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Investigation of cooperative cortical dynamics by multivariate autoregressive modeling of event-related local field potentials☆

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Abstract

To explore the operation of large-scale networks in the cerebral cortex, we sought to measure the functional interdependence of event-related local field potentials (LFPs) from different cortical areas in macaque monkeys performing a visuomotor pattern discrimination task. To track the transformation of functional interdependence accompanying rapid changes in cognitive state, we developed a method for spectral coherence analysis using multivariate autoregressive (MVAR) models of short-windowed LFP time series. MVAR modeling overcomes problems associated with direct coherence analysis of short-windowed data. Coherence and phase are shown to vary during task processing with spatial location, processing stage, and stimulus and response conditions.

Keywords: Cerebral cortex; Local field potentials; Multivariate autoregressive modeling; Coherence; Phase

1. Introduction

Understanding how areas of the cerebral cortex cooperate in large-scale networks during cognitive processing is an important problem in computational neuroscience [2]. The measurement of functional interdependence between event-related local field

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potentials (LFPs) from different cortical areas is an approach that can potentially allow us to characterize the cooperative dynamics of large-scale network operations. A technique that captures salient features of functional interdependence among distributed cortical areas is time-dependent spectral coherence analysis [3]. Here we report new findings on cooperative cortical dynamics from a recently developed method of spectral coherence analysis using multivariate autoregressive (MVAR) modeling. A sequence of short-time MVAR models provides a detailed depiction of the spatio-temporal dynamics of multiple cortical areas during cognitive processing.

2. Experimental methods

LFPs were recorded from highly trained macaque monkeys performing a visuomotor task in which they discriminated dot patterns arranged as either diamonds or lines. In each recording session, a Go response was contingent on one pattern type and a No–Go response on the other. The contingency was reversed across sessions. Trials from sessions having mixed response contingencies were pooled, forming balanced data sets that differed only in stimulus pattern (Diamond vs. Line) or response type (Go vs. No–Go). The analysis described here used 888 trials from one monkey (subject GE) balanced across 4 sessions.

LFPs were simultaneously sampled at 200 points/s from 115 ms pre-stimulus onset to 500 ms post-onset. They were recorded transcortically from bipolar electrodes chronically implanted at 15 sites distributed in striate, prestriate, inferotemporal, parietal, motor, and frontal areas of the cerebral hemisphere contralateral to the responding hand (Fig. 1).

3. Analysis

Since LFPs are highly nonstationary during cognitive processing, their analysis must proceed in short-time windows having local stationarity. However, spectral

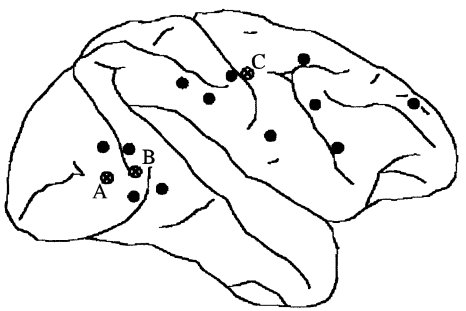

Fig. 1. Map of the right hemisphere of monkey GE showing the 15 electrode sites whose LFPs were used for MVAR modeling. Results are presented in this paper on the functional interdependence between a striate site (A) with a prestriate site (B) and a motor site (C).

analysis performed directly on short-time data is distorted due to bias [5]. We employed an alternative approach to spectral analysis based on MVAR modeling. The LFP time series were first normalized over the time points in each trial and over trials at each time point. An 80-ms window (16 time points) was then stepped point by point through the task. In each window, data from all trials and all electrode sites were used to estimate the MVAR model. Spectral coherence analysis was then based on the model coefficients.

The MVAR model is defined as

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

where $\boldsymbol{X}_t = [x(1,t), x(2,t), \ldots, x(p,t)]^{\mathrm{T}}$ are vectors containing p LFP channels (electrodes), $\boldsymbol{E}_t$ is a temporally uncorrelated noise vector, and $\boldsymbol{A}_k$ are p by p coefficient matrices. The model order m is determined from the Akaike Information Criterion (AIC).

Right-multiplying Eq. (1) by $\boldsymbol{X}_{t-k}^{\mathrm{T}}$ yields the multivariate Yule–Walker equations:

$$\boldsymbol{R}(-k) + \boldsymbol{A}_1\boldsymbol{R}(1-k) + \cdots + \boldsymbol{A}_m\boldsymbol{R}(m-k) = 0, \quad k = 1, 2, \ldots, m, \tag{2}$$

where $\boldsymbol{R}(s) = \langle \boldsymbol{X}_t\boldsymbol{X}_{t+s}^{\mathrm{T}} \rangle$ is the covariance matrix of lag s. The above set of mp^2 equations is solved for the set of model coefficient matrices $\boldsymbol{A}_k$ by using the LWR algorithm [6]. Data from multiple trials are incorporated in the calculation of $\boldsymbol{R}(s)$.

