Neural field model of binocular rivalry waves

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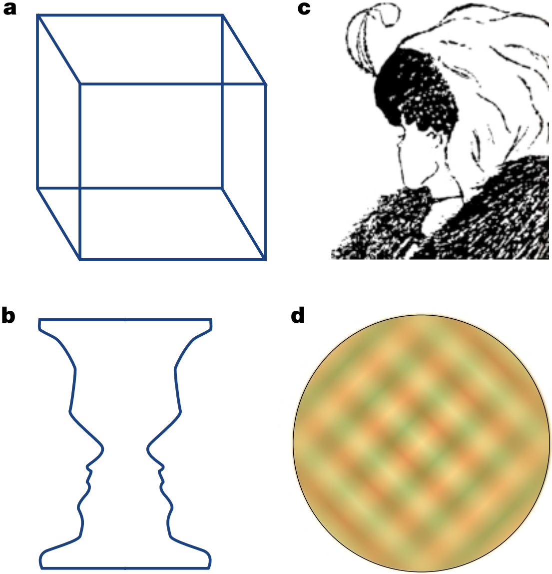
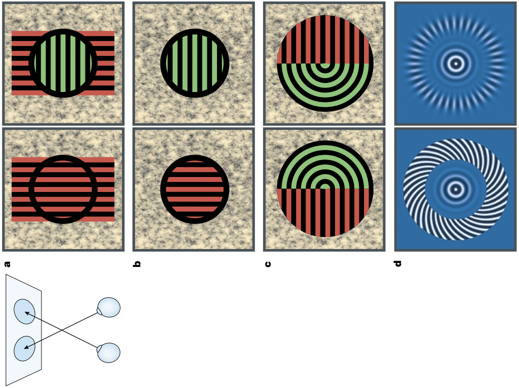
Part I. What is binocular rivalry?

AMBIGUOUS FIGURES - BISTABLE PERCEPTION



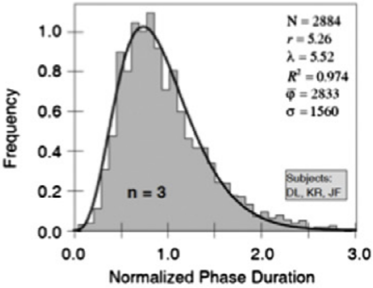
BINOCULAR RIVALRY



- Binocular rivalry: perception switches back and forth between different images presented to the two eyes
- Two images compete for perceptual dominance; one dominates for a few seconds before switching to the other

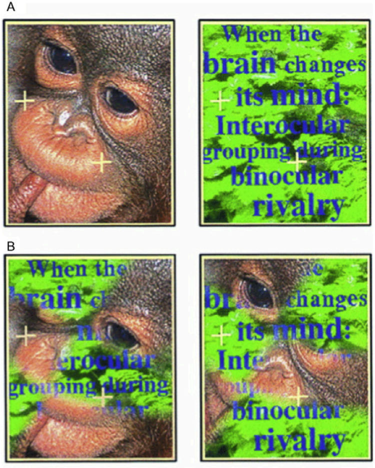
CHARACTERISTICS OF RIVALRY I

- Increasing the strength of one rival figure (brighter, moving rather than stationary, densely contoured) increases the percentage of time that it is dominant.
- Periods of suppression are decreased rather than period of dominance increased - Levelts propositions
- Fluctuations in dominance and suppression are irregular: switching times given by a Gamma distribution (Logethetis et al 1996)



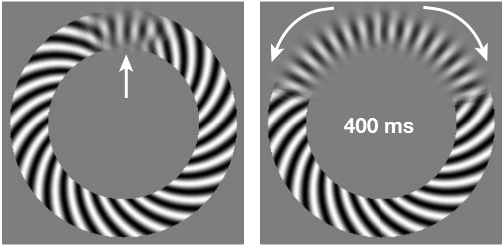
CHARACTERISTICS OF RIVALRY II

- Perceptual dominance can take on a 'patchy' appearance when the inducing figures are relatively large (Kovacs et al 1996)



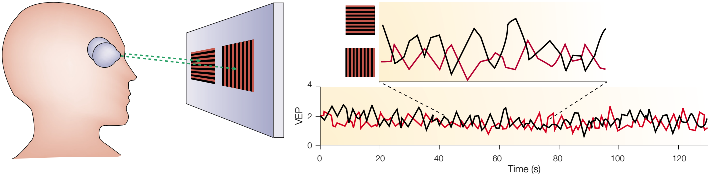
CHARACTERISTICS OF RIVALRY III

- Attending to one of the rivalry figures can increase its dominance - not possible to suppress other image completely
- Perceptual dominace transitions are not instantaneous.
- Instead, dominance emerges in a wave-like fashion, originating at one region of a figure and spreading from there throughout the rest of the figure (Wilson et al 2001)



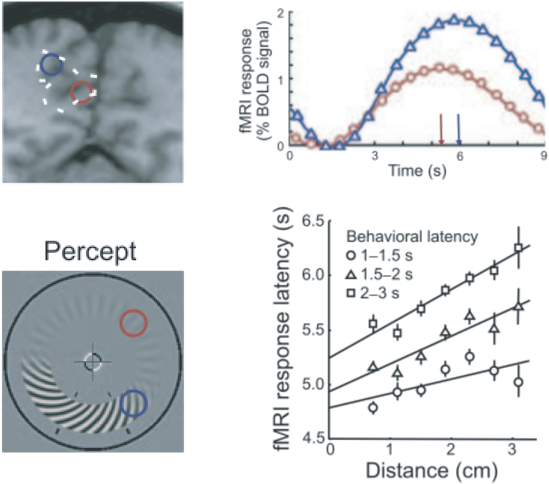
NEURAL CORRELATES OF BINOCUAR RIVALRY

- Visual evoked potentials recorded from scalp electrodes on occipital cortex



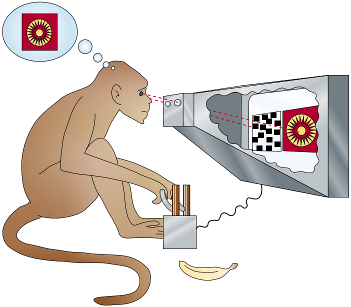
- Functional magnetic resonance imaging (fMRI) - used to identify brain regions in which blood oxygen level dependent (BOLD) signals fluctuate in synchrony with binocular rivalry
- Flutuating BOLD signals that are highly correlated with observers' perceptual reports have been found in primary visual cortex (grating stimuli) and higher-order visual areas (faces, buildings)

