Paying attention to correlated neural activity

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Correlations in firing rate between pairs of neurons can change depending on task and attentional demands. This new finding suggests that measuring correlations can help to reveal how neural circuits process information.

Any reasonable neuroscientist should avoid studying correlations in neuronal activity at any cost. They require an inordinate amount of data to be estimated properly and they affect information content of neural codes and downstream processing in ways that are remarkably complicated and counter-intuitive[1–5]. However, we have no choice. If we are to understand how neural activity relates to behavioral performance, we need to measure how much information is conveyed by populations of neurons, which depends heavily on the exact pattern of correlated activity among neurons. Here we specifically refer to 'noise correlation', which quantifies how the activity of different neurons covaries from moment to moment, independent of changes in sensory stimuli or motor responses. Such correlations can also help us uncover the computations performed by neural circuits, as computations depend on connectivity and connectivity strongly constrains correlations.

Fortunately, recent studies demonstrate that it is possible to extract valuable information from correlations and a recent paper by Cohen and Newsome[6] provides a particularly interesting example. The authors trained monkeys to discriminate between two opposite directions of visual motion (for example, left versus right) in a noisy random-dot display. On each trial, monkeys were presented with two response targets cueing the potential movement directions. Across trials, they switched between discriminating motion along two orthogonal axes (for example, left versus right and up versus down). While the monkeys performed the task, Cohen and Newsome[6] recorded from pairs of neurons in the middle temporal area, which has been causally linked to performance of this task[7]. Individual neurons in the middle temporal area preferentially respond to motion in a particular direction, with the population representing the full range of directions. Previous experiments in the middle temporal area have suggested that correlations between pairs of nearby neurons depend solely on the difference in direction preference between the two neurons[8]. Specifically, neurons with similar direction preferences have moderate positive correlations, whereas cells with widely divergent preferences have very weak positive correlations.

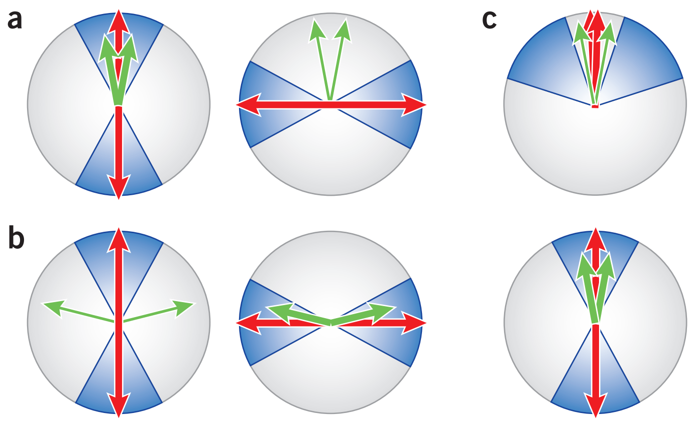

Figure 1 Interactions between correlations and attentional modulation as suggested by Cohen and Newsome[6]. (**a**) Left, the green arrows indicate the preferred directions of two neurons with similar preferred direction centered near upward motion. The task involves a discrimination between upward and downward motion (red double arrow). Feature-based attention (indicated by blue shading) predicts that neurons with preferred directions close to either upward or downward motion should be enhanced. This common drive to the neuronal pair should result in enhanced correlations (represented by the thickness of the green arrows). Right, as in the left panel, but this time the monkeys must discriminate rightward from leftward motion. The neurons are no longer affected by the attentional enhancement. As a result, their correlations are reduced compared with the left panel. (**b**) Diagrams are shown as in **a**, but for two neurons with widely different preferred directions that are both close to the right-left axis. This time, correlations are stronger when the task operates along the right-left axis (right) because both neurons are boosted by attention. (**c**) Prediction for an experiment in which the animal has to switch between a coarse-discrimination task (bottom) and a fine-discrimination task (top). If the theory of Cohen and Newsome[6] is correct, correlations should be weaker in the fine-discrimination task. This is because attention should be allocated to neurons that are tuned ±50 deg away from upward motion in the fine-discrimination task.

In their new study, Cohen and Newsome[6] show that correlations between middle temporal neurons also depend on the relationship between individual direction preferences and the axis of motion to be discriminated. Consider two neurons with direction preferences of –5 and +5 degrees (**Fig. 1a**). They found that correlated noise among responses of these two neurons was stronger when the monkey discriminated between upward versus downward motion than when the monkey discriminated between leftward versus rightward motion (**Fig. 1a**). For cells with widely different direction preferences (for example, –85 deg and +85 degrees), they found the opposite effect (**Fig. 1b**).

