

Population Code, Noise Correlations, and Memory

Frédéric E. Theunissen^{1,*} and Julie E. Elie^{1,*}

¹Department of Psychology & Helen Wills Neuroscience Institute, 3210 Tolman Hall, University of California, Berkeley, Berkeley, CA 94720, USA

*Correspondence: theunissen@berkeley.edu (F.E.T.), julie.elie@berkeley.edu (J.E.E.)

<http://dx.doi.org/10.1016/j.neuron.2013.04.012>

Changes in the correlated activity in the population code can increase neural discrimination by facilitating noise suppression. In this issue, [Jeanne et al. \(2013\)](#) observe learning-dependent changes in high-level avian auditory cortical neurons after a song discrimination task.

Neural activity recorded simultaneously across multiple neurons allows neuroscientists to study the importance of synchronous or correlated activity for the neural code. Although correlated neural activity had been shown to be important for information processing tasks such as visual feature integration ([Singer and Gray, 1995](#)) and top-down attention ([Mitchell et al., 2009](#)) including attention processes during learning ([Jones and Wilson, 2005](#)), its role in memory storage had remained unknown until very recently. In this issue of *Neuron*, [Jeanne et al. \(2013\)](#) show changes in the correlated activity of avian auditory cortical neurons in response to auditory cues as a result of an associative learning task.

In these experiments, starlings learned to discriminate song motifs in a two-alternative forced-choice experimental design. Once the task had been learned, simultaneous recordings of multiple neurons were obtained using 16- and 32-channel polytrodes. The researchers used a clever experimental design wherein a pair of song motifs was presented as a single stimulus for each trial but where only one of the two motifs was relevant for the behavioral task (task-relevant sound). During the learning experience, the set of second motifs (task-irrelevant sounds) was heard with the same frequency and could therefore be used to distinguish familiarity from learning effects. Thus, during the neurophysiological recordings, responses to task-irrelevant sounds could be considered to be surrogates for neural representations before learning and responses to the task-relevant stimuli to be neural representations from the same neurons after learning. The results were striking: the correlated activity in the population code resulted in increased neural discrimina-

tion for the task-relevant sounds relative to the correlations observed for both novel and task-irrelevant sounds. The study replicates similar findings in the primate visual system ([Gu et al., 2011](#)) and, together, these two studies show, for the first time, that the memory for behaviorally relevant stimuli could be reflected not only in changes in the magnitude of the average responses to the stimuli but also, and irrespective of whether such stimulus response effects occur, in changes in correlated activity across neurons.

To appreciate the role of correlated activity in the population code and in memory, it is useful to think of simple examples. Take first the case of two binary auditory neurons, 1 and 2, that represent four sounds A, B, C, and D in a noiseless fashion ([Table 1](#)). The information from neuron 1 can be used to distinguish A or B from C or D while the information from neuron 2 distinguishes A or D from B or C. When the responses of both neurons are taken together, the ensemble code can be used to perfectly discriminate the four sounds. Although new information seems to be available in the joint neural response, one can appreciate that this result can be obtained from independent characterization of the responses of neurons 1 and 2 to each stimuli (i.e., from

nonsynchronous recordings of neurons): all the information is embedded in the stimulus-response function of single neurons, yet it is the specifics of the *signal correlation* for neurons 1 and 2 (correlated or positive for A and C and anticorrelated or negative for B and D) that yield a highly informative scheme. In an information-theoretic framework, the mutual information between the stimulus, S, and the response, R, is only $I(R_1; S) = 1$ bit for neuron 1, and similarly for neuron 2, $I(R_2; S) = 1$ bit (each neuron can only code two states). In this case, the information in the ensemble response is $I(R_1, R_2; S) = 2$ bits and is exactly the sum of the information from the individual neurons. One can say that ensemble code is perfectly nonredundant (or perfectly complementary) but it is not synergistic in the sense that the information in the ensemble is not greater than the sum of the information present in the response of each neuron. Consider a second example of two noisy neurons, 1 and 2, that encode sounds A and B ([Table 2](#)). For both neurons, stimulus A elicits no spikes (0) 50% of the time and one spike (1) 50% of the time. Stimulus B elicits similarly ambiguous responses and thus these neurons appear to lack any stimulus selectivity. However, as it turns out, the neural activity between the two neurons

Table 1. The Joint Activity of Neuron 1 and Neuron 2 Can Perfectly Encode the Stimulus Identity in a Coding Scheme with Highly Informative Signal Correlation

| | Neuron 1 | Neuron 2 |
|---|----------|----------|
| A | 0 | 0 |
| B | 0 | 1 |
| C | 1 | 1 |
| D | 1 | 0 |

Table 2. The Joint Activity of Neuron 1 and Neuron 2 Can Perfectly Encode A versus B in a Coding Scheme with Highly Informative Noise Correlation

| | Neuron 1 | Neuron 2 |
|---------|----------|----------|
| A (50%) | 0 | 0 |
| A (50%) | 1 | 1 |
| B (50%) | 0 | 1 |
| B (50%) | 1 | 0 |

is positively correlated for A and negatively correlated for B such that pair responses (0,0) and (1,1) are only observed when A is presented and responses (0,1) and (1,0) are only observed when B is presented. Thus, A and B can be completely discriminated from the ensemble response but only if one takes into account these noise correlations. And note that these noise correlations could only be measured in simultaneous neural recordings. In the information-theoretic framework, $I(R_1; S) = 0$ bit and $I(R_2; S) = 0$ bit but $I(R_1, R_2; S) = 1$ bit; this is an extreme example of a synergistic code where extracting the information relies on the interpretation of the noise correlations. At this point, one can start to appreciate that changes in neural discrimination, such as those expected during a perceptual learning task, could come about either by changes in joint neural representation of the signal or by changes in

the correlated activity across neurons given a signal, i.e., changes in the correlated noise. The study by [Jeanne et al. \(2013\)](#) is a striking example of the second: while there appear to be only very small changes in the signal representation, the correlated activity changes significantly as a result of the learning, resulting in significant gains in neural discrimination.