Spectral coherence is obtained from the coefficient matrices as follows [4]. Applying the z-transform to both sides of Eq. (1) leads to

$$\boldsymbol{X}(z) = \boldsymbol{H}(z)\boldsymbol{E}(z), \tag{3}$$

where $\boldsymbol{H}(z) = (\sum_{j=0}^{m} \boldsymbol{A}_j z^{-j})^{-1}$. Letting $z = \exp(\mathrm{i}2\pi f)$, we obtain the spectral matrix:

$$\boldsymbol{S}(f) = \langle \boldsymbol{X}(f)\boldsymbol{X}^*(f) \rangle = \boldsymbol{H}(f)\boldsymbol{V}_e(f)\boldsymbol{H}^*(f), \tag{4}$$

where $\boldsymbol{V}_e(f)$ is the spectral matrix of the noise process. The auto-spectrum of the kth channel is $S_{kk}(f)$. The cross-spectrum between channels k and l is

$$S_{kl}(f) = G_{kl}(f)^{-\mathrm{i}F_{kl}(f)}, \tag{5}$$

where $G_{kl}(f)$ is the magnitude spectrum and $F_{kl}(f)$ is the phase spectrum. The coherence spectrum between channels k and l is the cross-spectrum normalized by the two auto-spectra:

$$C_{kl}(f) = \frac{G_{kl}(f)}{(S_{kk}(f)S_{ll}(f))^{1/2}}. \tag{6}$$

The value of coherence, $C_{kl}(f)$, can range from one, indicating maximum interdependence between channels k and l at frequency f, down to zero, indicating no interdependence.

4. Results

Spectral coherence analysis was performed on MVAR models of the 15 sites displayed in Fig. 1. Results are presented for: (1) the relation between a striate site (A) and a prestriate site (B), comparing the Diamond and Line conditions; and (2) the relation between the same striate site (A) and a motor site (C), comparing the Go and No–Go conditions. Each comparison was examined at two times: during early stimulus processing (120 ms following stimulus onset) and at response onset (265 ms post-stimulus).

The coherence between striate and prestriate sites was consistently low (below 0.05) prior to the arrival of stimulus-related activity at the cortex. During early stimulus processing (Fig. 2), it then developed a peak centered at 9 Hz (with 6 Hz half-amplitude width), indicating functional interdependence in this frequency range between these areas. The different magnitudes of coherence in the Diamond and Line conditions suggest a functional difference in the interdependence of these two sites in the processing of these two stimulus patterns. The slopes of the (roughly linear) phase spectra in the frequency range of elevated coherence indicate that striate activity preceded prestriate activity with a consistent time delay of about 10 ms.

By the time of response onset, the coherence spectrum became broad and unfocussed for both stimulus patterns, with only a small difference between stimulus patterns (Fig. 3). The phase is difficult to interpret because of the low level of coherence.

The striate and motor sites also developed (small) coherence peaks at 9 Hz during early stimulus processing (Fig. 4). Although the presence of the peak indicates that these sites became functionally interdependent at this frequency early in visuomotor

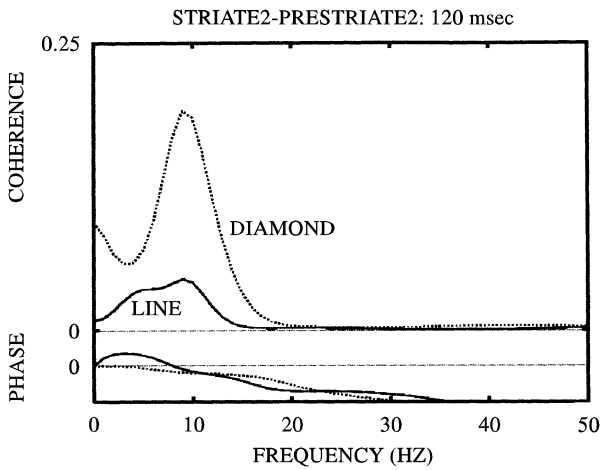

Fig. 2. Coherence and phase spectra between striate and prestriate sites, comparing Diamond and Line stimulus patterns in an 80-ms wide window centered at 120 ms post-stimulus. The total range of phase in this and subsequent figures is between $-180°$ and $180°$.

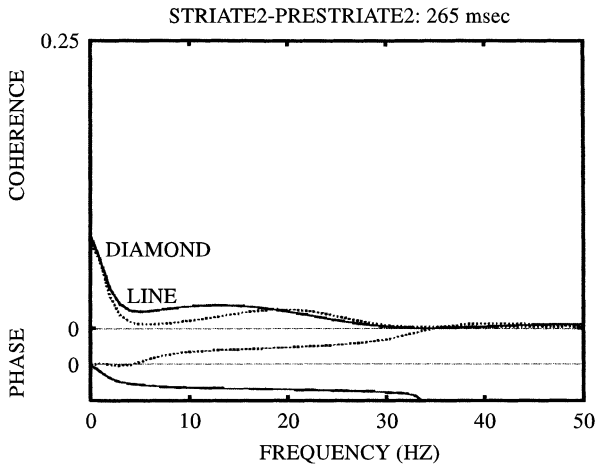

Fig. 3. Coherence and phase spectra between striate and prestriate sites, comparing Diamond and Line stimulus patterns in an 80-ms wide window centered at 265 ms post-stimulus.

