

# Short term synaptic depression improves information transfer in perceptual multistability

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networks connected by mutual inhibition, we consider the system (Laing and Chow, 2002; Moreno-Bote et al., 2007; Shpiro et al., 2007)

$$\dot{u}_R = -u_R(t) + f(I_R - q_L(t)u_L(t)) + \xi_1(t), \quad (6a)$$

$$\dot{u}_L = -u_L(t) + f(I_L - q_R(t)u_R(t)) + \xi_2(t), \quad (6b)$$

$$\tau \dot{q}_R = 1 - q_R(t) - \beta u_R(t)q_R(t), \quad (6c)$$

$$\tau \dot{q}_L = 1 - q_L(t) - \beta u_L(t)q_L(t), \quad (6d)$$

where  $u_j(t)$  represents the firing rate of the  $j = L, R$  population. The resource usage rate by synapse projecting from population  $j = L, R$  is specified by  $\beta u_j q_j$  and the resource recovery timescale is  $\tau$ . Fluctuations are introduced into population  $j$  with the independent white noise processes  $\xi_j$  with  $\langle \xi_j(t) \rangle = 0$  and  $\langle \xi_j(t) \xi_j(s) \rangle = \varepsilon \delta(t - s)$ . Units of time are taken to be 10 ms each. In numerical simulations,  $u_j(0)$  are initialized by randomly drawing from a uniform distribution on  $[0, 1]$ ;  $q_j(0)$  are initialized by randomly drawing from a uniform distribution on  $[1/(1 + \beta), 1]$ .

#### NUMERICAL SIMULATION OF STOCHASTIC DIFFERENTIAL EQUATIONS

The spatially extended model (Equation 1) is simulated using an Euler–Maruyama method with a timestep  $\Delta t = 10^{-4}$ , using Riemann integration on the convolution term with 2000 spatial grid points. A population is considered dominant if the peak of its activity bump is higher than the other; switches occur when the other bump attains a higher peak. The reduced network (Equation 6) was also simulated using Euler–Maruyama with a timestep  $\Delta t = 10^{-6}$ . Population  $j$  is considered dominant when  $u_j > u_k$  ( $j \neq k$ ); switches occur when the inequality switches direction. To generate histograms of dominance times, we simulated systems for 20,000s.

#### FITTING DOMINANCE TIME DISTRIBUTIONS

To generate the theoretical curves presented for exponentially distributed dominance times, we simply take the mean of dominance times and use it as the scaling in the exponential (Equation 28). For those densities that we presume are gamma distributed, we solve a linear system to fit the constants  $c_1$ ,  $c_2$ , and  $c_3$  of

$$f(T) = e^{c_1} T^{c_2} e^{-c_3 T} \quad (7)$$

an alternate form of Equation (30). Upon taking the logarithm of Equation (7), we have the linear sum

$$\ln f(T) = c_1 + c_2 \ln T - c_3 T. \quad (8)$$

Then, we select three values of the numerically generated distribution  $p^n(T^n)$  along with its associated dominance times:  $(T_1^n, p_1^n)$ ;  $(T_2^n, p_2^n)$ ;  $(T_3^n, p_3^n)$  where  $p_j^n = p^n(T_j^n)$ . We always choose  $T_2^n = \arg \max_T p^n(T)$  as well as  $T_1^n = T_2^n/2$  and  $T_3^n = 3T_2^n/2$ . It is then straightforward to solve the linear system

$$\begin{pmatrix} 1 & \ln T_1^n - T_1^n \\ 1 & \ln T_2^n - T_2^n \\ 1 & \ln T_3^n - T_3^n \end{pmatrix} \begin{pmatrix} c_1 \\ c_2 \\ c_3 \end{pmatrix} = \begin{pmatrix} \ln p_1^n \\ \ln p_2^n \\ \ln p_3^n \end{pmatrix}$$

using the `\backslash` command in MATLAB.

## RESULTS

We now present results that reveal the importance of synaptic depression in preserving information about bimodal stimuli. No previous work, to our knowledge, has studied how activity in a ring model with depression (Equation 1) can be collapsed to a

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(Laing and Chow, 2002; Kilpatrick and Bressloff, 2010a). Synaptic input  $u$  then tracks the slowly varying state of the synaptic scaling term  $q$ . We have also verified in simulations  $q$  is essentially piecewise constant in space, in the case of the Heaviside non-linearity (Equation 4), which yields

$$u(x, t) \approx \int_{-\pi/2}^{\pi/2} \cos(2(x-y))q(y, t)H(u(y, t) - \kappa)dy - I_0 \cos(4x), \quad (17)$$

and  $q$  is governed by Equation (1b). To start, we will also assume a symmetric bimodal input ( $I_a = 0$ ). This way, we can simply track  $q$  in the interior of one of the bumps, given  $q_i(t) = q(\pi/4, t)$ . Solving the resulting piecewise system of differential equations, we can derive an implicit formula for

$$q_0 = \frac{1}{1+\beta} + \frac{\beta}{1+\beta} e^{-T/\tau} - (1-q_0)e^{-2T/\tau}, \quad (18)$$

the value of the synaptic depression variable inside a bump just prior to a switch. We can rearrange (Equation 18) to yield a formula for the dominance time

$$T = \tau \ln \left[ \frac{\beta + \sqrt{\beta^2 - 4(1+\beta)(1-q_0)[(1+\beta)q_0 - 1]}}{2(1+\beta)q_0 - 2} \right], \quad (19)$$

so that we now must specify the value  $q_0$ . We can examine the fast Equation (17), solving for the form of the slowly narrowing right bump during its dominance phase

$$u(x, t) = q_i(t) [\sin^2(x + a(t)) - \sin^2(x - a(t))] - I_0 \cos(4x). \quad (20)$$

