

# Temporal Structure of Attention-Modulated Neuronal Synchronization in Macaque V4

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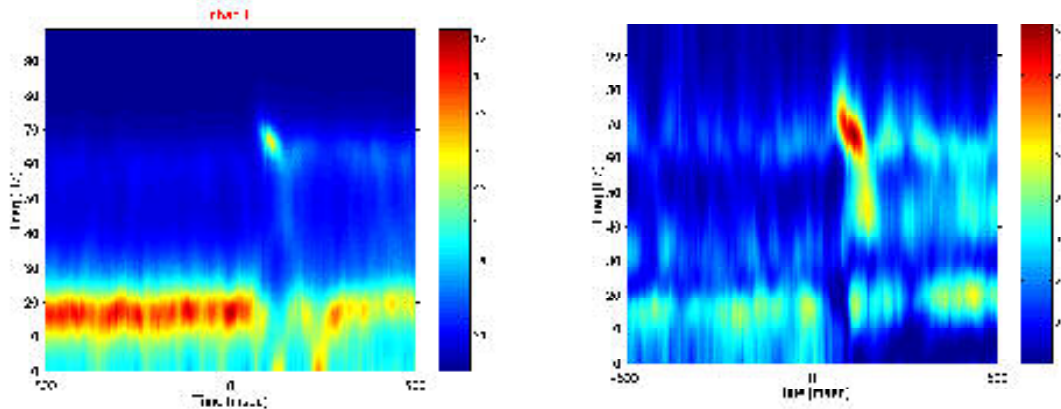
It has recently been shown that gamma band (35-90 Hz) synchronization is enhanced among V4 neurons activated by an attended stimulus as compared to neurons activated by distracters (Fries et al, Science, 2001). We studied the temporal structure of simultaneously recorded local field potentials from area V4 of monkeys performing a selective visual attention task. By use of Adaptive MultiVariate AutoRegressive (AMVAR) modeling we examined the temporal structure of attention-modulated neuronal synchronization and found elevated gamma power (~65 Hz) related to attention in episodes as brief as about 25 msec. We also found elevated coherent gamma synchronization at the same frequency as well as at a second gamma frequency (~45 Hz) among a subset of V4 recording sites. Analysis of the directional influences between pairs of V4 subpopulations for these two gamma-frequency events revealed that the influence in one direction could dominate over the other, and that the directional influence between some subpopulations was also larger when attention was directed to their receptive fields. These results support the idea that attention biases competition among visual stimuli in favor of those that are behaviorally relevant. The AMVAR method was instrumental in revealing the dynamics of gamma frequency synchronization with high temporal and frequency resolution.

Selective visual attention may be defined as the process whereby information is selected from multiple visual stimuli for further processing. In this process, attention is thought to bias competition among visual stimuli in favor of those that are most behaviorally relevant (Desimone & Duncan, 1995). It has recently been shown that gamma band (35-90 Hz) synchronization is enhanced among V4 neurons activated by an attended stimulus as compared to neurons activated by distracters (Fries et al, Science, 2001). The findings were obtained by examining the poststimulus interval between 50 to 150 ms with the spike triggered averaging technique. Here, we explored the temporal characteristics of attentional deployment by applying our recently developed Adaptive MultiVariate AutoRegressive (AMVAR) modeling technique (Ding et al, 2000) to Local Field Potentials (LFPs) recorded from multiple sites in V4.

The AMVAR procedure treated a collection of V4 LFP time series as the output of linear filters given white noise input. Thus the multi-site LFP signals were modeled as a multivariate autoregressive process for which the coefficients could be estimated by standard techniques (Morf et al, 1978). Our ability to capture the rapid dynamics of the multi-site LFPs lay in the treatment of the LFP signal from many repeated trials in a short time window as being generated by an underlying (approximately) stationary stochastic process. As such, the LFPs from different trials provided statistical samples for reliably estimating time series models over time intervals nearly as brief as that spanned by the MVAR model. Once the model coefficients were estimated, a battery of spectral quantities were derived.

