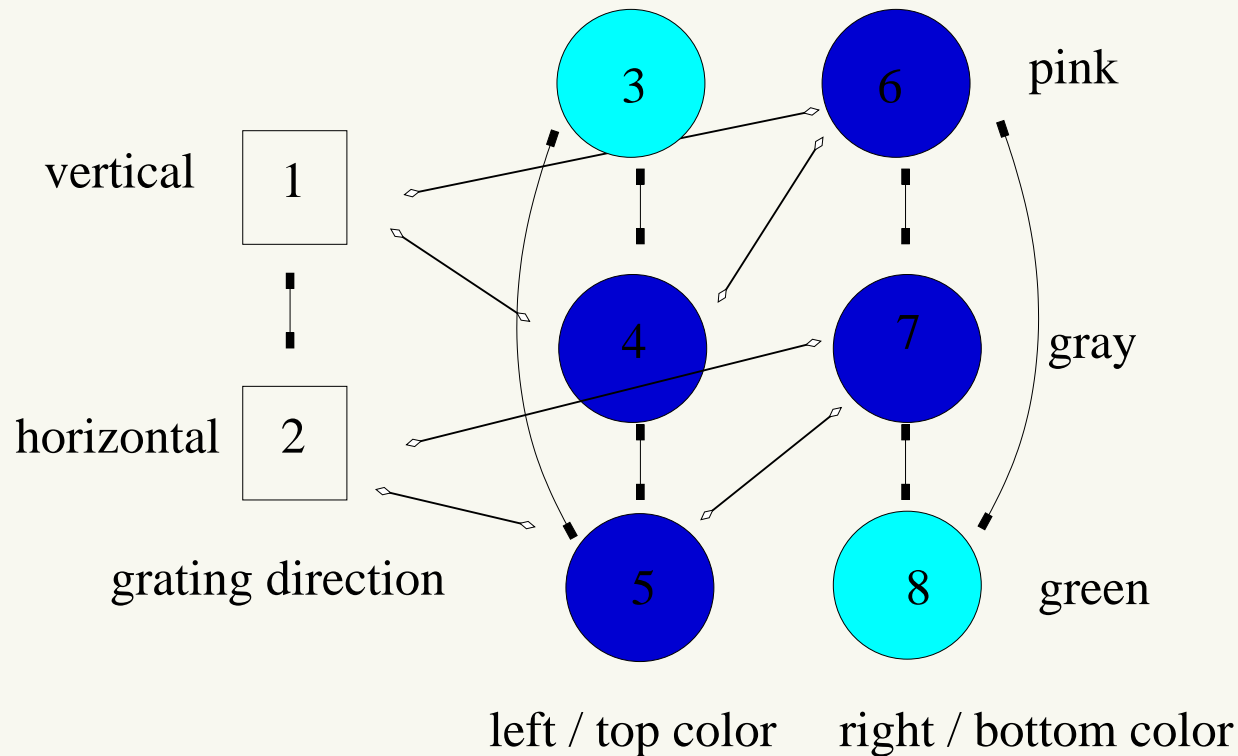


Network corresponding to simplified scrambled experiment

- Symmetry group is $\mathbf{D}_4 \times \mathbf{Z}_2(\rho)$
Learned & derived **interchanged** with conventional experiment