What accounts for these changes in correlated activity? Cohen and Newsome[6] carefully eliminated effects of the visual stimulus itself by restricting their analysis to identical stimuli (in which there was no coherent motion signal). Therefore, the only difference between the two task conditions was the axis of motion discrimination. On each trial, the response targets cue the animal as to which directions of motion are possible on a given trial. Cohen and Newsome[6] suggest that this setting of expectation could direct attention, inducing a change in coordinated top-down inputs to the middle temporal neurons. Indeed, when the animal has to discriminate between 0 and 180 degrees, it would make sense to focus attention on neurons tuned around 0 and 180 degrees, as these are most informative. Likewise, for discriminating between –90 and 90 degrees, attention should focus on neurons tuned around –90 and 90 degrees. This sort of modulation is known

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as feature-based attention. The effect of feature based attention on middle temporal neurons is well documented. When an animal pays attention to 0 degrees, it was found[9] that responses of cells preferring directions near 0 degrees are enhanced by about 10%, on average. As a result, two cells with direction preferences of –5 and 5 degrees would receive a common boost when the animal attends to 0 degrees. If this common boost varies slightly from trial to trial, it will induce additional positive correlations, which may explain why noise correlations are high for these cell pairs (**Fig. 1a**). In contrast, when the animal attends to 90-degree motion, the same neurons would no longer be boosted by attention and their correlation should decrease (**Fig. 1a**). Cohen and Newsome[6] simulated a neural model of attentional modulation in the middle temporal area that accounts for these findings by feature-based attention.

These simulations are encouraging but may not prove that feature-based attention is the main source of the changes in correlation. First, if attention boosts the response of neurons, one should see an increase in the mean firing rate of these neurons. This predicts that firing rates should increase when the preferred direction of the neurons is closely aligned with the axis of motion discrimination. Cohen and Newsome[6] did not find this effect but may not have had sufficient power in their analysis. Second, although attention is believed to increase the fidelity of sensory representations, the authors' model of attention degrades the quality of the code for the attended stimulus. This is because they apply attention as a multiplicative gain on a sample of middle temporal firing rates. Amplification of a sample of responses cannot increase information; it can only reduce it. It will therefore be important to determine whether the simulation results still hold for a model in which attention increases the information content of the representation. This could be implemented, perhaps, by having attention modulate the postsynaptic potentials of the middle temporal neurons caused by incoming spikes before the spike-generation nonlinearity.

The hypothesis that feature-based attention alters correlations could also be tested experimentally by manipulating the task to alter the effect of attention on neuronal responses. For instance, one could alternate between a coarse-discrimination task in which the monkey is trained to discriminate between 0 and 180 degrees and a fine-discrimination task in which the monkey must discriminate between –3 and +3 degrees (**Fig. 1c**). In the latter case, attention should boost the activity of neurons tuned around ±50 degrees, as these middle temporal neurons have the steep portion of their tuning curves centered around 0 degrees and thus show the largest changes in response between –3 and 3 degrees. A previous neurophysiological study showed that these off-axis neurons have maximal sensitivity and are most strongly correlated with perceptual decisions during fine direction discrimination[10], and a psychophysical study supports the notion that attention selectively boosts these responses[11]. A comparison between coarse and fine discrimination could therefore be a critical test of the effect of feature-based attention on correlations. For instance, cells with similar direction preferences near 0 degrees (for example, –5 and +5 degrees) should show strong response correlations when the animal performs the coarse discrimination along the 0/180-degree axis and should show weaker correlations when the animal performs the fine discrimination task around 0 degrees (**Fig. 1c**). Such a finding would reinforce the notion that attention drives changes in correlation while providing evidence that attention targets the most informative neurons.

Cohen and Newsome's[6] results are important because they establish the fact that measurement of correlations can provide insight into neural correlates of task-dependent processing. Similarly, previous studies of the relationship between single-unit responses and perceptual decisions (choice probability analysis) have suggested neural correlates of task strategy[12,13]. Notably, Cohen and Newsome[6] found that choice probabilities did not mirror changes in noise correlation, suggesting that these two measurements may provide somewhat independent assays of task-dependent processing. Thus, correlation measurements provide another tool for neuroscientists to explore the neural correlates of perception.

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A rose by any other name

No two roses smell exactly alike, yet we still perceive their scents as being the same. Most natural odors are made up of odorant mixtures that evoke complex patterns of neural activity, and it is rare for an odor to have the exact same components in the exact same proportions. Encoding these odorant mixtures therefore requires both the identification of individual odorants (pattern separation) and perceptual stability despite the presence of different odorant mixtures (pattern completion). In this issue (p 1378), Barnes and colleagues investigated the neural signals underlying these processes.

The authors recorded responses from neurons in both the anterior piriform cortex and the olfactory bulb in anesthetized rats to complex odorant mixtures that were variants of a core mixture. Some presentations were missing one or more odorants and other presentations involved a replacement of one or more of the odors. Repeated presentations of the same odor mixture elicited highly correlated responses from ensembles of olfactory bulb neurons, and small changes to the mixture (for example, removing or replacing even a single odorant) resulted in a significant decorrelation in the ensemble response. In contrast, cortical ensemble responses were not decorrelated by removing a single odorant. However, removing additional components or replacing even a single component did result in a significant decorrelation.

The authors then tested the ability of rats to discriminate between odor mixtures. As predicted by their electrophysiological results, they found that animals had difficulty discriminating between the full mixture and the mixture with one component missing, but not between the full mixture and a mixture with one component replaced (even though the two mixtures were nearly entirely overlapping). These results suggest that ensembles of piriform cortical neurons perform pattern completion, possibly providing a substrate for perceptual stability. ***Hannah Bayer***