

Journal Club

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Feature Configuration Modulates Effective Connectivity

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Review of Hirabayashi and Miyashita (<http://www.jneurosci.org/cgi/content/full/25/44/10299>)

Dynamic stimulus-dependent correlated spiking activity (on a millisecond scale) has been observed in several regions of the visual system, but dependencies have typically been limited to relatively simple integrative rules such as continuity and collinearity (Singer, 1999). Continuity is when features extend across multiple receptive fields (RFs) without interruption and collinearity is when features extend across aligned RFs. The notion that correlated firing might play a role in integrating visual features and solving the binding problem has been a controversial topic in neuroscience [an entire issue of *Neuron* (Vol. 24, Issue 1, 1999) was devoted to this debate]. The massive amount of physiological and anatomical data on the primary visual cortex (V1), as well as the accessibility to this area, have allowed researchers to characterize systematically stimulus-dependent correlated spiking activity in that structure. These data, together with retinotopic organization and the dependence of spike correlation on simple grouping rules, provide an intuitive idea about how this behavior might play a role in early stages of object recognition such as contour integration.

Inferior temporal (IT) cortex is viewed as one of the latest stages serving object recognition (Gross, 1992). IT neurons selectively respond to complex objects such as faces and this selectivity can be partially

invariant to spatial location and size. IT neurons can respond equally well to individual features isolated from complex objects. Correlated firing among V1 neurons tuned for orientated segments depends on collinearity and continuity among segments, which are ubiquitous configurations in natural scenes. Therefore, correlated firing among IT neurons tuned for complex features should depend on ecologically critical configurations of features such as faces. In a recent article in *The Journal of Neuroscience*, Hirabayashi and Miyashita (2005) tested this prediction by looking for differences in IT spike correlation between face-like objects (FO) and nonface-like objects (NFO) [Hirabayashi and Miyashita (2005), their Fig. 1 (<http://www.jneurosci.org/cgi/content/full/25/44/10299/FIG1>)].

The authors demonstrated a clear difference in cross-correlation peaks among IT pairs between FO and NFO stimuli comprised of the same features [Hirabayashi and Miyashita (2005), their Fig. 2 (<http://www.jneurosci.org/cgi/content/full/25/44/10299/FIG2>)]. Over 75% of the pairs had stronger spike correlation for the FO configuration versus the NFO configuration [Hirabayashi and Miyashita (2005), their Fig. 3A (<http://www.jneurosci.org/cgi/content/full/25/44/10299/FIG3>)], which was independent of firing rate changes [Hirabayashi and Miyashita (2005), their Fig. 4 (<http://www.jneurosci.org/cgi/content/full/25/44/10299/FIG4>)]. Over the population of pairs, the difference in correlation peaks between FO and NFO stimuli was more robust than the variance in correlation peaks across pairs

[Hirabayashi and Miyashita (2005), their Fig. 5 (<http://www.jneurosci.org/cgi/content/full/25/44/10299/FIG5>)]. Conversely, the ability of the firing rate to distinguish between FO and NFO stimuli at first glance appeared to be limited [Hirabayashi and Miyashita (2005), their Figs. 3B (<http://www.jneurosci.org/cgi/content/full/25/44/10299/FIG3>) and 5 (<http://www.jneurosci.org/cgi/content/full/25/44/10299/FIG5>)]. Approximately one-half of the pairs had larger firing rates for FO stimuli and the other one-half had higher firing rates for NFO stimuli.

There are two primary concerns that the authors addressed when interpreting these results. The first is about the magnitude of the spike correlation. If these correlated spikes signal feature configurations, the signal must be detectable among all spiking activity. The authors defined "correlation strength" as the percentage of their raw shift predictor-corrected peak measurement with respect to the average number of spikes fired by each cell (Fig. 1A). On average, this 1 ms peak is 1.6% for preferred FO stimuli and 1.1% for corresponding NFO stimuli. This means that there was only a 0.5% difference in the probability of any two spikes being within a 1 ms window of each other beyond chance. Although small, this difference between configurations was significant and consistent. In addition, expanding the temporal window to match integration times (~10 ms) results in greater spike correlation probabilities (Fig. 1A, gray area).

However, the difference between FO and NFO correlation strength is only one factor determining whether spike correla-

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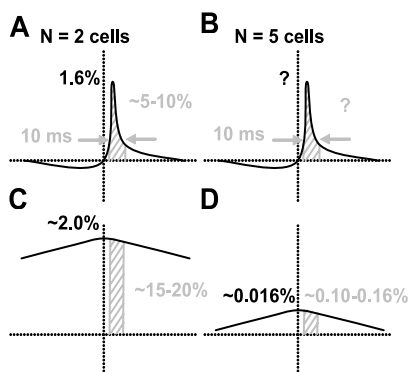


Figure 1. Distinguishing “effective connectivity” spike correlation from correlated spikes that arise from chance. **A**, Shift-predictor corrected cross-correlation (effective connectivity) for two cells. **B**, Shift-predictor corrected cross-correlation for five cells. **C**, Shift predictor (chance) for two cells. **D**, Shift predictor for five cells.

tion is a viable signal. It is also important to distinguish correlated spikes that may have functional significance from correlated spikes that simply arise from chance. A neuron that detects correlated spikes will be unable to discriminate between these two sources of correlation. Based on an average firing rate of 20 spikes per second, the percentage of correlated spikes within 10 ms that arise from chance is ~15–20% (or 2% for a 1 ms peak) (Fig. 1C). This corresponds to the magnitude of the shift predictor with respect to the average number of spikes [Hirabayashi and Miyashita (2005), their Fig. 2 (<http://www.jneurosci.org/cgi/content/full/25/44/10299/FIG2>)]. This percentage is proportional to firing rate. For one-half of the pairs that showed greater spike correlation for FO stimuli with respect to NFO stimuli, the firing rate actually decreased [Hirabayashi and Miyashita (2005), their Fig. 4 (<http://www.jneurosci.org/cgi/content/full/25/44/10299/FIG4>)]. This means the percentage of correlated spikes that arose from chance also decreased for FO stimuli with respect to NFO stimuli. Therefore, the two sources of correlation interfered with each for one-half of the pairs. Because the shift-predictor corrected spike correlation strength for a 10 ms window was ~5–10% (1.6% for a 1 ms peak) (Fig. 1A), there is some concern as to whether feature configuration-dependent spike correlation in IT can be distinguished from the conflicting correlated spikes that arise from chance.