Wilson Network for Shevell, St. Clair, and Hong



Symmetries

$$\rho = (1\ 2)(4\ 5)(6\ 7)$$

$$\tau = (3\ 8)(4\ 6)(5\ 7)$$

$$\rho\tau = (1\ 2)(3\ 8)(4\ 7)(5\ 6)$$

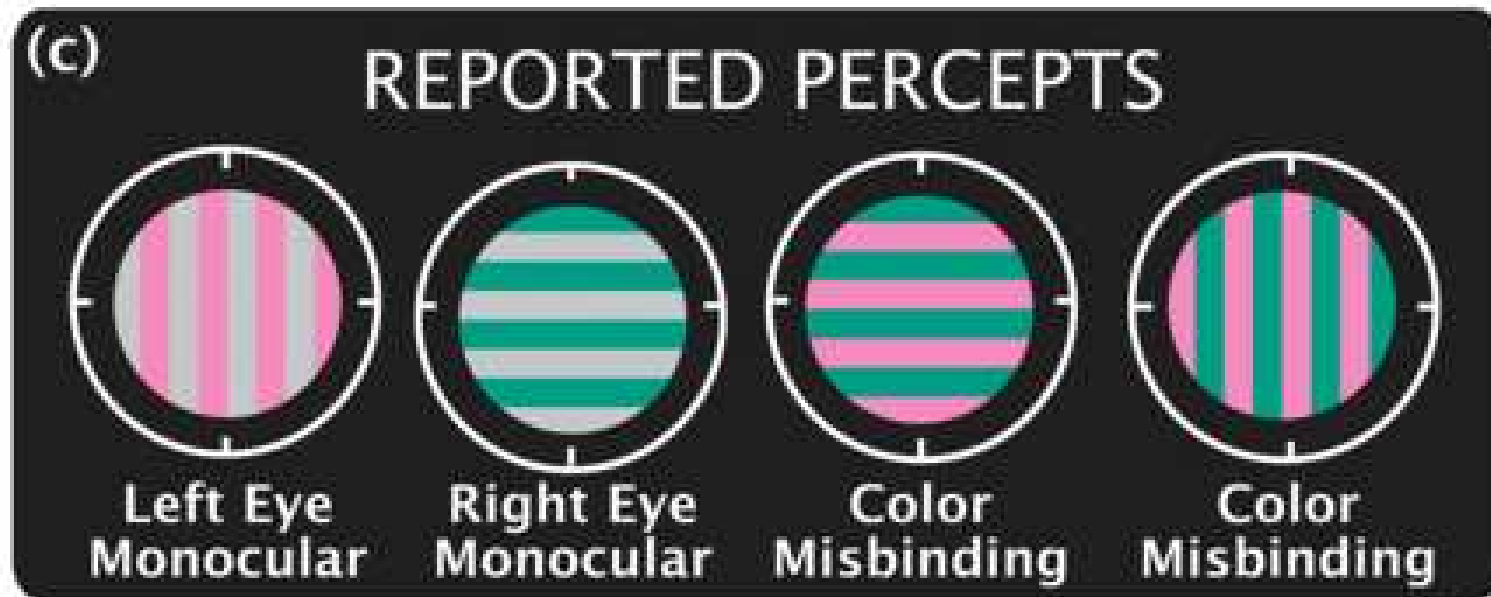
$$\rho = -1 = \rho\tau; \tau = +1$$

Fusion States

$$\begin{aligned} \text{Gray-Pink} &\leftrightarrow \text{Green-Gray} \text{ if } x_3^E < x_4^E = x_5^E \\ \text{Pink-Green} &\text{ if } x_3^E > x_4^E = x_5^E \end{aligned}$$

$$\text{Maximally fused states} = \{x_1 = x_2; x_3 = x_8; x_4 = x_5 = x_6 = x_7\}$$

Shevell, St. Clair & Hong 2008 Observed Percepts



Percepts observers reported during experiments

Synchrony and Synchrony Subspaces

RIGID PHASE-SHIFT SYNCHRONY

- $X(t) = (x_1(t), \dots, x_n(t))$ exhibits **partial synchrony** if

$$x_c(t) = x_d(t)$$

for two nodes c and d .

- **polydiagonal** = subspace

$$\Delta = \{x : x_c = x_d \text{ for some subset of pairs of cells } c, d\}$$

- **synchrony subspace** = polydiagonal **flow-invariant** \forall admissibles

All solutions in a synchrony subspace exhibit partial synchrony

Synchrony Subspaces from Network Symmetry

- σ is a **symmetry** of $\dot{X} = F(X)$ if it maps solutions to solutions

Equivalent to $F(\sigma x) = \sigma F(x)$

- **Fix**(Σ) = $\{x \in \mathbf{R}^n : \sigma x = x \quad \forall \sigma \in \Sigma\}$ is **flow-invariant**

