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Spatial attention decorrelates intrinsic activity fluctuations in Macaque area V4.

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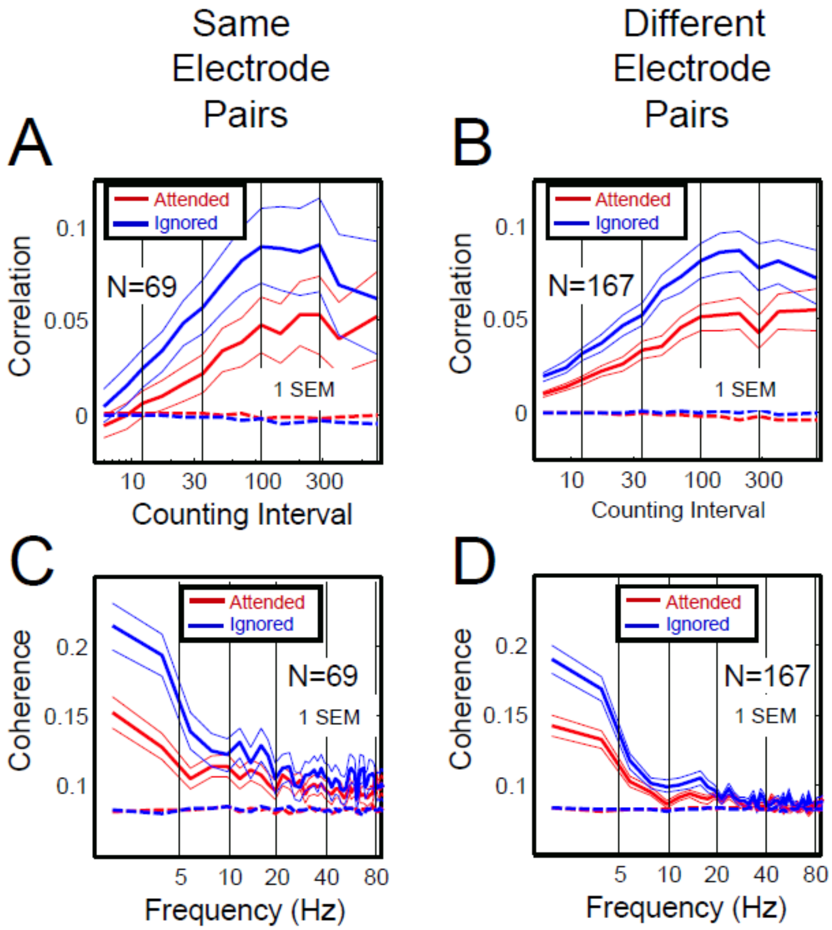
Supplemental Results:

Correlations for pairs isolated on the same or different electrodes.

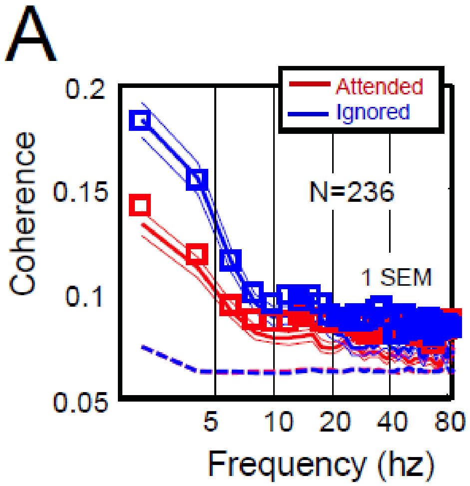
Our electrodes were typically separated by approximately 1-3 millimeters. However, because the electrodes are flexible and can bend, we are not confident of the separation of individual penetrations, and therefore cannot make a strong statement about how correlations varied as a function of distance. We can, however, separately analyze pairs recorded on the same electrodes versus different electrodes. This analysis is shown in Supplemental Figure 1.