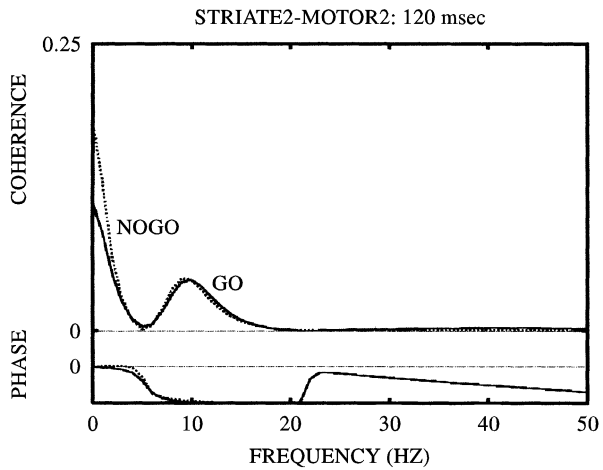

Fig. 4. Coherence and phase spectra between striate and motor sites, comparing Go and No–Go response types in an 80-ms wide window centered at 120 ms post-stimulus.

processing, the Go and No–Go conditions were not differentiated at this time. The phase spectrum shows an anti-phase relation between these sites in the region of the coherence peak that is not consistent with a fixed time delay.

At the time of response onset, the striate-motor coherence peak in the Go condition dropped in frequency to 3 Hz and increased in magnitude (Fig. 5). The phase relation also changed from anti-phase to in-phase. In the No–Go condition, coherence dropped to noise levels. This suggests a strong functional relation with no delay between striate and motor areas specific to active movement.

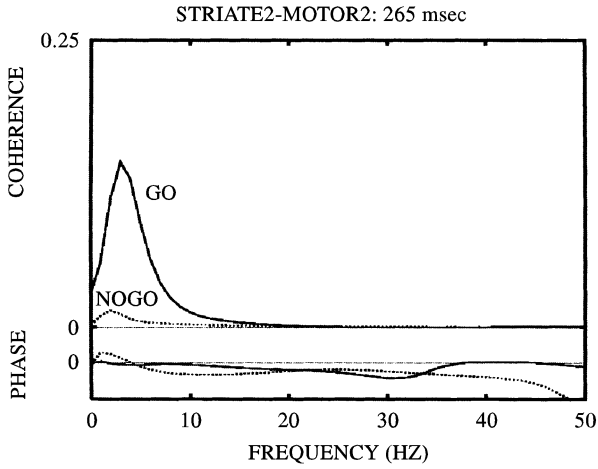

Fig. 5. Coherence and phase spectra between striate and motor sites, comparing Go and No–Go response types in an 80-ms wide window centered at 265 ms post-stimulus.

5. Conclusions

Short-time MVAR modeling is a new method that captures important dynamic aspects of LFP activity from distributed cortical sites during cognitive processing. In the preliminary, limited investigation described here, spectral coherence analysis of MVAR models revealed characteristic functional interdependence and timing relations of a site in striate cortex with a site in prestriate and another in motor cortex. During visuomotor task processing, interdependence and timing were observed to vary with spatial location, processing stage, and stimulus and response conditions.

The striate and prestriate sites were found to develop a 9 Hz peak in coherence specifically during early stimulus processing, with a phase spectrum suggesting transmission of information from striate to prestriate sites with a 10 ms time delay. The magnitude of coherence differentiated processing of the Diamond and Line stimulus patterns. These findings indicate that these two sites were engaged in processing stimulus-related information at this stage, most likely with a predominace of information transfer from striate to prestriate site. It would be incorrect to infer from this that all parts of the striate and prestriate areas maintained the same coherence and phase relation. In fact, spatial variation of interdependence between the two areas is expected from previous studies of the olfactory system [1]. Thus, the finding that the coherence peak in the Diamond condition was large as compared to that in the Line condition is specific to the two specific sites, and does not imply that striate and prestriate areas are in general more coherent for one condition than the other.

The striate and motor sites showed a different pattern of interdependence. Although a 9 Hz coherence peak did develop for these two sites during early stimulus processing, it was relatively small and did not differentiate the Go and No–Go conditions. These conditions were differentiated, however, at the time of response onset, with

a relatively large peak at 3 Hz specific to the Go condition. The striate-motor phase relation in the Go condition also changed, from anti-phase to in-phase.

These results are preliminary: the analysis is being expanded to systematically assess the statistical significance of coherence spectra for all pairwise combinations of sites in all conditions for these sessions, and other sessions, of this and other monkeys. Although preliminary, these findings suggest that spectral coherence and phase are useful measures of functional relation in the cerebral cortex. These measures have allowed us to demonstrate two different types of inter-areal relation. First, the relation between sites in two visual areas is specific to early stimulus processing, differentiates processing of two different stimulus patterns, and indicates information transfer in a feedforward manner. Second, the relation between striate and motor sites is specific to the time of response onset, differentiates the two response types, and shows a constant phase rather than constant timing relation. It is expected that further investigation will lead to a more comprehensive view of the spatio-temporal dynamics of the complex interactions occuring in large-scale cortical networks.

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