We solve for the slowly changing width  $a(t)$  by enforcing the threshold condition  $u(\pi/4 \pm a(t), t) = \kappa$  and using trigonometric identities to find

$$a(t) = \frac{1}{2} \tan^{-1} \left[ \frac{q_i(t) + \sqrt{q_i(t)^2 + 4(I_0^2 - \kappa^2)}}{2(I_0 + \kappa)} \right]. \quad (21)$$

We can also identify the maximal value of  $q_i(t) = q_0$  which still leads to the right bump suppressing the left. Once  $q_i(t)$  falls below  $q_0$ , the other bump escapes suppression, flipping the dominance of the current bump. This is the point at which the other bump of Equation (20) rises above threshold, as defined by the equation  $I_0 - q_0 \sin(2a_0) = \kappa$ . Combining this with Equation (21) and solving the resulting algebraic equation, we find

$$q_0 = \frac{2I_0 \sqrt{(I_0 - \kappa)(3I_0 + \kappa)}}{3I_0 + \kappa}. \quad (22)$$

The amplitude of synaptic depression is excluded from Equation (22), but we know  $q_0 \in (1 + \beta]$

$$\sqrt{\frac{1}{1+\beta}} \in [1, \infty) \implies \frac{1}{1+\beta} \in [1, \infty) \implies 1+\beta \in (0, 1] \implies \beta \in (-1, 0]$$

which we can solve explicitly for

$$a_R = \frac{1}{2} \cos^{-1} \left[ \frac{\kappa}{2I_0} + \frac{1}{2} \right]$$

We compute  $p[I_R > I_L | T^*(n)]$ , the predicted probability  $I_R > I_L$  based on sampling dominance time pairs from  $n$  cycles  $T^*(n) = \{T_R^{(1)}, T_L^{(1)}; T_R^{(2)}, T_L^{(2)}; \dots; T_R^{(n)}, T_L^{(n)}\}$ . As  $n \rightarrow \infty$ , the exponential distributions approximately defining the identical probability

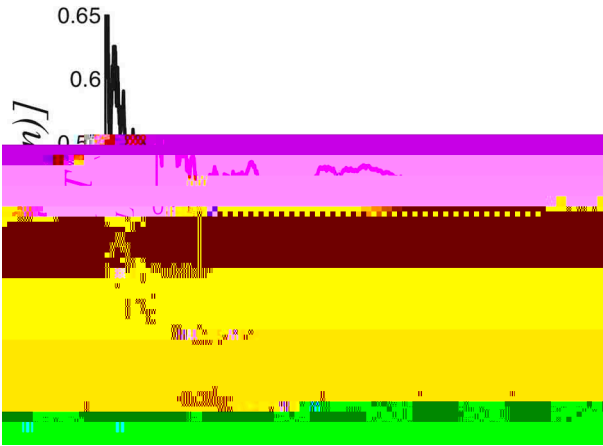


FIGURE 5, Predicted probability  $I_R$  is higher than the left  $I_L$ , based on the sampling cycles (2 s i ches be een percip s), for symmetric inputs  $I_L = I_R = 0.9$ . 2000 cycles,  $p[I_R > I_L | T^*(n)] \approx 0$ .







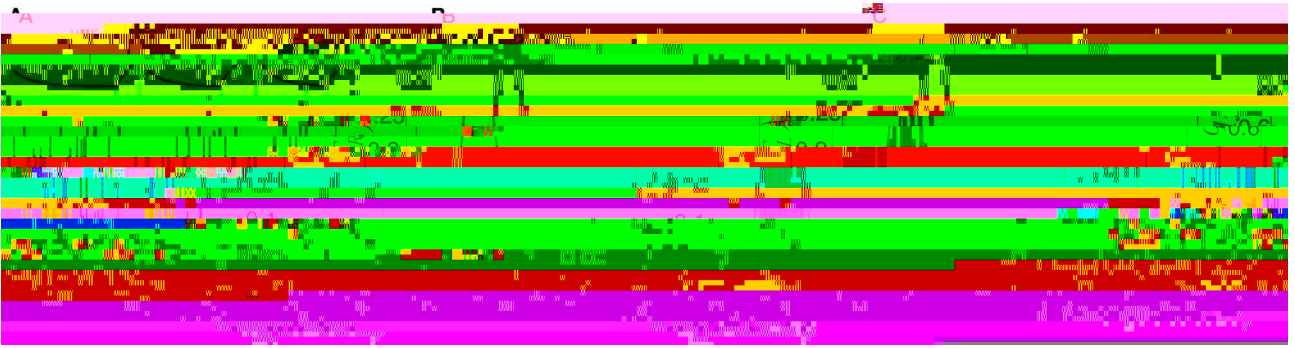


FIGURE 10, S i ching ind ced b noise and depression. (A)