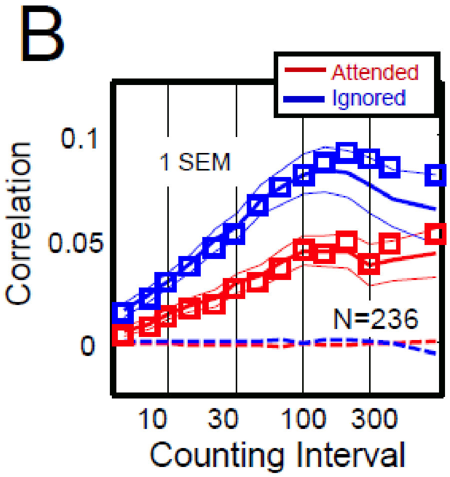


Supplemental Figure 1: *Attention-dependent modulation of spike-spike coherence and correlations for pairs recorded from the same or different electrodes.*

Eye movement analysis

It is important to verify that the effects on correlations in firing that we observe are not an eye movement artifact. The most direct way to test this is to ask whether the results change if we discard data that could be influenced by eye movements. Here we have computed coherence and correlation across the population after removing data recorded during the 400 msec. period that followed each fixational eye movement that we were able to detect using our eye monitoring system. Our eye monitoring system has sufficient resolution to detect fixational eye movements as small as 0.1 degrees of visual arc (dva). Details of the saccade detection algorithm and the source code with example data are provided at http://www.snl.salk.edu/~jude/. After removing fixational eye movements we find a significant attention-dependent reduction of coherence and correlation.



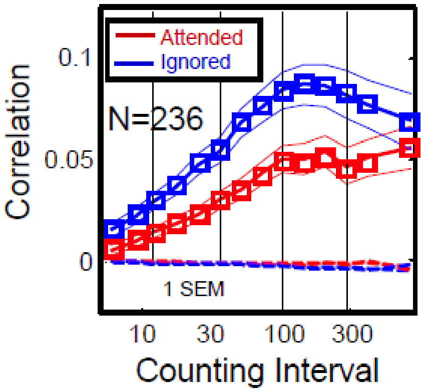


Supplemental Figure 2: *Attention-dependent modulation of spike-spike coherence and correlations after removing periods following fixation eye movements.*

Correcting for eye movements had very little systematic effect on our results, as seen in Supplemental Figure 2A and 2B. The lines show coherence (Panel A) and correlation (Panel B) before removing data following fixational eye movements. The square symbols show the values computed after the correction. Estimates of coherence and correlation are largely unaffected, and both measures are significantly reduced by attention, whether or not we exclude data following fixational eye movements. Therefore we conclude that our findings are not caused by fixational eye movements > 0.1 dva. Smaller eye movements would be expected to have a smaller effect on neuronal responses, so given the lack of an effect of fixational eye movements larger than 0.1 dva on our estimates of response correlation or their modulation by attention, it is unlikely that smaller eye movements strongly influence our findings.

The temporal scale of rate fluctuations and slow trends in firing rate.

Smoothing was used to remove slow variation across trials in computing correlations. Here, we were concerned that slow changes such as the alertness of the animal over a recording session might contribute to correlations in firing between units. Other studies performing similar analysis on correlations in firing across trials typically remove these slow trends in firing before computing the correlation (Bair et al., 2001; Cohen and Newsome, 2008). To control for these slow trends and make our data comparable to previous studies of spike count correlation, we implemented a similar procedure in computing the correlations. First, we computed the mean firing rate during the 800 ms sustained period on each trial, and then averaged over adjacent trials using a Gaussian smoothing window with a half-width of 10 trials. This smoothed firing rate was then subtracted from the spike counts of each trial to give normalized spike counts, which were used in computing correlation.