Proof: $F(x) = F(\sigma x) = \sigma F(x)$

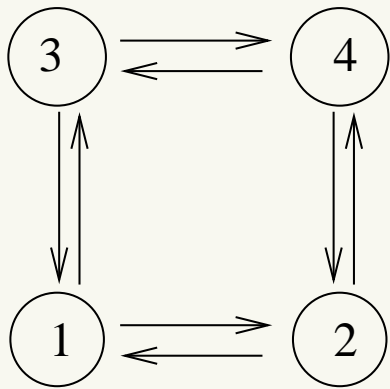
Synchrony Subspaces from Network Symmetry

- σ is a **symmetry** of $\dot{X} = F(X)$ if it maps solutions to solutions

Equivalent to $F(\sigma x) = \sigma F(x)$

- $\text{Fix}(\Sigma) = \{x \in \mathbf{R}^n : \sigma x = x \quad \forall \sigma \in \Sigma\}$ is **flow-invariant**

Proof: $F(x) = F(\sigma x) = \sigma F(x)$



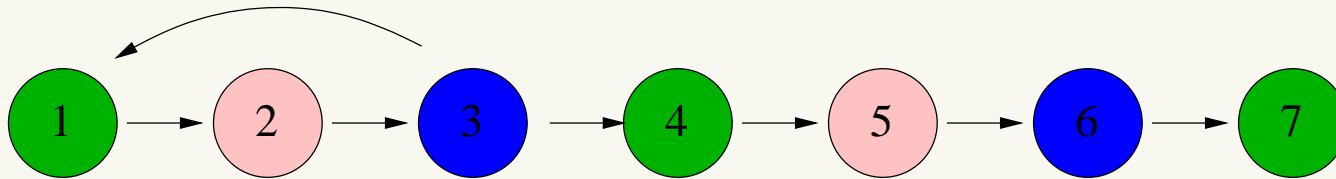
- If σ is **permutation**, then $\text{Fix}(\sigma)$ is polydiagonal

Example: $\text{Fix}((23)(14)) = \{x_2 = x_3; x_1 = x_4\}$

- If Σ is subgroup of permutation symmetries, then $\text{Fix}(\Sigma)$ is a **synchrony subspace**

Balanced Colorings

- Synchrony subspaces **do not** have to be fixed-point subspaces

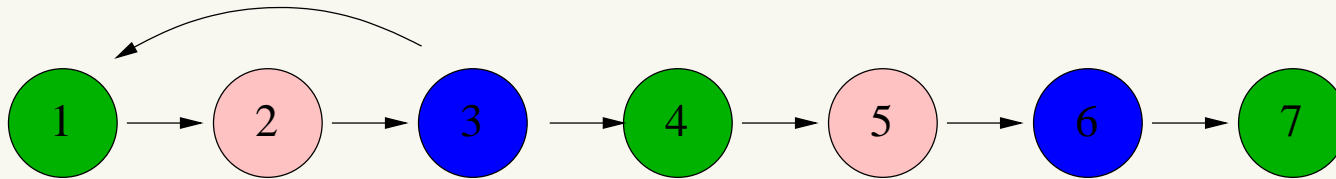


$$\begin{array}{lll} \dot{x}_1 = f(x_1, x_3) & \dot{x}_2 = f(x_2, x_1) & \dot{x}_3 = f(x_3, x_2) \\ \dot{x}_4 = f(x_4, x_3) & \dot{x}_5 = f(x_5, x_4) & \dot{x}_6 = f(x_6, x_5) \\ \dot{x}_7 = f(x_7, x_6) & & \end{array}$$

- $\Delta = \{x : x_1 = x_4 = x_7; x_2 = x_5; x_3 = x_6\}$ is flow-invariant

Balanced Colorings

- Synchrony subspaces **do not** have to be fixed-point subspaces



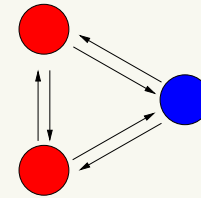
$$\begin{array}{lll} \dot{x}_1 = f(x_1, x_3) & \dot{x}_2 = f(x_2, x_1) & \dot{x}_3 = f(x_3, x_2) \\ \dot{x}_4 = f(x_4, x_3) & \dot{x}_5 = f(x_5, x_4) & \dot{x}_6 = f(x_6, x_5) \\ \dot{x}_7 = f(x_7, x_6) & & \end{array}$$