To interpret the results presented in the study, one needs to further understand how the relationship between stimulus representation and the correlated activity affects neural discriminability. As described previously ([Averbeck et al., 2006](#)), noise correlations could either increase or decrease neural discrimination depending on how the noise correlations covary with the signal representation (see also [Figure 1](#)). Succinctly, if the magnitude of the responses of neurons 1 and 2 varies in the same direction as one varies the stimulus identity (positive signal correlation), then, relative to uncorrelated

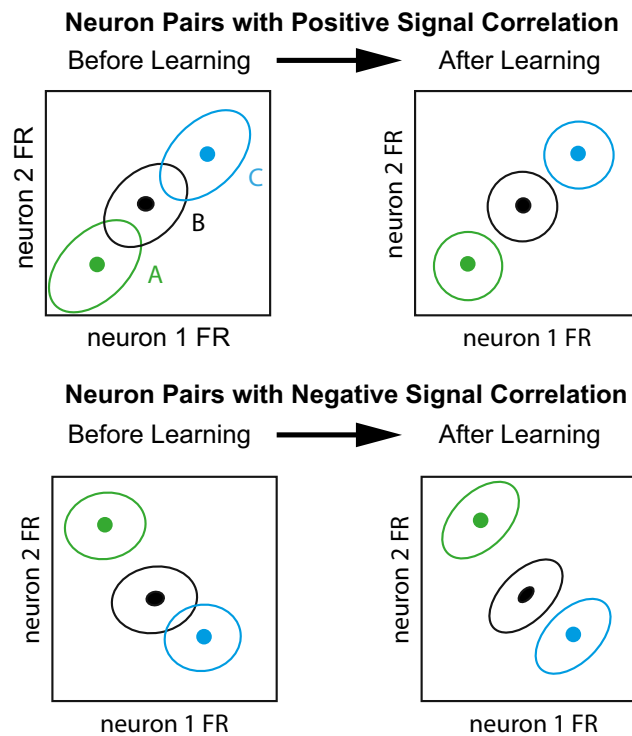


Figure 1. Noise Correlations Decreased as a Result of Learning for Neurons with Positive Signal Correlation and Increased for Neurons with Negative Signal Correlation

Top: positive signal correlation. Bottom: negative signal correlation. Both changes result in higher neural discrimination as illustrated by a reduction in response overlap for the three stimuli (A, B, and C). FR: firing rate.

noise, positive noise correlations will decrease neural discriminability while negative noise correlations will increase neural discriminability. The opposite is true for negative signal correlations. In the study by [Jeanne et al. \(2013\)](#), learning resulted in a decrease in the noise correlation for a pair of neurons with positive signal correlation and an increase in the noise correlation for a pair of neurons with negative correlations. As illustrated in [Figure 1](#), both of these changes lead to a gain in discriminability. Note, however, that in all cases the noise correlations remain positive; in this system at least, noise correlations appear to vary from values close to zero to relatively large positive values.

The biophysical mechanisms underlying the described changes in noise correlation are unknown but, as shown by the authors of the study, a realistic small network system where learning modulates the synaptic strength of common

input to noise-correlated neurons can easily reproduce the observed results. Thus, on one hand, as for other putative memory traces, local synaptic changes could be sufficient to explain the phenomenon. On the other hand, the origin of the “learning signal” and how it would modulate the synapses that affect noise correlation remain open questions. One also might wonder why noise correlations are not always in a form that maximizes neural discrimination as might be the case in the macaque visual cortex ([Ecker et al., 2010](#)). Therefore, maintaining optimal noise correlations must bear a cost or there might be other coding advantages for the nonoptimal noise correlation regime. A theory that unifies changes in correlated activity as they relate to sensory integration, attention, and now memory formation might shed light on this puzzle. And the wealth of population data that neurophysiologists are acquiring

and will acquire in the future might very well allow us to develop and test such theories ([Stevenson and Kording, 2011](#)).

REFERENCES

- Averbeck, B.B., Latham, P.E., and Pouget, A. (2006). *Nat. Rev. Neurosci.* 7, 358–366.
- Ecker, A.S., Berens, P., Keliris, G.A., Bethge, M., Logothetis, N.K., and Tolias, A.S. (2010). *Science* 327, 584–587.
- Gu, Y., Liu, S., Fetsch, C.R., Yang, Y., Fok, S., Sunkara, A., DeAngelis, G.C., and Angelaki, D.E. (2011). *Neuron* 71, 750–761.
- Jeanne, J.M., Sharpee, T.O., and Gentner, T.Q. (2013). *Neuron* 78, this issue, 352–363.
- Jones, M.W., and Wilson, M.A. (2005). *PLoS Biol.* 3, e402.
- Mitchell, J.F., Sundberg, K.A., and Reynolds, J.H. (2009). *Neuron* 63, 879–888.
- Singer, W., and Gray, C.M. (1995). *Annu. Rev. Neurosci.* 18, 555–586.
- Stevenson, I.H., and Kording, K.P. (2011). *Nat. Neurosci.* 14, 139–142.