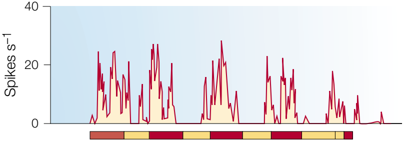
WAVES MEASURED BY FMRI (LEE ET AL 2005)



Red (blue) circles indicates subregion of V1 corresponding to upper (lower)-right quadrant of low-contrast stimulus

SINGLE UNIT RECORDINGS IN AWAKE PRIMATES

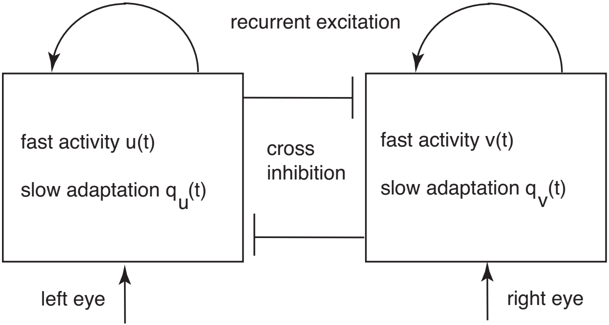




- Primate trained to operate a lever to indicate which of two competing monocular stimuli is dominant over time
- Activity recorded in single cells correlated with animal's perceptual reports.
- Experiments showed that inhibition of reponses is evident as early as primary visual cortex (Leopold and Logethetis 1996).

Part II. Models of binocular rivalry

COMPETITIVE NETWORK MODEL (NO SPACE)



- Two populations of cells driven by left and right eye stimuli, respectively
- Recurrent excitatory connections within a population, mutual inhibition between populations
- Each population exhibits some form of slow adaptation - spike frequency adaptation or synaptic depression

COMPETITIVE NETWORKS II

Many studies of rivalry in competitive networks

- Laing and Chow (2002)
- Taylor, Cottrell and Kristan (2002)
- Wilson (2003)
- Shpiro et al (2007,2009)
- Moreno-Bote, Rubin and Rinzel (2007)
- Kilpatrick and Bressloff (2010)
- Seely and Chow (2011)
- Diekman et al (2012)

Issues include

- noise vs. adaptation
- type of adaptation
- Levelt's propositions
- escape vs. release

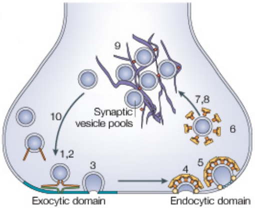
COMPETITIVE NETWORK WITH SYNAPTIC DEPRESSION

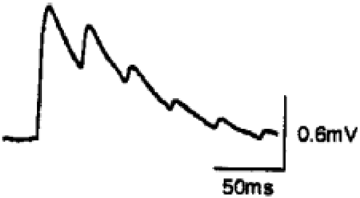
- Population activity variables u, v (current,voltage)

$$\begin{aligned}\dot{u}(t) &= -u(t) + a_e q_u(t) F(u(t)) - a_i q_v(t) F(v(t)) + I_L \\ \dot{v}(t) &= -v(t) + a_e q_v(t) F(v(t)) - a_i q_u(t) F(u(t)) + I_R\end{aligned}$$

- Depression variables q_u, q_v represent the short-term depletion of presynaptic resources (slow recovery $\tau_s \gg 1$)

$$\tau_s \dot{q}_j(t) = (1 - q_j(t)) - \beta q_j(t) F(u_j(t)), \quad j = u, v,$$





FIXED POINTS FOR HEAVISIDE RATE FUNCTION

- Off state $U^* = V^* = I$ and $Q_u^* = Q_v^* = 1$
- On-state or fusion state

$$(U^*, V^*) = \left(\frac{a_e - a_i}{1+\beta} + I, \frac{a_e - a_i}{1+\beta} + I \right), \quad (Q_u^*, Q_v^*) = \left(\frac{1}{1+\beta}, \frac{1}{1+\beta} \right),$$

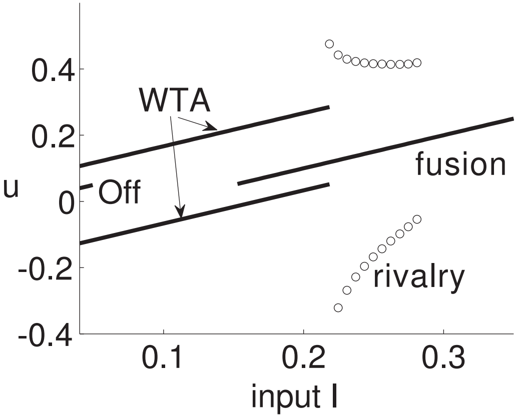
- Left eye dominant state:

$$(U^*, V^*) = \left(\frac{a_e}{1+\beta} + I, I - \frac{a_i}{1+\beta} \right), \quad (Q_u^*, Q_v^*) = \left(\frac{1}{1+\beta}, 1 \right)$$

- Right eye dominant state

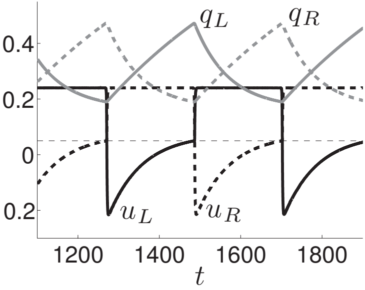
$$(U^*, V^*) = \left(I - \frac{a_i}{1+\beta}, \frac{a_e}{1+\beta} + I \right), \quad (Q_u^*, Q_v^*) = \left(1, \frac{1}{1+\beta} \right)$$

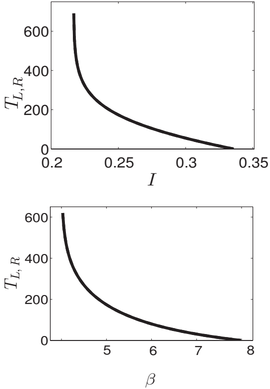
BIFURCATION DIAGRAM (KILPATRICK/PCB 2010)