- $\Delta = \{x : x_1 = x_4 = x_7; x_2 = x_5; x_3 = x_6\}$ is flow-invariant
- Color cells the same color if cell coord's in polydiagonal Δ are equal
- Coloring is **balanced** if all cells with same color receive equal number of inputs from cells of a given color
- **Theorem 1:** synchrony subspace \iff balanced

Stewart, G., and Pivato (2003); G., Stewart, and Török (2005)

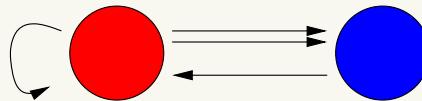
Quotient Networks with Self-Coupling & Multiarrows

- Synchrony subspace $\text{Fix}(1\ 2)$ in bidirectional ring



$$\begin{aligned}\dot{x}_1 &= f(x_1, x_2, x_3) \\ \dot{x}_2 &= f(x_2, x_3, x_1) \\ \dot{x}_3 &= f(x_3, x_1, x_2)\end{aligned}\quad \text{where } f(x, y, z) = f(x, z, y)$$

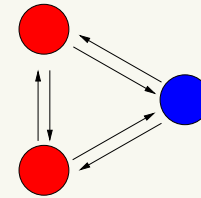
- **Quotient network:**



$$\begin{aligned}\dot{x}_1 &= f(x_1, x_1, x_3) \\ \dot{x}_3 &= f(x_3, x_1, x_1)\end{aligned}\quad \text{where } f(x, y, z) = f(x, z, y)$$

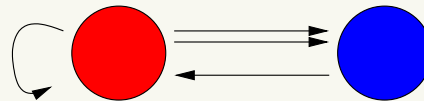
Quotient Networks with Self-Coupling & Multiarrows

- Synchrony subspace $\text{Fix}(1\ 2)$ in bidirectional ring



$$\begin{aligned}\dot{x}_1 &= f(x_1, x_2, x_3) \\ \dot{x}_2 &= f(x_2, x_3, x_1) \\ \dot{x}_3 &= f(x_3, x_1, x_2)\end{aligned}\quad \text{where } f(x, y, z) = f(x, z, y)$$

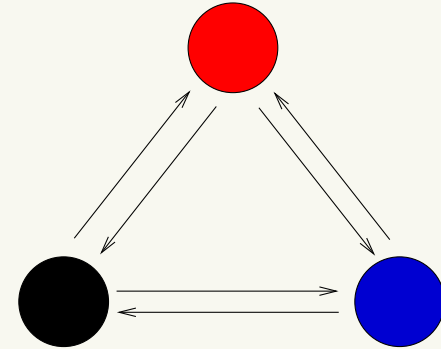
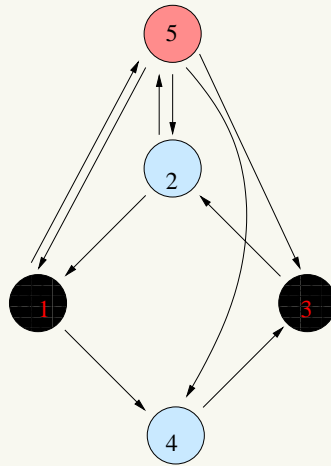
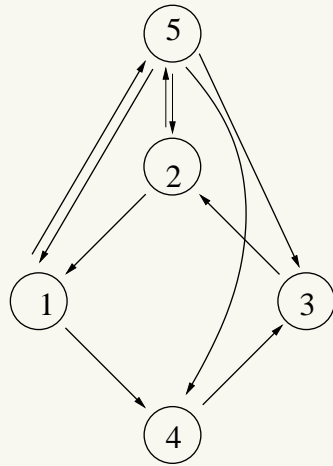
- **Quotient network:**



