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On the tracking of dynamic functional relations in monkey cerebral cortex

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Abstract

To track and characterize the temporal dynamics of functional interdependence among cortical areas, we developed an adaptive multivariate autoregressive (AMVAR) modeling approach to the analysis of multichannel event-related local field potentials (LFPs) in macaque monkeys. We demonstrate the effectiveness of the approach by showing event-related dynamic change of power, coherence and directed transfer functions derived from the AMVAR models during a cognitive task. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

It is commonly accepted that perceptually and behaviorally relevant events are reflected in changes of the activity in large-scale distributed neuronal networks [2]. However, it is much less clear how these networks organize dynamically to cope with momentary computational demands. To extract information about the many processing functions arising in a cognitive task from a single or a few recording sites is difficult, since at any instant only a small fraction of the brain's hundreds of simultaneously active major cortical areas might be performing processing related to the function of interest. The situation is further complicated by the fact that the state of any particular cortical area and the relation between cortical areas can shift rapidly on

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a time scale of tens of milliseconds. Thus, tracking and characterization of the temporal and spatial interactions among various cortical areas is required for a greater understanding of the information processing of the brain. In order to decipher the dynamic organization of cortical ensembles, we utilized a suite of tools for event-related potential (ERP) analysis based on a recently developed technique called adaptive multivariate autoregressive (AMVAR) modeling that has been proven to be useful for studying short-term cognitive processing [3].

The event-related local field potentials (LFP) data used in this paper were recorded from one monkey by using 15 transcortical electrodes distributed in striate, prestriate, parietal, inferior temporal, motor and frontal areas in the right cerebral hemisphere. The monkey performed a visuomotor pattern discrimination task with GO/NOGO motor response of the left hand. The computer-generated stimulus set consisted of four-dot patterns forming a diamond or line. Each pattern could be either right- or left slanted. The LFPs were sampled at 200 Hz from around 115 ms prior to stimulus onset to 500 ms after stimulus onset in each trial of a session. A data set of 888 trials balanced for stimulus direction (right vs. left) was used in the analysis described below. For a more detailed description of the recordings, see [1].

We shall show that, on a time scale of 80 ms (or even shorter), the temporal dynamics of regional activity and inter-regional functional coupling can be clearly revealed during the different stages of visuomotor pattern discrimination. We shall then show that the strength of the coupling and especially the direction of influence between two cortical areas can be directly observed. This very remarkable observation could contribute to the understanding of signal transmission between different regions of the brain.

2. Methods

In this section we briefly review the AMVAR modeling technique introduced in [3] and describe powerful spectral quantities that can be derived from the AMVAR models.

Suppose that $\boldsymbol{X}_t = [x(1,t), x(2,t), \cdot, x(p,t)]^{\mathrm{T}}$ are p channels of LFPs. The multivariate autoregressive (MVAR) model is given by

$$\boldsymbol{X}_t + \boldsymbol{A}_1 \boldsymbol{X}_{t-1} + \cdot + \boldsymbol{A}_m \boldsymbol{X}_{t-m} = \boldsymbol{E}_t, \tag{1}$$

where $\boldsymbol{E}_t$ is uncorrelated noise with covariance matrix $\boldsymbol{\Sigma}$, and $\boldsymbol{A}_k$ are $p \times p$ coefficient matrices which can be obtained by solving the multivariate Yule–Walker Equations (of size mp^2) using the Levinson, Wiggins and Robinson (LWR) algorithm [7]. The model order m is determined by the akaike information criterion (AIC) [6].

The AMVAR analysis was applied in an 80-ms analysis window that was stepped point by point through the task. In each window, data from all trials were used to estimate the MVAR model. Once having obtained the model coefficients $\boldsymbol{A}_k$ and $\boldsymbol{\Sigma}$, the spectral matrix can be written [3] as

$$\boldsymbol{S}(f) = \boldsymbol{H}(f)\boldsymbol{\Sigma}\boldsymbol{H}^*(f), \tag{2}$$

where the asterisk denotes matrix transposition and complex conjugation. Based on the spectral matrix, a suite of tools for spectral analysis can be derived [4] as follows:

- *Auto power and partial power spectrum*: The auto power spectrum of channel i, $S_{ii}(f)$, is the ith diagonal element of the spectral matrix $\boldsymbol{S}(f)$. The partial power spectrum of channel i is defined by

  $$S_{ii}^{p}(f) = |\boldsymbol{S}(f)|/|M_{ii}(f)|,$$

  where M_{ii} is the minor of $\boldsymbol{S}(f)$ corresponding to $S_{ii}(f)$.
- *Ordinary coherence*: The ordinary coherence between channel i and channel j is given by

  $$C_{ij}(f) = |S_{ij}(f)|/(S_{ii}(f)S_{jj}(f))^{1/2}.$$

- *Directed transfer function* [5]: The directed transfer function is defined as

  $$\gamma_{ij}(f) = \left(|H_{ij}(f)|^2 \Big/ \sum_{k=1}^{p} |H_{ik}(f)|^2\right)^{1/2},$$

  which measures the information flow from channel j to i.

3. Results

The application of the tools described above to reveal the dynamic aspects of LFP activity will be illustrated in this section.

The simplest yet most used measure is the estimate of power as a function of frequency at each site. Thus, the power spectrum reveals how the activity at a site is distributed in frequency. Fig. 1 demonstrates the power spectrum as a function of time for a site in the parietal cortex. Its dynamical characteristic is starkly resolved: there is preferred resonance around 22 Hz during the pre-stimulus period, but it shifts to 12 Hz during the early stimulus processing. Here the switch occurs in response to stimulus presentation.

Whereas, the power spectra reflects the regional activity of neuronal assemblies, the ordinary coherence reflects the inter-regional functional coupling of neuronal activity between two cortical areas. An example of a dynamic ordinary coherence profile between striate and inferotemporal sites is shown in Fig. 2, where the larger coherence (darker region), corresponding to stronger association, occurs at around 120 ms and 12 Hz.

A topographic map of the overall inter-site coherence is plotted in Fig. 3 which shows a large-scale network coordinated at 12 Hz around 120 ms. The lines connecting cortical sites have significant coherence, with line thickness proportional to their values.

To characterize the direction of influence between cortical areas, we show an example of the DTF in Fig. 4, where the feedforward influence (dashed line) from lower (striate) to higher (inferotemporal) visual cortical areas typically begins earlier than the feedback influence (solid line) in the opposite direction. The significance of

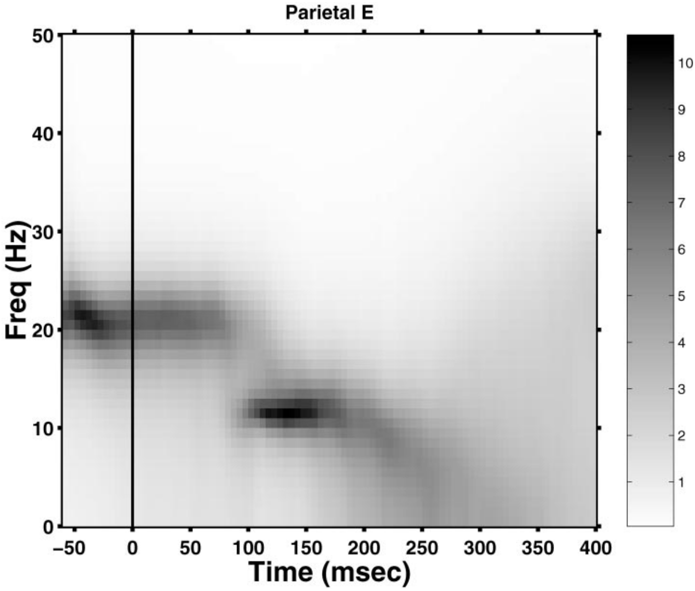

Fig. 1. Power spectrum time–frequency plot for a site in the parietal cortex (E). During the pre-stimulus period, the power is largely distributed at 22 Hz. Following stimulus presentation, it shifts to 12 Hz. The vertical solid line indicates the stimulus onset.