- Coexistence of rivalry oscillations and the fusion state ($\tau_s = 500, \beta = 5, a_e = 0.4, a_i = 1.0, \kappa = 0.05$)

DOMINANCE TIMES

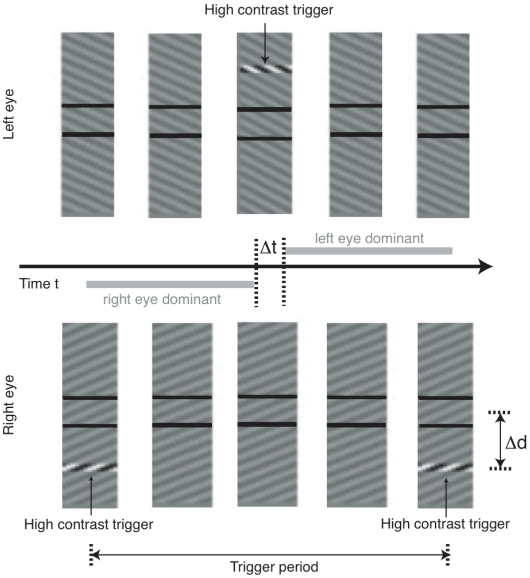




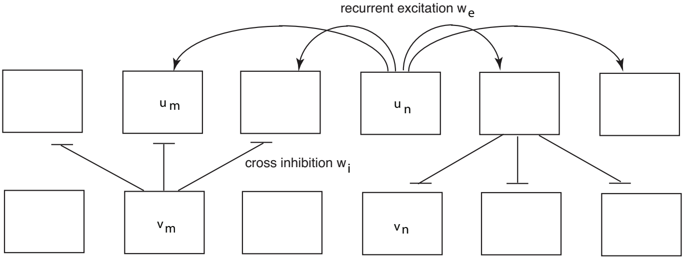
- Oscillations arise through an escape rather than a release mechanism – suppressed population's activity crosses threshold before dominant population ceases firing

- Can construct explicit solution and determine dominance times T_L and T_R.

1D RIVALRY WAVES (KANG ET AL 2009)



SPATIALLY EXTENDED COMPETITIVE NETWORK (1D)



$$\tau \frac{du_m}{dt} = -u_m + I_u + \sum_n \left([w_e]_{mn} q_{u,n} F(u_n) - [w_i]_{mn} q_{v,n} F(v_n) \right)$$

$$\tau \frac{dv_m}{dt} = -v_m + I_v + \sum_n \left([w_e]_{mn} q_{v,n} F(v_n) - [w_i]_{mn} q_{u,n} F(u_n) \right)$$

$$\tau_s \frac{dq_{j,m}}{dt} = 1 - q_{j,m} - \beta q_{j,m} F(v_m), \quad j = u, v$$

SPATIALLY EXTENDED COMPETITIVE NETWORK (1D)

- $[w_e]_{mn}$ is the strength of excitation from the nth to the mth population with the same eye preference
- $[w_i]_{mn}$ is the strength of cross-inhibition between populations with opposite eye preferences.
- The weights are assumed to decrease with distance of separation $|m-n|$ according to an exponential or Gaussian distribution.
- Sigmoidal firing rate function

$$F(u) = \frac{F_0}{1 + \mathrm{e}^{-\eta(u-\kappa)}}$$

- Discrete model useful for simulations. For analytical insights take a continuum limit $\implies$ neural field model

NEURAL FIELD MODEL (PCB AND WEBBER 2012)

Left eye network:

$$\begin{aligned}
\tau \frac{\partial u(x,t)}{\partial t} &= -u(x,t) + \int_{-\infty}^{\infty} w_e(x-x')q_u(x',t)F(u(x',t)))dx' \\
&- \int_{-\infty}^{\infty} w_i(x-x')q_v(x',t)F(v(x',t)))dx' + I_u(x,t) \\
\tau_s \frac{\partial q_u(x,t)}{\partial t} &= 1 - q_u(x,t) - \beta q_u(x,t)F(u(x,t))
\end{aligned}$$

Right eye network:

$$\begin{aligned}
\tau \frac{\partial v(x,t)}{\partial t} &= -v(x,t) + \int_{-\infty}^{\infty} w_e(x-x')q_v(x',t)F(v(x',t)))dx' \\
&- \int_{-\infty}^{\infty} w_i(x-x')q_u(x',t)F(u(x',t)))dx' + I_v(x,t) \\
\tau_s \frac{\partial q_v(x,t)}{\partial t} &= 1 - q_v(x,t) - \beta q_v(x,t)F(v(x,t)).
\end{aligned}$$

Part III. Traveling fronts

TRAVELING FRONT WITH SLOW ADAPTATION I

- Suppose system is initially in a right dominated WTA state.
- Perturbation of system initiates a propagating front that generates a switch from right to left eye dominance
- Adiabatic approximation ($\tau_s \gg 1$): If L is size of domain and c is wavespeed then $L/c \ll \tau_s$ so that $q_j(x,t) \approx Q_j, j = u, v$
- Consider a traveling wave front solution of the form

$$u(x,t) = U(\xi), \quad v(x,t) = V(\xi), \quad \xi = x - ct$$

$$(U(\xi), V(\xi)) \to \mathbf{X}_L = (Q_u a_e + I, I - Q_v a_i) \text{ as } \xi \to -\infty,$$

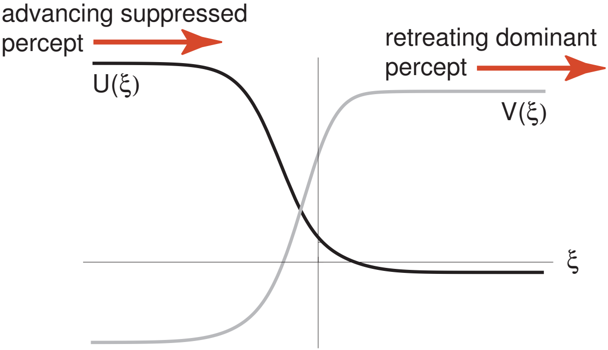
$$(U(\xi), V(\xi)) \to \mathbf{X}_R = (I - Q_u a_i, Q_v a_e + I) \text{ , as } \xi \to \infty$$

TRAVELING FRONT WITH SLOW ADAPTATION II

- Threshold conditions

$$U(0) = \kappa, \quad V(X) = \kappa$$

- If $c > 0$ then the front represents a solution in which activity invades a suppressed left eye network and retreats from a dominant right eye network.