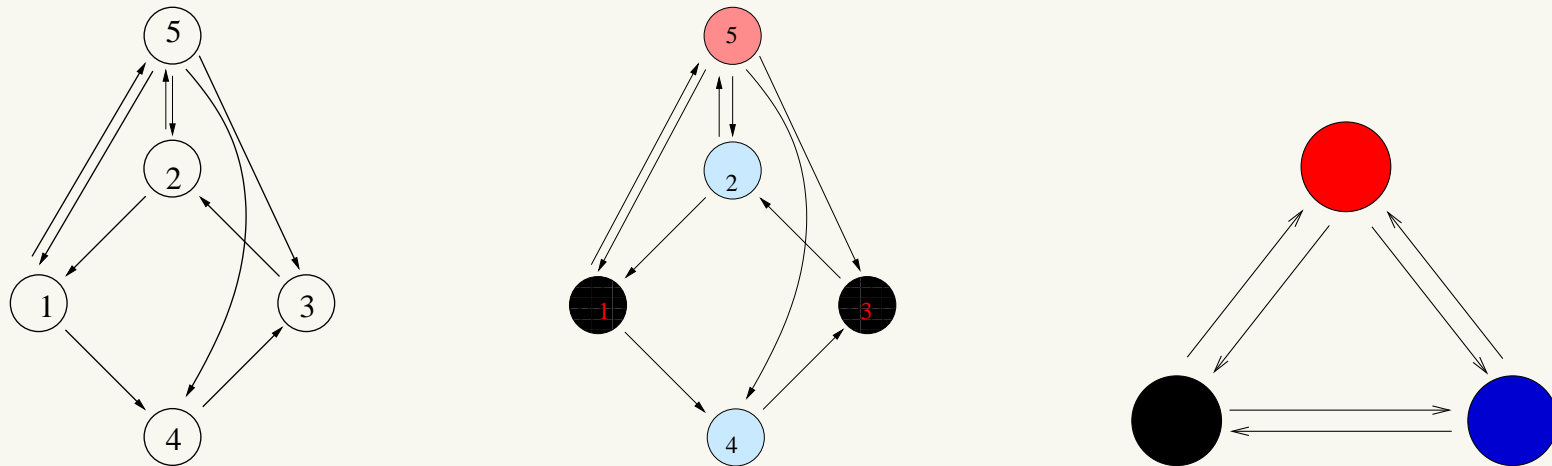
$$\begin{aligned}\dot{x}_1 &= f(x_1, x_1, x_3) \\ \dot{x}_3 &= f(x_3, x_1, x_1)\end{aligned}\quad \text{where } f(x, y, z) = f(x, z, y)$$

- Cell network with synchrony subspace leads to **quotient network**
- **Theorem 2:** Admissible ODE restricts to quotient admissible ODE
Quotient admissible ODE lifts to admissible ODE