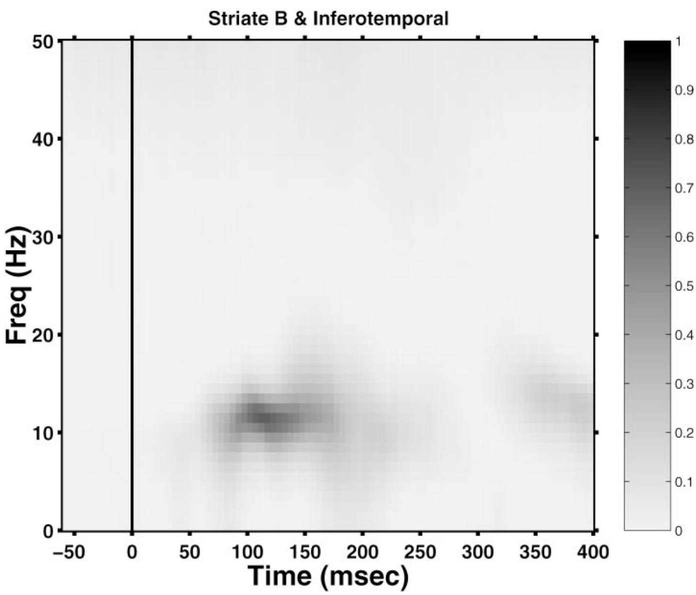

Fig. 2. Ordinary coherence time–frequency plot between striate B and inferotemporal sites. The vertical solid line indicates the stimulus onset.

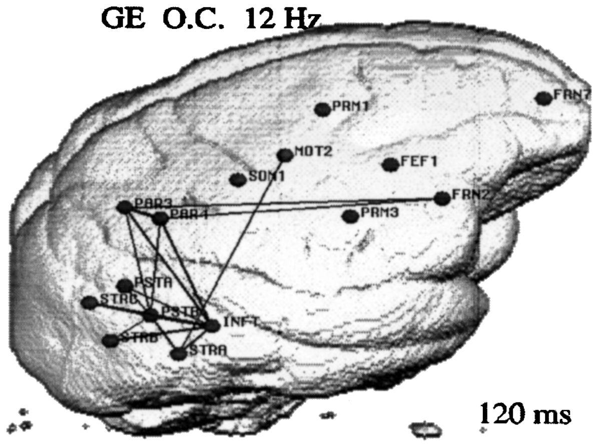

Fig. 3. Ordinary coherence reveals a large-scale coordinated 12 Hz network during visual feature extraction, demonstrating the functional coupling among multimodalities. The lines connect site pairs having significant coherence values with line thickness proportional to the values.

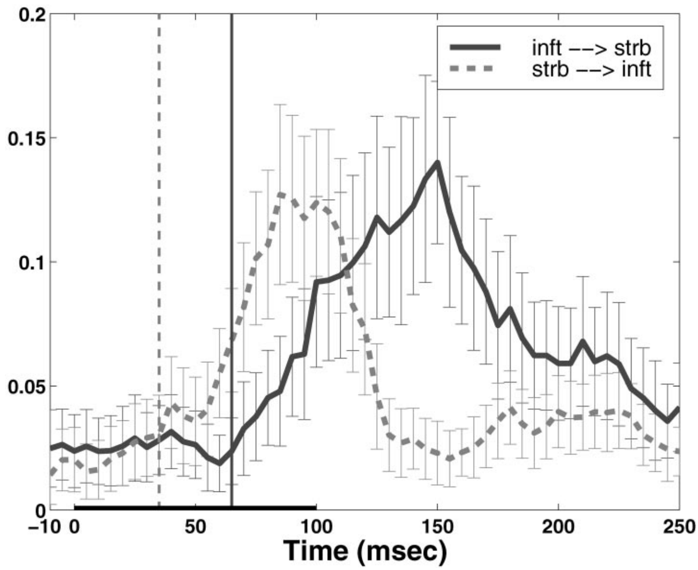

Fig. 4. Feedforward and feedback DTFs at 12 Hz with error bar obtained by boot-strap method. The feedforward influence (dashed line) from striate site B to an inferotemporal site occurs earlier than the feedback influence (solid line) in the opposite direction. The vertical lines indicate the onset times of these influences; the horizontal thick bar shows the stimulus duration.

the DTF measure is shown by the error bars which were obtained by the bootstrap resampling method [3]. An automatic procedure was developed, based on these statistics, to identify the onset times of the influences (two vertical lines).

We note that the differential onset times seen above are generally observable for all pairs involving visual cortical areas. Moreover, the feedforward influences from lower to higher areas always precede those of the feedback.

4. Conclusions

In summary, a suite of tools for ERP analysis was utilized to analyze multichannel LEPs during cognitive processing. Viewed as a function of time, they allows us to reveal various aspects of cortical dynamics. The temporal description of a cognitive process was demonstrated by dynamic power, coherence and DTFs. The results clearly show the effectiveness of the techniques by revealing task-relevant patterns of cortical interdependency during different stages of cognitive processing.

Acknowledgements

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