ANALYTICAL SOLUTION I

- Substitute the traveling wave solution into NF equations for fixed Q_u, Q_v and $F(u) = H(u - \kappa)$:

$$\begin{aligned}
-c\frac{dU}{d\xi} + U \quad &= Q_u \int_{-\infty}^{0} w_e(\xi - \xi')d\xi' - Q_v \int_{X}^{\infty} w_i(\xi - \xi')d\xi' + I \\
-c\frac{dV}{d\xi} + V \quad &= Q_v \int_{X}^{\infty} w_e(\xi - \xi')d\xi' - Q_u \int_{-\infty}^{0} w_i(\xi - \xi')d\xi' + I.
\end{aligned}$$

- Rewrite equations in integral form

$$\begin{aligned}
U(\xi) \quad &= \quad \mathrm{e}^{\xi/c}\left[\kappa - \frac{1}{c}\int_0^{\xi} \mathrm{e}^{-z/c}\Psi_X(z)dz - I(1 - \mathrm{e}^{-\xi/c})\right], \ \xi > 0 \\
V(\xi) \quad &= \quad \mathrm{e}^{(\xi-X)/c}\left[\kappa - \frac{1}{c}\int_0^{\xi-X} \mathrm{e}^{-z/c}\Phi_X(-z)dz\right], \\
&\qquad -I(\mathrm{e}^{(\xi-X)/c}), \ \xi > X
\end{aligned}$$

ANALYTICAL SOLUTION II

- Ψ_X and Φ_X defined by

$$\Psi_X(z) = Q_u \int_z^\infty w_e(y)dy - Q_v \int_{-\infty}^{z-X} w_i(y)dy.$$

$$\Phi_X(z) = Q_v \int_z^\infty w_e(y)dy - Q_u \int_{-\infty}^{z-X} w_i(y)dy.$$

- Boundedness of solution as $\xi \to \infty$ (assuming $c > 0$) implies the threshold conditions

$$\begin{aligned} \kappa &= \int_0^\infty \mathrm{e}^{-s}\Psi_X(cs)ds + I, \\ \kappa &= \int_0^\infty \mathrm{e}^{-s}\Phi_X(-cs)ds + I. \end{aligned}$$

SYMMETRY BREAKING

- If $Q_u = Q_v = 1$ (no synaptic depression) then

$$\kappa = \int_0^\infty e^{-s}\Psi_X(cs)ds + I, \quad \kappa = \int_0^\infty e^{-s}\Psi_X(-cs)ds + I.$$

- Subtracting equations shows that

$$\int_0^\infty e^{-s}\left[\Psi_X(cs) - \Psi_X(-cs)\right]ds = 0$$

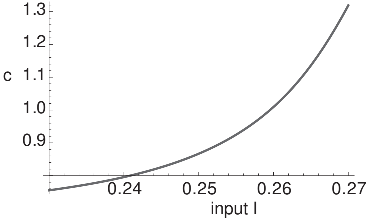
- No traveling wave solution, since if $c \neq 0$ then

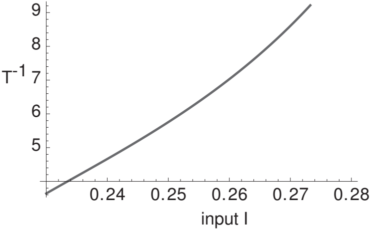
$$\Psi_X(cs) - \Psi_X(-cs) = -\int_{-cs}^{cs} w_e(y)dy - \int_{-cs-X}^{cs-X} w_i(y)dy < 0$$

  for all $s \in [0, \infty)$.

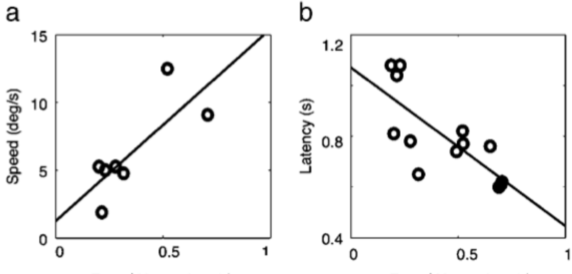
- Slow synaptic depression ($Q_u \neq Q_v$) breaks the symmetry of the threshold crossing conditions, leading to a unique (stable) solution for c, X as a function of the network parameters.

WAVESPEED COVARIES WITH ALTERNATION RATE $1/T$





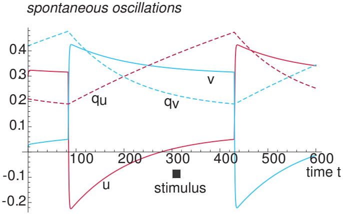
- Default parameters: $a_i = 1, a_e = 0.4, \sigma_i = 1, \sigma_e = 2, \beta = 5, \kappa = 0.05, I = 0.24, Q_u = 0.42, Q_v = 0.25$

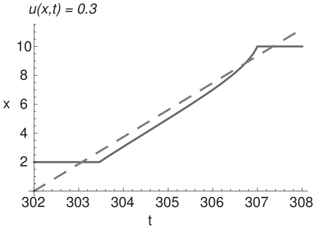


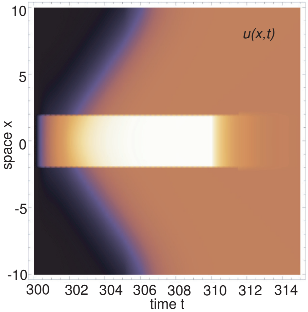
NUMERICS

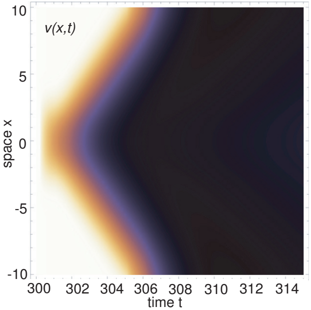
- Fix units by setting $\sigma_e = 2, \tau = 1$. Wavespeed $c = 1$ in dimensionless units corresponds to $c = \sigma_e / 2\tau$ in physical units.
- Kang *et. al.* (2009) find speeds of order 10 mm/sec. This is consistent with $c = 1$ if we take $\sigma_e \sim 200\mu$m and $\tau \sim 10$msec.
- Trigger stimulus switched on at time t_0 and has duration $\Delta t = 10$, corresponding to 200ms as in Kang *et. al.* (2009)
- Size of the excited region $\Delta x \sim \sigma_e$. This is consistent with the size of perturbation used in the experiments by Kang *et. al.*, which was of size 0.2 degrees, corresponding to 0.8mm of cortical tissue.

