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)

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

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

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

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

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 τ. Fluctuations are introduced into population j with the independent white noise processes ξ_j with $\langle x_j(t)\rangle = 0$ 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 $\mathtt{dt} = 10^{-4}$, 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 $\mathtt{dt} = 10^{-6}$. 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

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

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

$$\ln f(T) = c_1 + c_2 \ln T - c_3 T. \tag{8}$$

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\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 low dimensional oscillation. The oscillation results from a combination of depression and mutual inhibition, which produces population dominance times and can thus be sampled to give information about the strength of the stimulus that produced them. Once noise is added to these low dimensional oscillations, dominance time distributions still remain relatively tight, which can be sampled to infer relative contrasts of each input. We contrast this with a previous cue orientation selective model which used a heterogeneous population of spiking neurons with lateral inhibition and slow adaptation, so chaos rather than noise produced apparent stochasticity in dominance times (Laing and Chow, 2002). We can use an energy function for a reduced system to approximate the relative effect of depression and noise on dominance times. These energy methods are also useful in the study of perceptual tristability, where we also show depression introduces a history dependence in dominance transitions.

DETERMINISTIC SWITCHING IN THE RING MODEL

To start we consider the ring model with depression (Equation 1) in the absence of noise, so $\xi \equiv 0$. In previous work, noise-free versions of Equation (1) have been analyzed to explore how synaptic depression can generate traveling pulses (York and van Rossum, 2009; Kilpatrick and Bressloff, 2010b), self-sustained oscillations (Kilpatrick and Bressloff, 2010b), and spiral waves in two-dimensions (Kilpatrick and Bressloff, 2010c). Here, we will extend previous work that explored input-driven oscillations in two-layer networks possessing statistics matching binocular rivalry (Kilpatrick and Bressloff, 2010a). We think of Equation (1) as a model of *monocular rivalry*, since oscillations can be due to competition between representations in a single orientation column (Ben-Yishai et al., 1995). Competition between ocular dominance columns (Kilpatrick and Bressloff, 2010a) is not necessary for our theory. For exposition, we will employ specific functional forms: cosine weight (Equation 2); a Heaviside firing

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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

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

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

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

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

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

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

$$u(x,t) = q_i(t)\left[\sin^2(x+a(t)) - \sin^2(x-a(t))\right] - I_0\cos(4x). \tag{20}$$

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

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

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

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

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

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 $T^*(n) = \{T_R^{(1)}, T_L^{(1)}; T_R^{(2)}, T_L^{(2)}; \ldots; T_R^{(n)}, T_L^{(n)}\}$. As $n \to \infty$, the exponential distributions approximately defining the identical probability

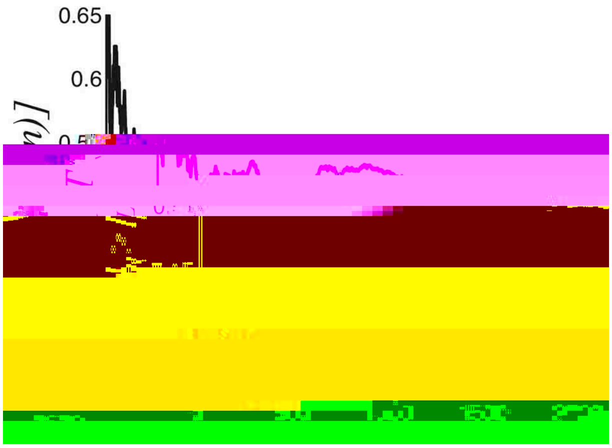

FIGURE 5 | Predicted probability right input I_R is higher than the left input I_L, based on the sampling cycles (2 switches between percepts), for symmetric inputs $I_L = I_R = 0.9$. 2000 ,
$p[I_R > I_L|T^*(n)] \approx 0$.

FIGURE 10. Switching induced by noise and depression. (A) … u_L. **(B)** … **(C)** … (q …) … u_R (…) … u_L (…) … 0 … 1, … q_R ( ) … q_L ( ) … u_R

percepts that contains the same percept twice (e.g., 1 → 3 → 1). This is opposed to a "switch forward," which contains all three percepts (e.g., 1 → 3 → 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

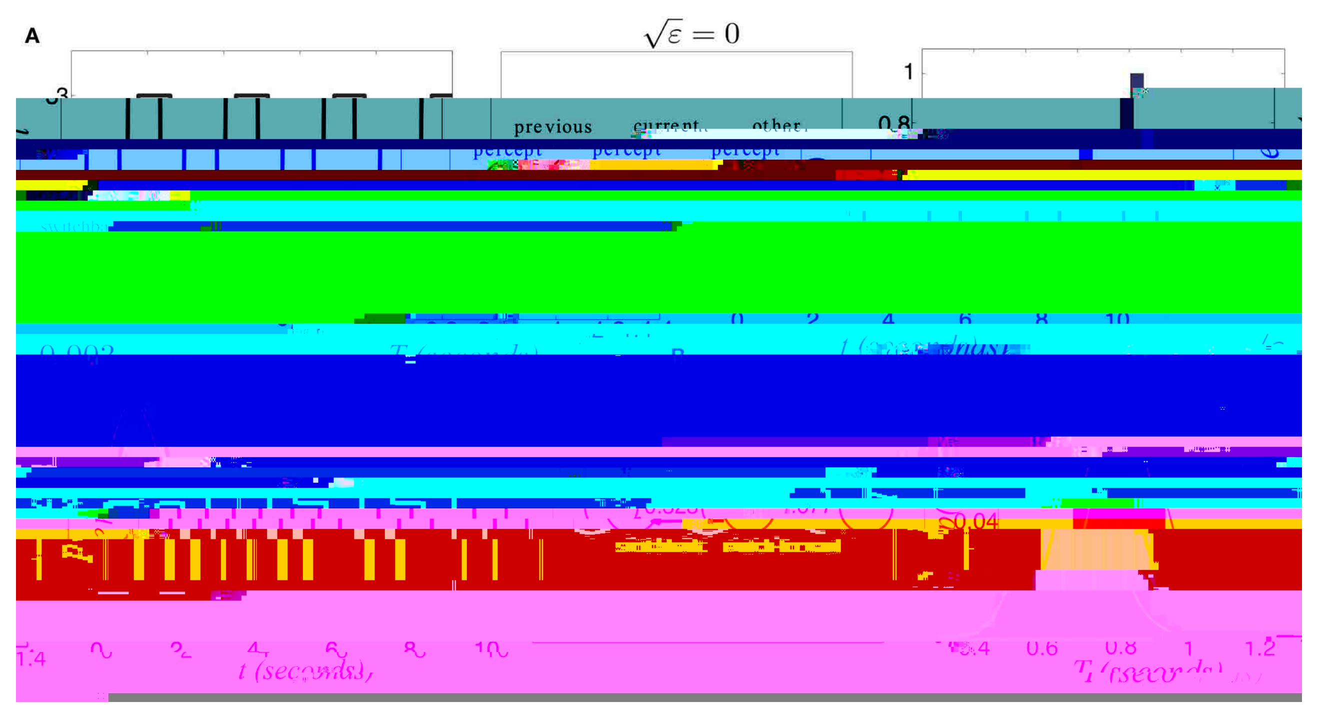

FIGURE 13. Noise degrades two sources of information provided by dominance switches. (A) h . (B( )-13.3(i)-6.8(0p( )2-465dc83 nce)-466

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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