This first concern can be tempered by the fact that the authors were observing only two simultaneously recorded neurons. The relatively weak synaptic connections in IT likely require larger numbers of

correlated spikes for effective transmission of information (Gochin et al., 1991). The percentage of correlated spikes that arise from chance will decrease substantially when synchronous events involve increasing numbers of neurons (e.g., for $n = 5$ cells, ~0.10–0.16%) (Fig. 1D). It is unknown whether or not the percentage of correlated spikes that arise beyond chance for five neurons is substantially higher than 0.16% (Fig. 1B).

The second concern is about the consistency of response measurements to repeated presentations of stimuli. The differences in firing rate for the two stimuli, regardless of the direction, were reliable across stimulus trials (based on information measurements). In addition, changes in firing rate were substantially more reliable than changes in spike correlation for repeated presentations. This raises the question of whether spike correlation is behaviorally relevant, because a relatively small population of IT neurons (<100) can accurately identify and categorize objects based on distributed firing rate representations alone (Hung et al., 2005).

However, correlation that may have functional significance was not separated sufficiently from correlation that arose from chance (i.e., shift predictor correction) in the information estimates. A single-trial correlation-coefficient calculation will be underestimated or overestimated if the firing rate changes within the trial, which is typical for neuronal responses [Hirabayashi and Miyashita (2005), their Fig. 2 (<http://www.jneurosci.org/cgi/content/full/25/44/10299/FIG2>)]. Considering that these two sources of correlation are many times contradictory and on the same order of magnitude as discussed above, the available information that either might provide about feature configuration could be cancelled out. Whether spike correlation is informative in IT will require observing larger numbers of cells or performing a correction similar to the shift predictor for single trials that accounts for within trial nonstationarity.

These two concerns do not limit the significance and importance of Hirabayashi and Miyashita's results. As the authors pointed out in their introduction, we do not have to view spike correlation and firing rate as two mutually exclusive mechanisms for neural signaling. Spike correlation can affect integration and shape the flow of information in IT. Successful identification and categorization of objects based on firing rates depended on appropriately weighted summation (Hung et al., 2005). Spike correlation can

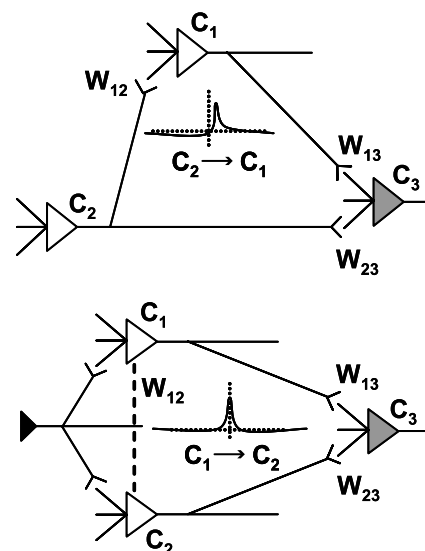


Figure 2. Dynamic “effective connectivity.” When C_1 and C_2 are driven by FO configurations, the spike correlation between these two cells (inset histograms, W_{12}) is stronger than for NFO configurations (whether directly connected or mediated through a common input). This increased correlation results in more effective integration and stronger effective connections (W_{13} and W_{23}) for C_1 and C_2 with C_3 . W , Connection weight.

be an indicator of “effective connectivity” or weighting between IT neurons (Fig. 2). Hirabayashi and Miyashita's results suggest the possibility that this weighting is dynamic. These dynamic weights can in turn influence the weighting with other neurons. For example (Fig. 2), if a simultaneously recorded IT pair with significant spike correlation [cell 1 (C_1) and cell 2 (C_2)] converges to the same neuron at a subsequent processing level [cell 3 (C_3)], the spike correlation between the pair will affect the weighting for each neuron with this hypothetical integrator (Alonso et al., 1996). This could occur regardless of whether the spike correlation is caused by direct connectivity or common input (feedforward or feedback) (Fig. 2).

Although the stimulus-dependent spike correlation in IT parallels the behavior in V1, there are some important differences. In V1, neurons with similar tuning properties tend to have spike correlation and stronger effective connections. This can be attributed to relatively small V1 RFs for local processing, along with Gestalt predictions of gradual changes in simple features with respect to space. However, at the level of IT, there is more global integration with larger RFs involving more complex features. Indeed, spike correlation in IT is not biased toward neuron pairs with similar tuning characteristics (Gochin et al., 1991). This raises inter-

esting questions about the organization and role of intracortical connectivity in IT. Hirabayashi and Miyashita begin to answer these questions and also provide an intriguing example of how spike correlation and effective connectivity are not static properties of IT cortical networks. Cortical networks are made up of complex dynamic synaptic connections and cannot be defined by single-neuron tuning and anatomy alone. This additional dimension likely

plays a critical role in object recognition throughout the visual system.

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