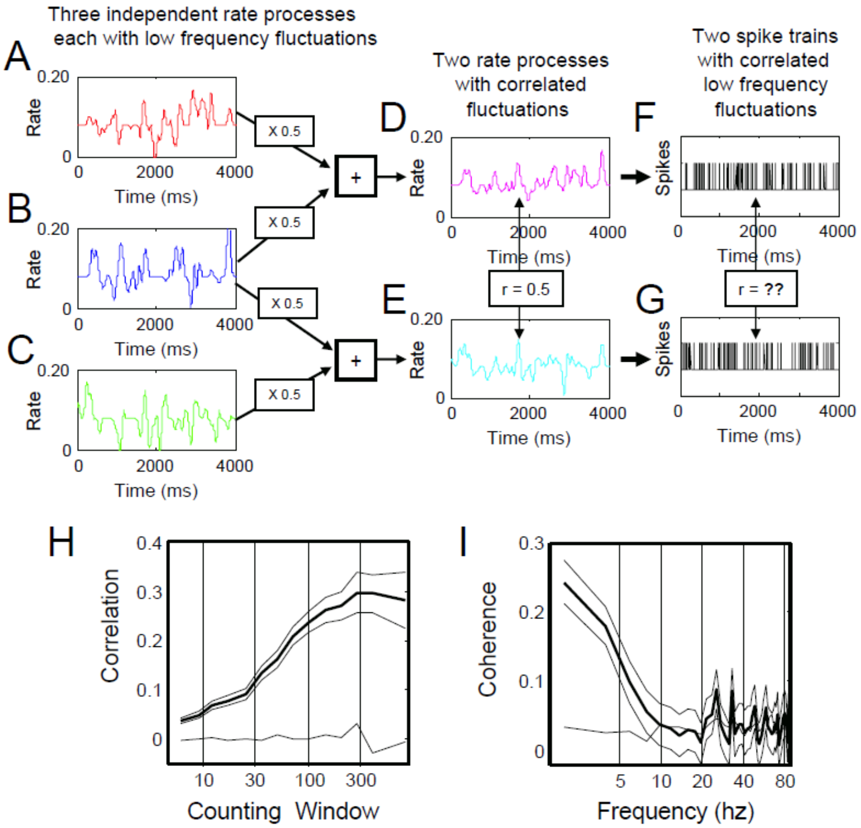


Supplemental Figure 3: *Attention-dependent modulation of correlations without factoring out slower trends in firing rate by smoothing rate across trials.*

Here we have undertaken a new analysis to verify that this did not give rise to any the effects we have observed. The results of this are shown as Supplemental Figure 3. The blue and red lines are taken from the manuscript, and show our estimates of correlation for ignored and attended responses. The blue and red squares show the estimates computed if we do not first subtract the smoothed average responses. The symbols fall almost perfectly along the lines, showing that the effort we made to exclude any slow fluctuations had very little effect, neither giving rise to the effects we observe, nor affecting the estimated time scale of the correlations.

Matching rate between attention conditions prior to computing correlation and coherence

The question of how to control for this spike count bias in correlation and coherence estimates has not been addressed adequately in the literature. The problem is present not only for coherence estimates, but also for estimates of the correlation of spike counts. Whereas coherence projects spikes onto sine and cosine basis functions, and then computes their correlation, in a similar fashion, one can regard correlations of spike counts simply as projecting spikes onto square counting windows before computing correlations. Thus the two methods exhibit similar biases and are very much related to each other.