SOLITARY BINOCULAR RIVALRY WAVE

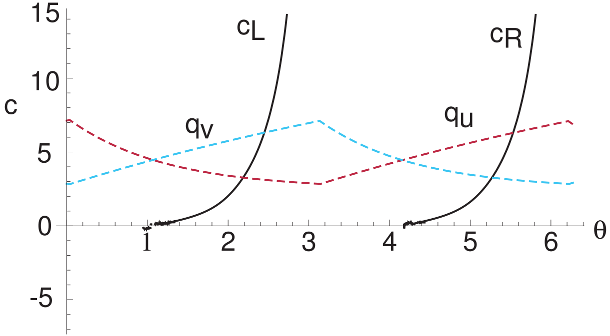








WAVESPEED DEPENDS ON PHASE OF STIMULUS ONSET



Kang *et al.* (2009) used periodic trigger stimuli and averaged over multiple cycles so lost phase information. Also need to take into account the effects of noise.

PERIODIC TRIGGER STIMULI AND ADDITIVE NOISE

Introduce additive white noise to the depression dynamics:

$$\tau_s \frac{\partial q_u(x,t)}{\partial t} = 1 - q_u(x,t) - \beta q_u(x,t) f(u(x,t)) + \sigma \xi_u(x,t)$$
$$\tau_s \frac{\partial q_v(x,t)}{\partial t} = 1 - q_v(x,t) - \beta q_v(x,t) f(v(x,t)) + \sigma \xi_v(x,t)$$

with

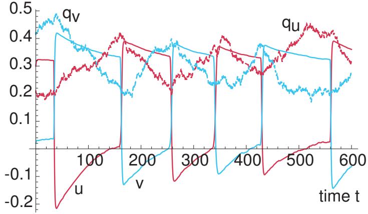
$$\langle \xi_u(x,t) \rangle = \langle \xi_v(x,t) \rangle = 0$$

and

$$\langle \xi_i(x,t) \xi_j(x',t') \rangle = \delta(x-x')\delta(t-t')\delta_{i,j}, \quad i,j = u,v$$

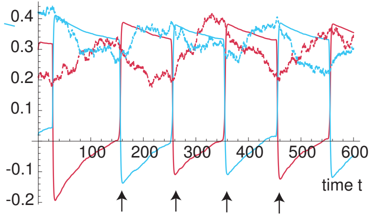
Consider alternating, periodic trigger stimuli

SPONTANEOUS VS. PERIODICALLY FORCED SWITCHING



Spontaneous switching

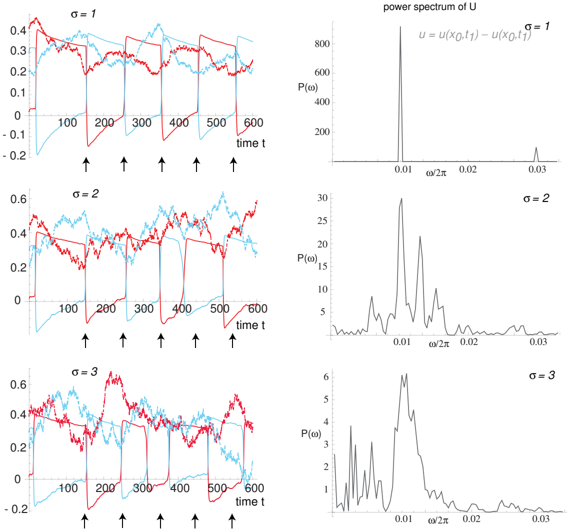
Noise strength σ = 1



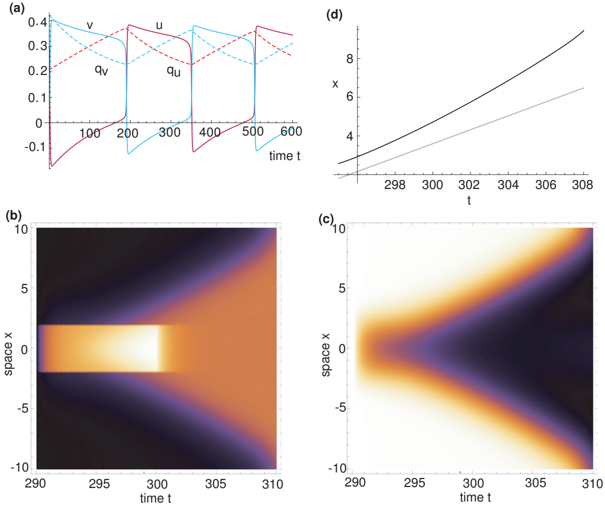
Periodically forced switching
$T_0 = 100$

Noise strength σ = 1

BREAKDOWN OF MODE–LOCKING AS NOISE INCREASES



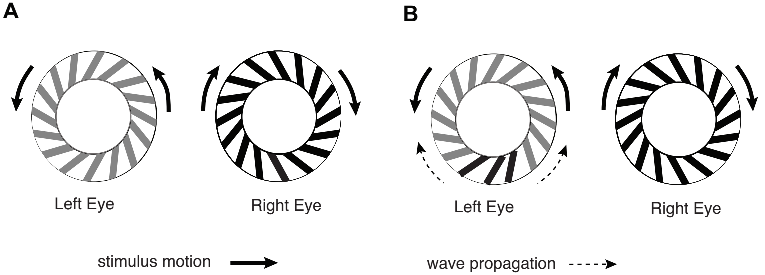
RIVALRY WAVES PERSIST FOR SIGMOIDAL FIRING RATE FUNCTION



Part IV. Moving stimuli

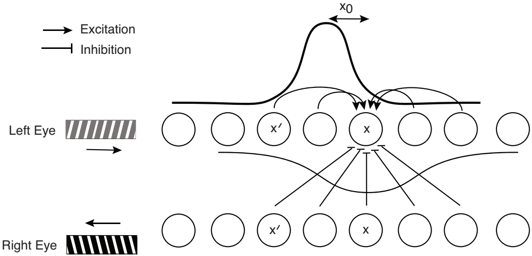
ROTATING STIMULI

- The left (right) eye is presented with a low (high) contrast carrier (mask) stimulus rotating in an anti-clockwise (clockwise) direction.
- A transient increase in the contrast of the carrier stimulus induces a pair of counter propagating waves.
- The wave traveling in the same direction as the stimulus reaches the top first, indicating that it has a higher speed