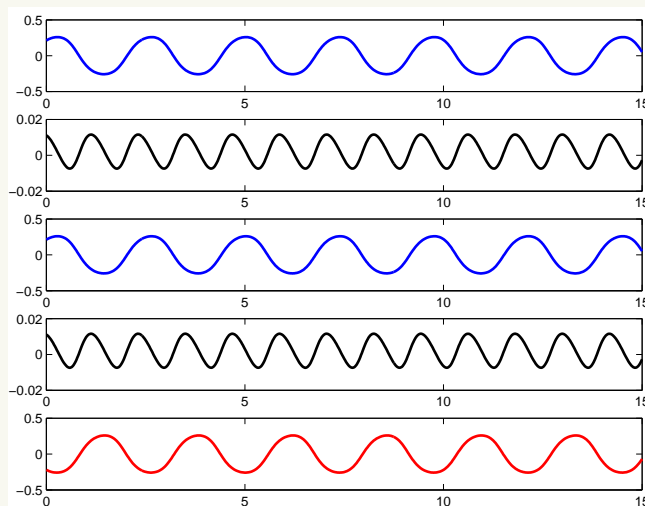
Asymmetric Network; Symmetric Quotient



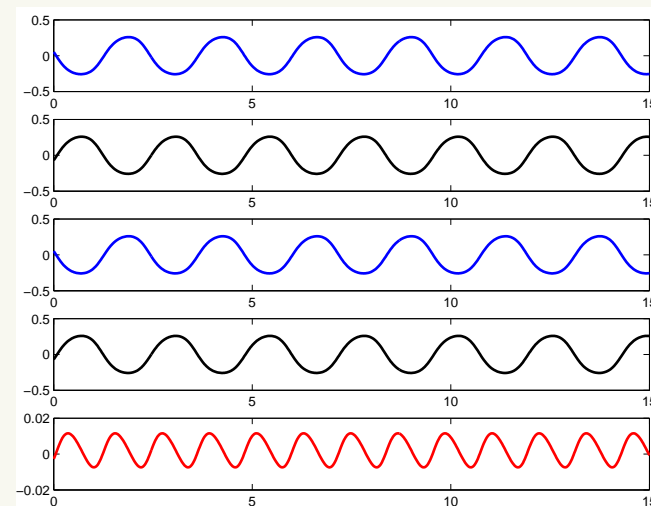
Asymmetric Network; Symmetric Quotient



- **Quotient** is bidirectional 3-cell ring with S_3 symmetry



swap red and blue



swap blue and black

- **Rigid phase shift; no symmetry**

Rigid Phase-Shift \Leftrightarrow Pattern of Phase-Shift Synchrony

Theorem 3: Assume network is **transitive**.

Nonzero **rigid** phase-shift synchrony
if and only if
phase-shift forced by **symmetry on quotient network**

- Let $Z(t)$ be the periodic solution.
Quotient network corresponds to the synchrony subspace

$$\Delta_Z = \{x_i = x_j \quad \text{if} \quad z_i(t) = z_j(t) \quad \forall t\}$$

Stewart and Parker (2008, 2009); G., Romano and Wang (2010, 2011)

Thanks

Luciano Buono	<i>UOIT</i>	Gaits
Jim Collins	<i>Boston University</i>	Gaits
Ian Stewart	<i>Warwick</i>	Gaits, Phase-Shift Synchrony
David Romano	<i>Grinnell</i>	Phase-Shift Synchrony
Yunjiao Wang	<i>Texas Southern</i>	Phase-Shift Synchrony, Rivalry
Tyler McMillen	<i>Cal State Fullerton</i>	Rivalry
Casey Diekman	<i>NJIT</i>	Rivalry

Wilson Networks

Coupled cell networks have nodes and arrows & equivalence classes of nodes and arrows. **Wilson network** = coupled cell network such that

- (a) Nodes partition into **attribute columns**: $\mathcal{C} = A_1 \cup \dots \cup A_m$ where all nodes in an attribute column are cell equivalent.

Example: Attribute might be color of a dot

- (b) **Pattern** = choice of one node in each attribute column

Learned patterns given; other patterns **derived**

Binocular rivalry has two learned patterns

- (c) Two types of arrows: *inhibitory* and *excitatory*

- Nodes in same attribute column connected by inhibitory arrow
- Nodes in same learned pattern connected by excitatory arrow
- Inhibitory arrows and excitatory arrows are not arrow equivalent

Wilson considers networks where nodes are cell equivalent, inhibitory arrows are arrow equivalent, and excitatory arrows are arrow equivalent

Rivalry Networks

A **rivalry network** is a Wilson network such that

- (a) Attributes partition into **attribute types**
Nodes in attribute equivalent columns are cell equivalent
Inhibitory arrows are equivalent iff have equivalent attributes
- (b) **Feature** is property of pairs of nodes in different attribute columns
Excitatory arrows equivalent iff connect nodes with same features

Examples:

- Dot experiments have *distance feature*: assigns to pair of nodes distance between dots
Arrows can be equivalent only if connect equidistant nodes
- Dot experiments have *color feature*
Excitatory arrows connecting nodes of same color and arrows connecting nodes of different colors are not equivalent