$h(q_c)$   $h$   $u_R(c)$   $u_L(c)$   $q$   $0$   $1$   $c$   $q_R(c)$   $q_L(c)$   $h$   $h$   $u_R$

$u_L$  (B)  $h$  (C)  $m$   $m$   $h$   $em$

percepts that contains the same percept twice (e.g.,  $1 \rightarrow 3 \rightarrow 1$ ). This is opposed to a “switch forward,” which contains all three percepts (e.g.,  $1 \rightarrow 3 \rightarrow 2$ ). Statistics like these were analyzed from psychophysical experiments of perceptual tristability, using an image like **Figure 11A** (Naber et al., 2010). The main finding of Naber et al. (2010) concerning this property is that switch forwards occur more often than chance would suggest. Therefore, they proposed that some slow process may be providing a memory of the previous image. Memory in perceptual rivalry has also been observed in experiments where ambiguous stimuli are presented intermittently (Leopold et al., 2002; Pastukhov and Braun, 2008; Gigante et al., 2009). We suggest short term depression as a candidate substrate for this memory. As seen in **Figure 13B**, the bias in favor of switching forward persists even for non-zero levels

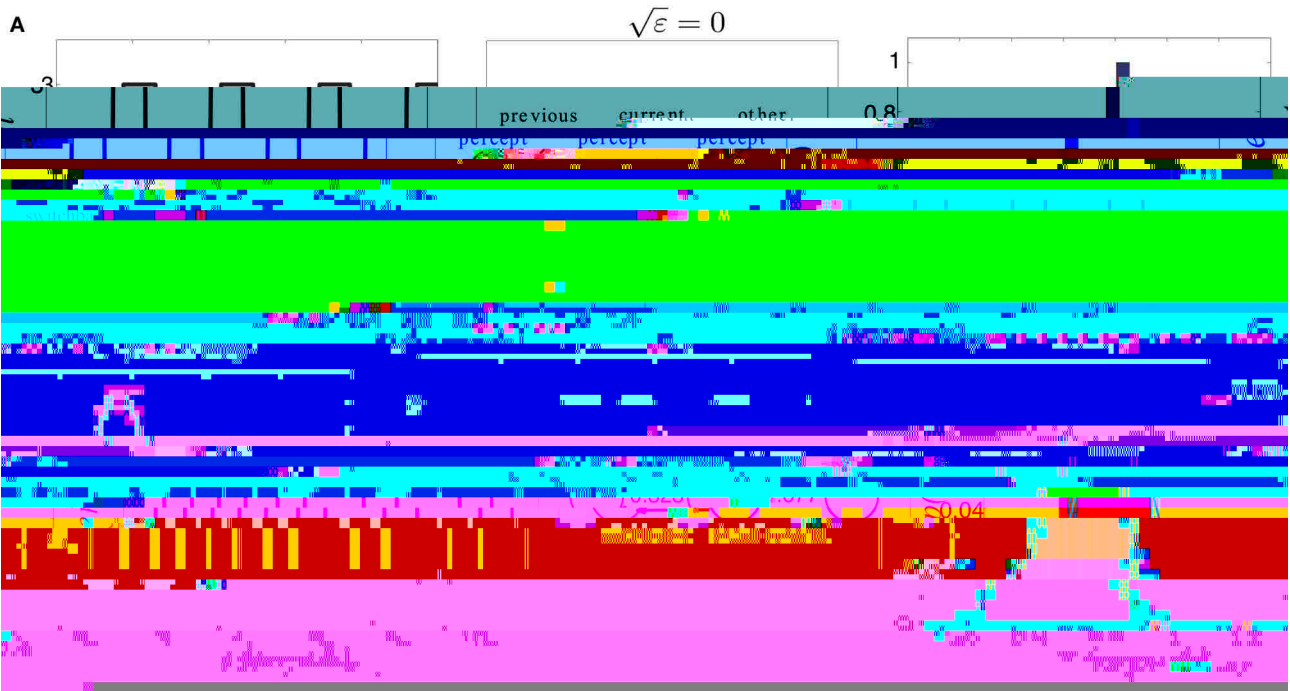


FIGURE 13, Noise degrades sources of information provided by dominance switches. (A) Hierarchical model of the human visual system. The model is a feedforward network of layers of neurons. The input is a grayscale image of a face. The output is a set of activation values for the neurons in the final layer. The model is trained on a large dataset of faces. (B) The model's performance is degraded by noise. The noise is added to the input image. The model's performance is measured by the percentage of correct classifications. The performance is significantly lower when noise is present.

states, leading to the slow timescale that defines the peak in depression-noise generated switches. Finally, using a three population space-clamped neural network, we analyzed depression and noise generated switching that may underlie perceptual tristability. We found this network also sustained some of the same relationships between input contrast and dominance times as

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