Synergy in Cortical Networks

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A dot in this text can simultaneously stimulate thousands of neurons in primary visual cortex, a response that may seem unnecessarily redundant. Contrary to such a view, in this issue of *Neuron*, Nigam et al. (2019) demonstrate that these co-activated neurons generate abundant synergistic interactions that help to decode the stimulus.

Redundancy is good. If you need a pen in your desk, it is helpful to have two just in case one stops working. Similarly, when neurons start dying from disease or just old age, it is good to have neurons with similar functions to keep the brain working and delay the onset of symptoms. Redundancy can also be bad. If we only have three neurons to discriminate three stimulus features but two of them signal the same feature, we can only discriminate two features instead of three. Because the visual brain needs to discriminate millions of stimulus variations, having redundancy in the neuronal signals could be a problem. Puzzlingly, brains seem to have evolved disregarding this concern. The primary visual cortices of primates and carnivores are made of columns of neurons that are heavily interconnected and signal the same stimulus features such as spatial position, eye input, orientation, and contrast polarity (Hubel and Wiesel, 1977; Kremkow and Alonso, 2018). Because each cortical column has thousands of neurons responding to the same stimulus properties, it was frequently assumed that the interactions between neurons within cortical columns were either redundant or, at best, independent. This assumption is no longer valid. In this issue of *Neuron*, Nigam et al. (2019) demonstrate that neurons within the same cortical column show abundant synergistic interactions that are significant enough to increase the accuracy of stimulus decoding.

The authors simultaneously recorded the electrical activity from multiple neighboring neurons within the same cortical column of primary visual cortex in awake macaques. They stimulated all neurons with a circular grating pattern of white and black bars and measured the joint information transmitted by each neuronal pair about the stimulus. The joint information can be the same, lower, or higher than the sum of the individual information from each neuron (Barlow, 2001; Brenner et al., 2000). Consequently, a pair of neurons can process information independently if the difference between joint and summed information is zero (Figure 1A, black dotted line), redundantly if the difference is negative (Figure 1A, blue solid line), and synergistically if the difference is positive (Figure 1A, red solid line). Past studies concluded that most pairs of cortical neurons process information independently or redundantly even if they have different stimulus preferences (Montani et al., 2007; Reich et al., 2001). Therefore, it was assumed that redundancy was highest in neurons within the same cortical column because they have very similar stimulus preferences. Remarkably, Nigam et al. demonstrate that only half of the neuronal pairs within the same cortical column show redundant interactions (Figure 1A, blue) while the other half show synergy (Figure 1A, red). Because the number of redundant and synergistic interactions is similar, the average information difference for all pairs of neurons within the column is close to zero even if independent neuronal interactions are rare (Figure 1A, black).

Cortical connections do not average all the information within a column. Instead, they form highly specific networks that vary as a function of cortical layer, cell type, and cell stimulus preferences (Callaway, 1998). Consistent with this anatomical specificity, Nigam et al. demonstrate that synergy and redundancy are not randomly distributed throughout the column but form neuronal hubs (Figure 1C). Synergy hubs have more neurons interacting synergistically, redundancy hubs have more neurons interacting redundantly, and the interactions between synergy hubs are more synergistic than interactions between redundancy hubs. Importantly, they also show that the accuracy of stimulus decoding increases with the percentage of synergy hubs included in the decoder (Figure 1C). The synergistic interactions that Nigam et al. measured are more than three times stronger than those measured in the past (Montani et al., 2007) and provide 45% more information than the sum of the information transmitted by individual neurons.

Several technical advances allowed Nigam et al. to obtain more reliable measurements of cortical synergy than in the past. The first advance was to obtain their measurements in awake brains to overcome the difficulty of interpreting the information content of neuronal interactions in a cortex synchronized by general anesthesia (Montani et al., 2007; Reich et al., 2001). The second advance was to perform simultaneous neuronal recordings through the entire depth of a cortical column instead of recording from small neuronal clusters or neurons horizontally separated. This advance is important because Nigam et al. demonstrate that neurons within the same cortical column show less redundant interactions than neurons located in different columns (Figure 1B). Finally, the third advance was to measure joint information with longer time windows than in the past to match the 300 ms duration of their stimulus and the average duration of visual fixation.

As with any scientific advance, the work from Nigam et al. raises new questions that will need to be addressed in future experiments. The first question is whether

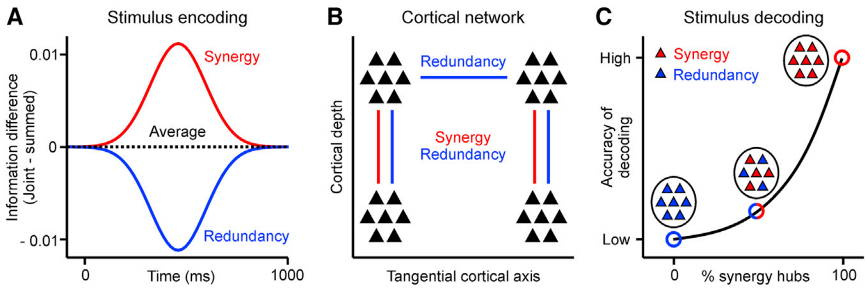

Figure 1. Neuronal Interactions within a Visual Cortical Column Improve Stimulus Decoding
(A) For each pair of neurons within the same cortical column, A and B, the authors measured their joint information (A&B) and the sum of information from the individual neurons (A+B). They found synergy in half of the neuronal pairs (red, A&B > A+B), redundancy in the other half (blue, A&B < A+B) and independence in the average across all pairs (black, A&B ≈ A+B).
(B) The authors also found that neuronal interactions can be redundant or synergistic across the depth of the same cortical column but are much more frequently redundant across the tangential axis of the superficial cortical layers.
(C) Stimulus decoding accuracy increases with the percentage of synergy hubs included in the decoder. Figure adapted from Nigam et al. (2019).

the values of synergy that they measured are large enough to facilitate stimulus decoding. The authors convincingly argue that their values are small because they optimized the stimuli to drive all neurons within the column, and that more natural stimuli should generate sparser responses with larger synergy. The second question is whether the different types of neuronal hubs that they describe reflect different connectivity patterns or just different stimulation conditions. Consistent with an origin in different connectivity patterns, redundant interactions are less common within the same column than across columns, and vertical intracolumnar connectivity is also very different from horizontal inter-columnar connectivity. However, synergy and redundancy hubs are similar in all cortical layers even if the inputs and connectivity patterns are very different in each layer. Because the amount of synergy changes with the stimulus conditions, redundancy and synergy hubs could also originate from differences in sensory stimulation. As shown by Nigam et al., synergy increases when the stimulus co-activates most effectively the neurons within the same cortical column. Moreover, some stimuli may require more synergy for decoding than others. For example, brief stimuli shorten the timescale of the neural code and their decoding may increase the need for synergy and spike timing (Butts et al., 2007). It is also worth noticing that neurons sharing the strongest retinal input and having the most similar receptive fields within the thalamus (i.e., same position, contrast polarity, size, and response time course) generate the strongest thalamic synergy when stimulated with white noise (Dan et al., 1998). If white-noise stimulation also drives the largest synergy in cortical neurons with the strongest common inputs and most similar receptive fields, strong common inputs may not reduce the neuronal information about the stimulus but increase it. That would explain why brains show such a stubborn tendency to cluster and interconnect neurons with the most similar stimulus preferences in both cortex and thalamus (Hubel and Wiesel, 1977).

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