

Optimizing Working Memory with Heterogeneity of Recurrent Cortical Excitation

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A neural correlate of parametric working memory is a stimulus-specific rise in neuron firing rate that persists long after the stimulus is removed. Network models with local excitation and broad inhibition support persistent neural activity, linking network architecture and parametric working memory. Cortical neurons receive noisy input fluctuations that cause persistent activity to diffusively wander about the network, degrading memory over time. We explore how cortical architecture that supports parametric working memory affects the diffusion of persistent neural activity. Studying both a spiking network and a simplified potential well model, we show that spatially heterogeneous excitatory coupling stabilizes a discrete number of persistent states, reducing the diffusion of persistent activity over the network. However, heterogeneous coupling also coarse-grains the stimulus representation space, limiting the storage capacity of parametric working memory. The storage errors due to coarse-graining and diffusion trade off so that information transfer between the initial and recalled stimulus is optimized at a fixed network heterogeneity. For sufficiently long delay times, the optimal number of attractors is less than the number of possible stimuli, suggesting that memory networks can under-represent stimulus space to optimize performance.

tion at a specific degree of network heterogeneity. For a large number of stimulus locations and long retention times, we show

into synaptic conductance by the spatially decaying functions (Fig. 1A) expressed:

$$W_{\beta,\alpha}(\theta_j, \theta_k) = \exp \left[\cos \right]$$

Diffusion in the potential well model. To analyze the diffusive dynamics of the bump, we studied an idealized model of bump motion. In this model, the bump position $\phi(t)$ obeys the stochastic differential equation,
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To calculate the probability density $p(\phi, t)$, we simulated 10,000 realizations of Equation 2 using an Euler–Maruyama integration scheme with a timestep $dt = 0.001$ from $t = 0$ to $t = 10$ s (Fig. 4 B, C). The effective diffusion coefficient was calculated as the gradient of the variance across

both fast-acting AMPA and slow-acting NMDA components (see Materials and Methods). Third, feedback connections from interneurons are broadly tuned (Fig. 1A, blue line). With these architectural features, neurons in the network respond to a transient stimulus (Fig. 1

and diffusion over the potential landscape occurs in a punctuated fashion. Across many trials, the probability $p(\theta, t)$ of finding the particle at position θ at time t

The transition $Y(0) \ni Y(T)$ involves diffusion across the network, which also degrades storage. To compute the proba-

Figure 6. N a v p — M. M. a .A, L a . p b a p b w a . . a M. A a p (), a M. a M. a b v . p b . . .B, P. v G a a p bab. a v a = 4 a σ² = 0.16. T a a a v p p p bab. a . . a v a a a a v .E a a a p p bab. a . . M. . a a a a a 3 . , F = 8,

$n_{\max} < m$ in both the potential well model and the spiking model (Fig. 7 A, B; $T = 10$ s). The value n_{\max} marks a compromise between quantization and diffusion errors. For the potential well model, the optimal heterogeneity n_{\max} decreases as the delay time T increases (Fig. 7 C), since diffusion error grows as T increases. In total, we find that for sufficiently long delay times the degree of heterogeneity n should be less than the stimulus size m to optimize information transfer.

For a fixed delay time T , varying the number of possible inputs m also shifts n_{\max} . Diffusion error is independent of the number of possible inputs m ; however, the total possible information increases with the number of inputs m . For small m , we have that $n_{\max} = m$ since when $n \geq m$, the quantization error is always zero and network diffusion increases with n (Fig. 8 A, B; $m = 4$). However, for larger m , we find $n_{\max} < m$, due to a compromise between quantization error and diffusion (Fig. 8 A, B; $m = 16$). These results hold for the potential well model over a wide range of m (Fig. 8 C). Overall, we highlight that a combination of varying T and m uncovers the effect of diffusion and quantization

error on mutual information in a working memory network. In particular, for many combinations of T and m , an optimal spatial heterogeneity for information transfer can be found.

The information $I(X, Z)$ measures the general relation between X and Z , one that is decoder independent. However, in psychophysical experiments, a reward is only given when the recall is correct, i.e., $X = Z$. Thus, it is important to consider how the probability of correct recall depends on the spatial heterogeneity of excitatory connections. In both the potential well and spiking network models, the probability of correct recall is maximized for a fixed $n < m$ when T is sufficiently long (Fig. 9 A, B), consistent with observations of $I(X, Z)$ (Fig. 7 A, B). The n that maximizes the probability of correct recall decreases as storage time increases (Fig. 9 C), also in agreement with results using $I(X, Z)$ (Fig. 7 C). The probability of correct recall provides a quantification of error that weights all incorrect responses the same. To use knowledge of the spatial organization of the cue set in determining error, we also measure the impact of the number of attractors on the angular difference between the recalled and cued

stimulus position. Specifically, we compute the variance of the difference between the recalled and input cue location $X - Z$. The magnitude of the recall error is minimized for a fixed $n < m$ (Fig. 9D,E), corroborating our findings for $I(X, Z)$ and proportion correct. Thus, our core finding that information transfer across the memory network is maximized for a specific degree of spatial heterogeneity also holds for a measure of task performance.

Discussion

We have outlined how both neural architecture and noisy fluctuations determine error in working memory codes. In working memory networks, the position of a bump in spiking activity encodes the memory of a stimulus, and input fluctuations cause diffusion of the bump position, which degrades the memory. Spatially heterogeneous recurrent excitation reduces the diffu-

of information between the stimulus and the memory output by tuning the spatial heterogeneity of recurrent excitation. We found that the ideal heterogeneity gives a number of attractors in the network n_{max} , which can be less than the number of possible inputs to the network m .

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Networks whose dynamics lie on a continuum attractor have steady-state activity that can be altered by arbitrarily weak noise and input (Bogacz et al., 2006). The advantage of this feature is that two stimuli with an arbitrarily fine distinction can be reliably stored and distinguished upon recall. However, this structure requires fine-tuning of network architecture, since any paramet-

position is possible, but motion between attractors will depend on θ and will be difficult to interpret as a simple diffusion process. Nevertheless, we expect that the specifics of spatially uneven heterogeneous coupling will significantly impact both the attractor