NETWORK MODEL OF DIRECTION SELECTIVITY

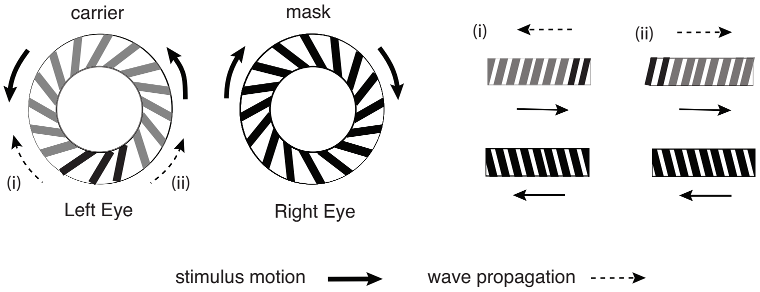
- Simplified stimuli: The left (right) eye is shown an oriented grating moving rightwards (leftwards).
- Pair of 1D neural fields that represent the activity of neurons responding maximally to the orientation and motion of the corresponding grating.
- Gaussian excitatory recurrent connections, cross-inhibition and slow synaptic depression.
- Introduce an asymmetric shift in excitation of size x_0 in the left network and a shift of $-x_0$ in the right network.



TRIGGERING STIMULUS

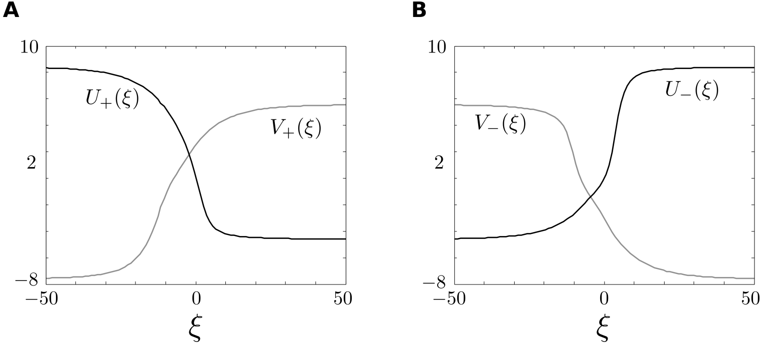
- Induction of a wave moving in (i) the opposite direction to stimulus motions and (ii) the same direction as stimulus motion.
- For annuli stimuli, a local increase in the contrast of the carrier can induce both waves

- For linear gratings, a local increase in contrast has to be induced separately at either one end or the other of the stimulus



TRAVELING WAVEFRONTS (PCB AND SAM CARROLL)

- Plot of profiles in the co-moving frame $\xi = x - ct$ for wave fronts traveling in the positive (left) and negative (right) direction.

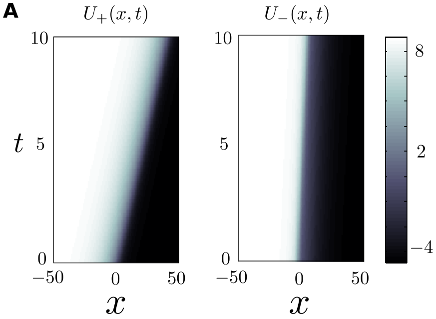


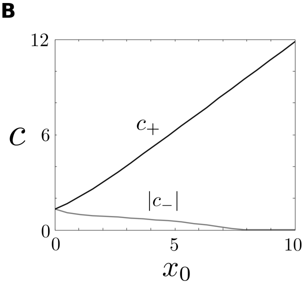
DIRECTIONAL SYMMETRY BREAKING I

A Space-time plot of traveling fronts with positive wave speed (left) and negative wave speed (right) with $x_0 = 3$

- Note that $U_-(x,t)$ has been reflected about the $x = 0$ axis for visual comparison against $U_+(x,t)$.

B Plot of analytically computed positive and negative wave speeds against x_0





DIRECTIONAL SYMMETRY BREAKING II

- Introducing asymmetric shift in cross-inhibition rather than excitation does not generate observed directional symmetry breaking
- Same result holds if a different form of asymmetry is introduced eg. an asymmetric shift in the spatial rate of decay in the weights.
- Sensitive to source of slow adaptation - asymmetric cross-inhibition works in the case of spike frequency adaptation

Part V. Stochastic rivalry waves

STOCHASTIC MODEL I (PCB AND WEBBER 2012)

- Langevin equation (or stochastic PDE) for the stochastic activity variables $U(x,t)$ and $V(x,t)$:

$$\begin{aligned} dU &= \Big[-U + Q_u \int_{-\infty}^{\infty} w_e(x-y)F(U(y,t))dy \\ &\quad -Q_v \int_{-\infty}^{\infty} w_i(x-y)F(V(y,t))dy + I_u\Big] dt + \epsilon^{\frac{1}{2}} dW_u \end{aligned}$$

$$\begin{aligned} dV &= \Big[-V + Q_v \int_{-\infty}^{\infty} w_e(x-y)F(V(y,t))dy \\ &\quad -Q_u \int_{-\infty}^{\infty} w_i(x-y)F(U(y,t))dy + I_v\Big] dt + \epsilon^{\frac{1}{2}} dW_v \end{aligned}$$

with Q_u, Q_v fixed.

