

Random compressed coding with neurons

According to the efficient coding hypothesis, neural responses represent information so as to enable the most accurate readout possible, constrained by neuronal resources and neuronal noise. To date, much of the theoretical work on efficient neural coding has focused on relatively simple models of neural activity, characterized by smooth, often unimodal tuning curves [1, 2]. Real neurons, however, often exhibit more complex tuning curves. For instance, in the entorhinal cortex, the periodicity of grid cell tuning curves, as well as their functional organization in modules, imparts the population code with an exponentially large dynamic range, defined as the ratio between the range of represented stimuli and resolution [3]. Recently, multiple other examples of neurons with complex, but unstructured tuning curves have been identified [4, 5]. These findings lead us to ask whether highly efficient neural codes require fine organization, as in grid cells, or whether they can be realized with more complex and irregular tuning curves. We approached this question with a benchmark model: a shallow neural network in which irregular tuning curves emerge due to random synaptic weights. The synapses project from a large population of sensory neurons with unimodal tuning curves in response to a one-dimensional stimulus onto a smaller neural population. A trade-off is observed between two qualitatively different types of readout errors: ‘local’ errors whereby two nearby stimuli are confused, and ‘global’ errors causing complete loss of information about the stimulus. When balancing the two error rates, we obtain an optimal solution in which a population code with irregular tuning curves achieves exponentially large dynamic range. We argue that compression balancing local and global errors takes place in the motor cortex, based on primate cortex recordings [6]. Our results show that highly efficient codes do not require finely tuned response properties, and can emerge even in the presence of random synaptic connectivity.

Additional detail. We study the benchmark case of random tuning curves as obtained in a two-layer neural network: L ‘sensory’ neurons uniformly tile a one-dimensional input space with unimodal tuning curves of width σ , and project to N ‘representation’ neurons with random synaptic weights. We consider the regime $N \ll L$ to investigate how efficient compressed representations can emerge. Because of randomness in synaptic weights, the tuning curves of representation neurons are irregular; analytically, we show that each neuron’s tuning curve can be viewed as a sample from a Gaussian process with Gaussian kernel with width equal to σ . As a result σ , the width of the tuning curves in the sensory layer, controls random tuning curves smoothness in the representation layer, and thus shapes the curve of mean population responses in the N -dimensional space of representation neuron activity (Fig. 1A).

Coding properties of representation neurons are investigated when their responses are corrupted by independent noise. Analytically, we compute the *local* error by approximating the curve of mean responses by a smooth function. As for the *global*, or catastrophic, error, we carry out an approximate calculation, by considering the distance between two segments of the mean response curve representing stimuli distant by more than σ as random, and then calculating the probability of two of these segments to be close to each other. We check these results with numerical Monte Carlo simulations, computing the error as obtained from an ideal Bayesian decoder which minimizes the mean squared error. We find that an optimal tuning width balances the two error types (Fig. 1B). At optimality, the mean squared error decreases exponentially with population size, similarly to a grid cell coding scheme (Fig. 1C). This result is not qualitatively affected by the introduction of independent noise in the sensory layer, which we show to have a modest impact (on the order of N/L) on the magnitude of the decoding error (Fig. 1D). Thereby, we demonstrate that highly efficient coding properties in terms of accuracy of the stimulus representation, comparable to finely designed coding schemes such as grid cells, obtain more generally in neurons with irregular and unstructured tuning curves.

Next, we illustrate the merit of irregular tuning curves in empirical neural recordings. Indeed, irregular tuning curves were reported to describe the neural responses during encoding of hand position in the monkey primary motor cortex [6], contrary to the classic theory which modelled them as linear functions of hand position [7]. After extending our random network model to encode multi-dimensional stimuli, we fit the tuning width σ , as well as noise amplitude parameters, to empirical data of [6] in order to capture the distribution of irregularity across tuning curves. Here, the sensory layer models parietal neurons, while the representation layer corresponds to motor neurons.