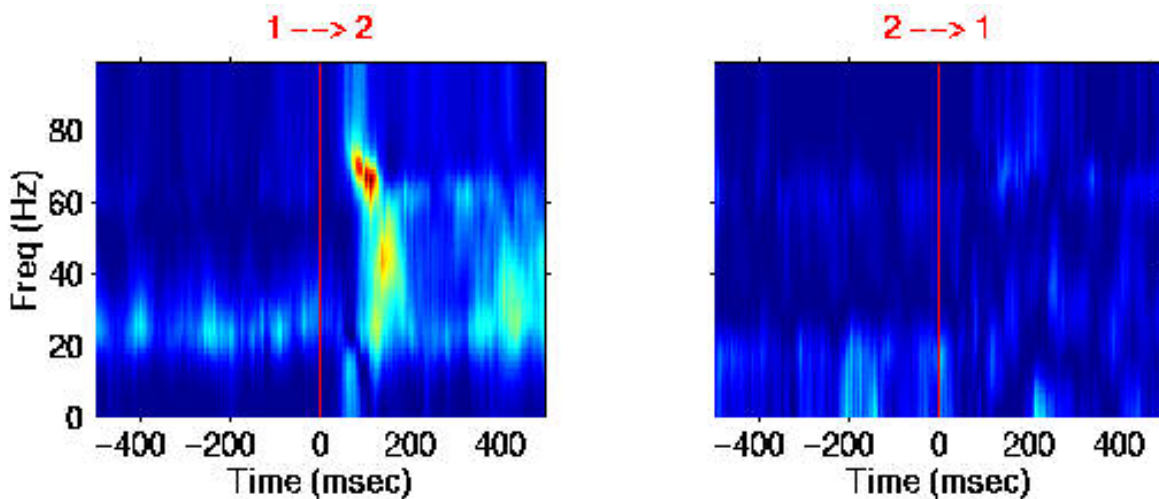
Power, coherence and Directed Transfer Function (DTF – a statistical measure of directional influence between two given recordings) spectra were computed from LFPs simultaneously recorded from multiple V4 sites with overlapping receptive fields (RFs). The monkey fixated a central spot on the display screen, and after a short delay, two stimuli were presented at equal eccentricity, one inside and one outside the RFs. On alternate trials, the monkey was cued to attend to either stimulus location. The V4 LFP data were down-sampled to 200 Hz.

We fitted LFPs within a 50-ms sliding window by AMVAR models. An example of the power spectrum from one recording site (Fig.1, left) and coherence between two sites (Fig.1, right) for attention within the RF (“attention inside” condition) is shown for illustration. At approximately 115 ms poststimulus, there was a brief, narrow-band oscillatory event detected as a peak in power around 65 Hz (Fig.1, left). This gamma power peak was accompanied by a peak in coherence among a subset of recording sites (Fig.1, right). At about 160 ms poststimulus, a second coherence peak occurred at approximately 45 Hz, but with no corresponding power peak. We further observed enhanced gamma power and coherence in the “attention inside” condition as compared to attention outside the RF.



**Fig. 1.** Time-frequency plots generated by the AMVAR procedure for site 1 spectral power (left) and spectral coherence between sites 1 and 2 (right) for attention inside the receptive field, using a 50-ms (10 point) sliding window.

Results obtained by DTF for the “attention inside” condition are shown in Fig. 2. A similar pattern to the coherence plots (Fig. 1, right), showing 65-Hz and 45-Hz poststimulus gamma peaks, is present for the influence from site 1 to site 2 (Fig. 2, left). However, both peaks are largely absent in the reverse (2→1) direction (Fig. 2, right). Therefore, both the 65-Hz and 45-Hz coherences could be attributed exclusively to the directional influence from site 1 to site 2. Like power and coherence, the 1→2 directional influence was greater the “attention inside” condition than when attention was directed outside the RFs.



**Fig. 2.** Time-frequency plots of the Directed Transfer Functions between sites 1 and 2 for attention directed inside the receptive field, using the AMVAR technique with a 50-ms (10 point) sliding window.

These results support the idea that attention biases competition among visual stimuli in favor of those that are behaviorally relevant (Desimone & Duncan, 1995), and suggest that increased gamma frequency synchronization to attended stimuli may enhance the impact of activated V4 neurons on their targets. The AMVAR method was instrumental in revealing the dynamics of gamma frequency synchronization with high temporal and frequency resolution.

## References

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