STOCHASTIC MODEL II

- W_u, W_v represent independent Wiener processes

$$\begin{aligned}\langle dW_{\{u,v\}}(x,t)\rangle &= 0,\\ \langle dW_i(x,t)dW_j(x',t')\rangle &= 2\delta_{i,j}C([x-x']/\lambda)\delta(t-t')dtdt'\end{aligned}$$

  where $i,j = u,v$ and $\langle\cdot\rangle$ denotes averaging with respect to the Wiener processes.

- λ is the spatial correlation length of the noise such that $C(x/\lambda) \to \delta(x)$ in the limit $\lambda \to 0$, and ϵ determines the strength of the noise, which is assumed to be weak

SEPARATION OF TIME-SCALES I

- Fluctuations generate two distinct phenomena that occur on different time–scales (Geier et al 1983,Sagues, Sancho and Garcia-Ojalvo 2007)

  [A] Diffusive–like displacement of the wave from its uniformly translating position at long time scales

  [B] Fast fluctuations in the wave profile around its instantaneous position at short time scales

- Decompose solution as ($\xi = x - ct$)

$$\begin{aligned} U(x,t) &= U_0(\xi - \Delta(t)) + \epsilon^{1/2} U_1(\xi - \Delta(t), t), \\ V(x,t) &= V_0(\xi - \Delta(t)) + \epsilon^{1/2} V_1(\xi - \Delta(t), t). \end{aligned}$$

where (U_0, V_0) is deterministic wave solution

SEPARATION OF TIME-SCALES II

- Substitute into NF equations and expand to $\mathcal{O}(\epsilon^{1/2})$

$$dU_1(\xi,t) - L_u(U_1(\xi,t),V_1(\xi,t)) = \epsilon^{-\frac{1}{2}} U_0'(\xi) d\Delta(t) + g(U_0) dW_u$$

$$dV_1(\xi,t) - L_v(U_1(\xi,t),V_1(\xi,t)) = \epsilon^{-\frac{1}{2}} V_0'(\xi) d\Delta(t) + g(V_0) dW_v$$

with $U_1 = U_1(\xi,t)$ and $\Delta(t) = \mathcal{O}(\epsilon^{1/2})$.

- L_u, L_v are non-self-adjoint linear operators

$$\begin{aligned}
L_u(A_1,A_2) &= c\frac{dA_1}{d\xi} + A_1 + Q_u \int_{-\infty}^{\infty} w_e(\xi-\xi')F'(U_0(\xi'))A_1(\xi')d\xi' \\
&\quad -Q_v \int_{-\infty}^{\infty} w_i(\xi-\xi')F'(V_0(\xi'))A_2(\xi')d\xi' \\
L_v(A_1,A_2) &= c\frac{dA_2}{d\xi} + A_2 + Q_v \int_{-\infty}^{\infty} w_e(\xi-\xi')F'(V_0(\xi'))A_2(\xi')d\xi' \\
&\quad -Q_u \int_{-\infty}^{\infty} w_i(\xi-\xi')F'(U_0(\xi'))A_1(\xi')d\xi'
\end{aligned}$$

SEPARATION OF TIME-SCALES III

- Let **L** denote the vector-valued operator with components L_u, L_v. That, is

$$\mathbf{L}\begin{pmatrix} A_1 \\ A_2 \end{pmatrix} = \begin{pmatrix} L_u(A_1, A_2) \\ L_v(A_1, A_2) \end{pmatrix}$$

- **L** has a 1D null space spanned by $(U_0'(\xi), V_0'(\xi))^T$
- Solvability condition for the existence of a nontrivial solution: the inhomogeneous part is orthogonal to all elements of the null space of the adjoint operator $\mathbf{L}^*$.
- The latter is defined with respect to the inner product

$$\int_{-\infty}^{\infty} \mathbf{B}(\xi) \cdot \mathbf{L}\mathbf{A}(\xi) d\xi = \int_{-\infty}^{\infty} \mathbf{L}^*\mathbf{B}(\xi) \cdot \mathbf{A}(\xi) d\xi$$

SEPARATION OF TIME-SCALES IV

- Find that

$$\mathbf{L}^* \begin{pmatrix} B_1 \\ B_2 \end{pmatrix} = \begin{pmatrix} L_u^*(B_1, B_2) \\ L_v^*(B_1, B_2), \end{pmatrix}$$

  where

$$\begin{aligned} L_u^*(B_1, B_2) &= -c\frac{dB_1}{d\xi} + B_1 + F'(U_0)Q_u \int_{-\infty}^{\infty} w_e(\xi - \xi')B_1(\xi')d\xi' \\ &\quad -F'(V_0)Q_v \int_{-\infty}^{\infty} w_i(\xi - \xi')B_2(\xi')d\xi' \end{aligned}$$

and

$$\begin{aligned} L_v^*(B_1, B_2) &= -c\frac{dB_2}{d\xi} + B_2 + F'(V_0)Q_v \int_{-\infty}^{\infty} w_e(\xi - \xi')B_2(\xi')d\xi' \\ &\quad -F'(U_0)Q_u \int_{-\infty}^{\infty} w_i(\xi - \xi')B_1(\xi')d\xi' \end{aligned}$$

SDE FOR $\Delta(t)$

- The adjoint operator $\mathbf{L}^*$ also has a one-dimensional null-space spanned by $\mathcal{V}(\xi)$.
- Obtain solvability condition

$$\begin{aligned} 0 &= \int_{-\infty}^{\infty} \mathcal{V}_1(\xi)\left[U_0'(\xi)d\Delta(t) + \epsilon^{1/2} dW_u(\xi,t)\right] d\xi \\ &\quad + \int_{-\infty}^{\infty} \mathcal{V}_2(\xi)\left[V_0'(\xi)d\Delta(t) + \epsilon^{1/2} dW_v(\xi,t)\right] d\xi. \end{aligned}$$