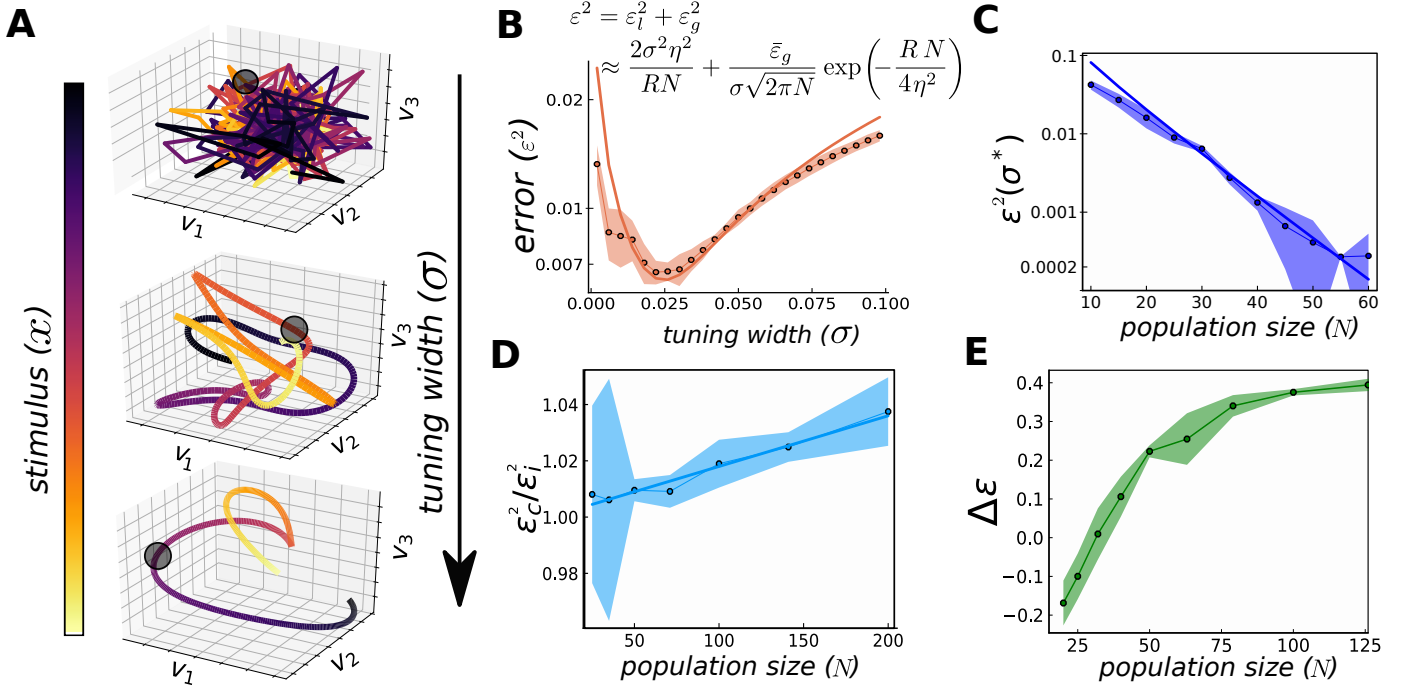


Figure 1: **(A)** Geometrical interpretation of a coding scheme: mean activity of three representation neurons as a function of stimulus, x (colored according to the legend), for three increasing values of the tuning width, σ (from top to bottom). Noise is represented as a grey disk of possible responses around the mean. Local error magnitude is proportional to the ratio between the radius of the disk and the length of the curve, while global errors occur when the curve comes close to intersecting itself on the scale of the noise. **(B)** Mean squared error (MSE), ϵ^2 , as a function of σ , for a given population size, N , and signal-to-noise ratio, R/η^2 (with R and η^2 signal variance and noise variance, respectively), averaged over synaptic weights realizations: comparison between theoretical prediction (formula on top, solid line) and numerical simulations (circles). The two contributions to the error exhibit a different dependence on σ . ($\bar{\epsilon}_g$ is a constant of order 1.) **(C)** Exponential scaling of the MSE at the optimal σ , as predicted by the minimization of the equation in **(B)**. **(D)** Ratio between MSE with (ϵ_c^2) and without (ϵ_i^2) sensory noise, for a given N and σ ; comparison between theoretical predictions (solid line) and numerical simulations (circles). The addition of input noise results in correlated output noise with a deleterious effect, yet quantitatively modest. **(E)** Relative advantage ($\Delta\epsilon = (\epsilon_{\text{irr}}^2 - \epsilon_{\text{lin}}^2)/\epsilon_{\text{lin}}^2$) of a population code with irregular tuning curves, as obtained in our model by fitting σ to the data of [6], and an encoding model with linear tuning curves, as proposed for motor neurons by the authors of [7].

With this neural-response model in hand, we compare the relative advantage of a population code with irregular tuning curves with respect to smooth, linear ones. The advantage of irregular coding schemes grows with population size N , as global errors are gradually suppressed and local error is thwarted by fine irregularities along the tuning curves (Fig. 1E). Interestingly, the difference between coding errors with irregular and with linear tuning curves no longer grows with N when the number of representation neurons becomes comparable to the number of neurons which controls a single muscle, a number estimated for M1 neurons in [6] through the decoding of EMG signals of individual muscles from subsets of motor neurons. Our results suggest that biological neural systems achieve a balance between high local accuracy, which can be obtained from complex, irregular neural codes and robustness against catastrophic errors, as obtained from smooth, simple neural codes.

References

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