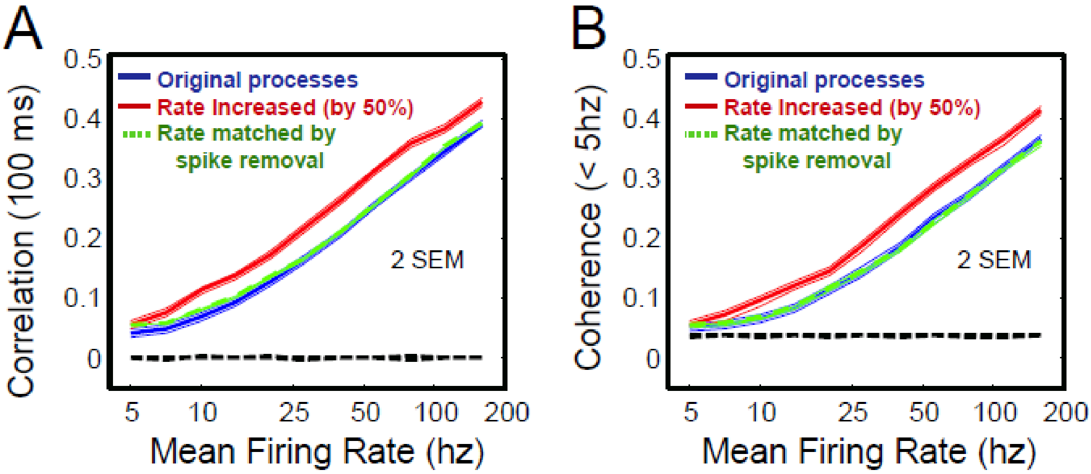


Supplemental Figure 4: *Simulated spike trains with know correlated low frequency fluctuations in rate and their corresponding estimates of correlation and coherence.*

In order to illustrate the problem for both coherence and correlations, we have included Supplemental Figures 4 and 5. In Supplemental Figure 4, we have created a pair of spike trains (Panel F and G) that have a well defined underlying correlation in their firing rates. To create the correlations in firing, we first created three independent continuous rate processes (labeled A, B, C) that had low frequency fluctuations in rate. Low frequency rate fluctuations were included independently for each process by the following method: we created a Poisson train of events with a mean rate of 10 Hz and then replaced each event with a Gaussian profile that was added to the flat mean rate of the process. The Gaussian profile for each event had a random amplitude (positive or negative, with σ equal to half the mean firing rate) and had a random temporal half-width (2σ) uniformly distributed from 50-150ms. If the rate process took on a value less than zero it was truncated at zero. We discuss shortly why this choice of rate fluctuations is a suitable model of our data. The first and second rate processes were then multiplied by 0.5 and summed (i.e., averaged) to yield a new rate process labeled in D, and the second and third processes were similarly averaged to give the processes labeled in E. The correlation between these two rate process is exactly 0.5 as half of their signal is shared. Each of these rate processes, r(t), are then used as input to generate the Poisson spiking processes, s(t), labeled in F and G by the rule

$$s(t) = \begin{cases} 1 & \text{with prob } r(t) \\ 0 & \text{else} \end{cases}$$

Having built a known correlation of 0.5 into the rate processes driving spiking in this model, we can now estimate correlation and coherence based on finite model spike trains, and ask how these compare to the true underlying correlation. To do this, we simulated 250 pairs of spike trains, each of which was 800 msec in duration, each with a mean firing rate of 100 Hz. The resulting correlation is shown, as a function of counting window, in Panel 4H. There are several points worth noting. First, correlation saturates at longer time windows, reflecting the time scale of the fluctuations that were built into the model. Second, it saturates at a value well below the true correlation of 0.5. Similarly, coherence is also underestimated (Panel 4I).