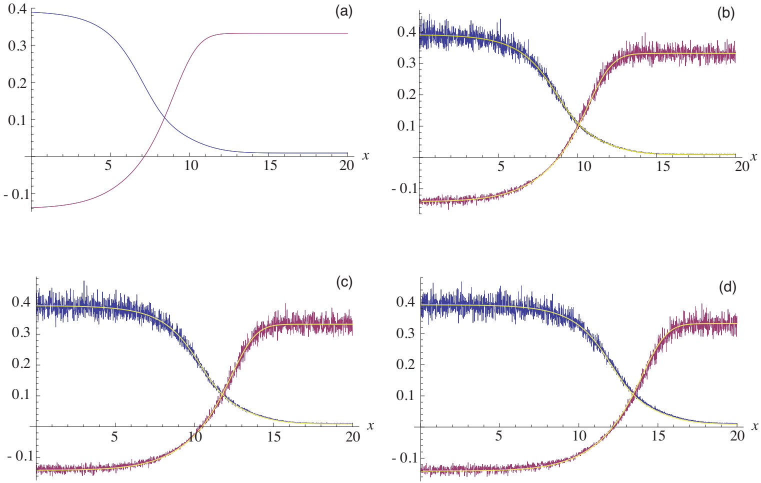
- Thus $\Delta(t)$ is a Brownian process with

$$\langle \Delta(t) \rangle = 0, \quad \langle \Delta(t)^2 \rangle = 2D(\varepsilon)t$$

$$D(\epsilon) = \epsilon \frac{\displaystyle\int_{-\infty}^{\infty} \left(\mathcal{V}_1(\xi)^2 + \mathcal{V}_2(\xi)^2\right) U_0^2(\xi) d\xi}{\left[\displaystyle\int_{-\infty}^{\infty} \left(\mathcal{V}_1(\xi)U_0'(\xi) + \mathcal{V}_2(\xi)V_0'(\xi)\right) d\xi\right]^2}.$$

RESULTS I: HEAVISIDE $F(u) = H(u - \kappa)$

- Snapshots of a stochastic composite wave

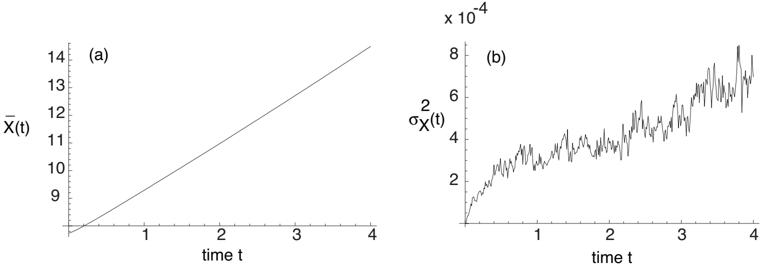


RESULTS II

- Determine the stochastic positions $X_a(t)$ such that $U(X_a(t), t) = a$, for various level set values $a \in (0.5\kappa, 1.3\kappa)$
- Mean and variance

$$\overline{X}(t) = \mathbb{E}[X_a(t)], \quad \sigma_X^2(t) = \mathbb{E}[(X_a(t) - \bar{X}(t))^2]$$

  averaged with respect to a and over N trials.
- $\overline{X}(t) \sim c_\varepsilon t$ and $\sigma_X^2(t) \sim 2D(\varepsilon)t$ (after initial transients)



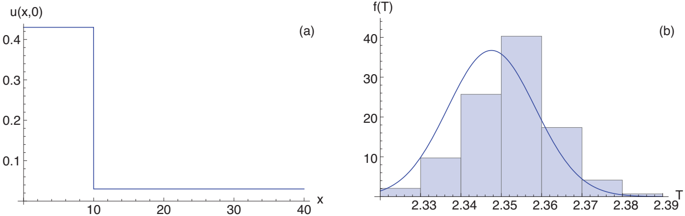
RESULTS III

- Let T_L denote the first passage time (FPT) for the wave to travel a distance L: $cT_L + \Delta(T_L) = L$ given $\Delta(0) = 0$.
- FTP density is given by an inverse Gaussian or Wald distribution:

$$f(T_L) = \mathcal{F}(T_L; \frac{L}{c}, \frac{L^2}{D}),$$

where

$$\mathcal{F}(T; \mu, \lambda) = \left[\frac{\lambda}{2\pi T^3}\right]^{1/2} \exp\left(-\frac{\lambda(T-\mu)^2}{2\mu^2 T}\right).$$

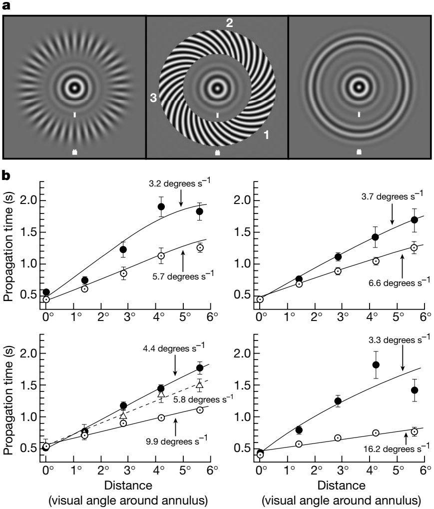


Part VI. Future directions

OVERSIMPLIFIED MODEL OF V1

- The model only represents neurons that fire maximally with respect to the given monocular image
- For example, in the case of a vertical grating, we only consider neurons that fire maximally to vertical orientations
- Neglects orientation tuning due to recurrent connections between neurons with different orientation preferences.
- 1D model cannot handle annulus experiment of Wilson et al (2001) with varying orientations
- Speed of wave depends on colinearity of image - orientation-dependence of long-range horizontal connections

ORIENTATION-DEPENDENCE OF WAVESPEED (WILSON ET AL 2001)



REFERENCES AND ACKNOWLEDGEMENTS

1. P. C. Bressloff and S. Carroll. Binocular Rivalry Waves in a Directionally Selective Neural Field Model. *Physica D* . In press (2014).
2. P. C. Bressloff and M. Webber. The effects of noise on binocular rivalry waves: a stochastic neural field model. *J. Stat. Mech: special issue* (2012).
3. P. C. Bressloff and M. Webber. Front propagation in stochastic neural fields. *SIAM J. Appl. Dyn. Syst.* (2012).
4. P. C. Bressloff and M. Webber. Neural field model of binocular rivalry waves. *J. Comput. Neurosci.* (2012).
5. P. C. Bressloff. Spatiotemporal dynamics of continuum neural fields: Invited topical review. *J. Phys. A* **45** 033001 (109pp.) (2012).
6. Z. P. Kilpatrick and P. C. Bressloff. Binocular rivalry in a competitive neural network with synaptic depression. *SIAM J. Appl. Dyn. Syst.* **9**, 1303–1347 (2010).

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