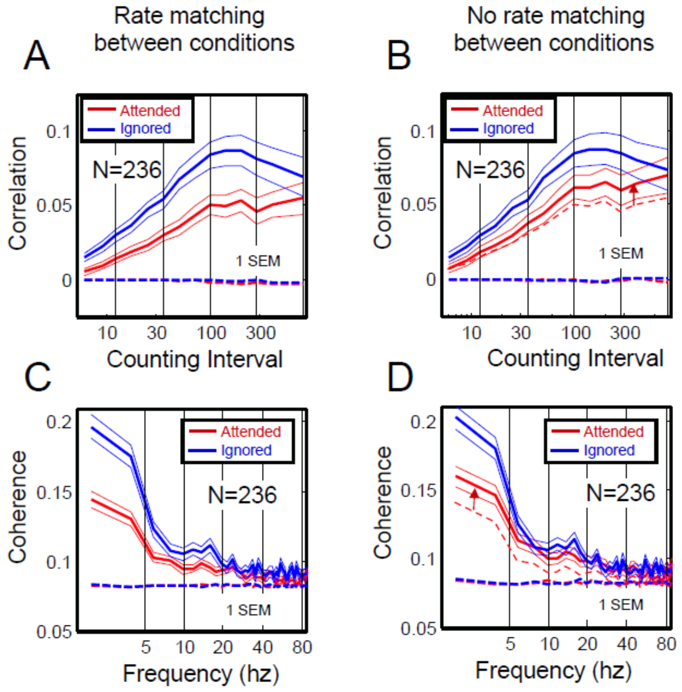


Supplemental Figure 5: *Correlation (at 100 ms intervals) and coherence (<5hz) estimated from the same underlying rate processes but as a function of mean firing rate of the generated spiking processes.*

The degree to which these measures underestimate the true underlying correlation depends on the number of spikes used in computing the estimates. This is illustrated in Supplemental Figure 5, which shows estimated correlation and coherence for a model with a fixed underlying correlation of 0.5, as a function of spike rate. The blue line in Panel A shows the estimated correlation computed with 100 ms counting bins as a function of the mean firing rates of the two model neurons. Estimated correlation increases monotonically with spike rate. This shows that simply increasing firing rates, without in any other way altering the rate processes driving the model neurons, results in an increase in estimated correlation. A very similar pattern is observed for the coherence measure that is shown in panel B.

This rate dependence is a basic limitation of coherence and correlation measures, and there is currently no way to correct for it. But, in the context of the present experiments, the key is not the absolute level of correlation but rather the relative level of correlation with and without attention. Since the two attention conditions differed in total spike count, the two conditions were differentially susceptible to this rate artifact. We therefore randomly removed spikes to equate total spike count across the two conditions. While this does not remove the artifact (estimated coherence is still a lower bound on true coherence), it removes the differential effect of the artifact, enabling us to see the effect of attention on coherence and correlation.

To verify this procedure does not introduce a new source of bias, we repeated our simulations with the spike trains having 50% higher firing rates (red lines, Supplemental Figure 5), and removed spikes randomly to match their firing rates to that of the original processes (blue lines). That is, we took the original model, increased the rate parameters driving the two neurons by 50%, and recomputed estimated coherence. The resulting coherence estimates are shown in red, and are plotted as a function of the firing rate before the 50% increase. We then randomly removed spikes from the resulting spike trains, with probability 2/3. This resulted in spike trains whose mean rate matched the rates that held before the 50% increase. The resulting correlations and coherences of the rate matched spike trains are shown by the green dashed line, which as expected, falls exactly on top of the original shown in blue. Thus, rate matching corrected for the rate artifact we introduced by increasing firing rates used in our simulation.



Supplemental Figure 6: *Attention-dependent modulation of correlations and coherence with and without rate matching.*

Although we are confident that it is appropriate to use rate matching to correct for this differential bias, we have also verified that our main results are not an artifact of applying the rate matching procedure. That is, attention reduces estimated correlation and coherence whether or not we use the rate matching procedure to correct for differences in firing rate. This is shown in Supplemental Figure 6. Panels A and C show the estimates of correlation and coherence if we do not implement rate matching. Both correlation and coherence are significantly reduced with attention. Thus, our findings are not an artifact of the steps we have taken to correct for the spike-count artifact.

Supplemental References

Bair, W., Zohary, E. & Newsome, W. T. (2001) Correlated firing in Macaque visual area MT: time scales and relationship to behavior. J. Neurosci., 21, 1676–1697.

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