Top-Down Cortical Influences in Visual Expectation

Steven L. Bressler, Craig G. Richter, Yonghong Chen, and Mingzhou Ding

Abstract—Visual perception depends on prior experience. Previous encounters with visual objects allow an organism to form expectations about future encounters, and to use those expectations to tune the visual system to more efficiently process expected visual inputs. This paper explores the proposition that visual expectation involves top-down modulation of neurons in low-level areas of visual cortex in anticipation of expected stimuli. It reports evidence that topdown modulation occurs within task-specific coherent oscillatory networks in the visual cortex of a macaque monkey, and that this modulation is related to stimulus processing efficiency.

I. INTRODUCTION

TOP-DOWN influences on sensory cortices have long been postulated to play a role in a variety of different cognitive processes [1]-[7]. Recent evidence has implicated synchronized population activity in the mediation of topdown effects in the visual system [8], [9], particularly in anticipation of an expected visual stimulus [10], [11].

We previously discovered that synchronized oscillatory population activity in the beta frequency range (13-30 Hz) carries causal influences (defined statistically by time series analysis) between cortical areas of the sensorimotor system in macaque monkeys while they maintain a lever press with the hand during the wait period of a visuomotor pattern discrimination task [12]. We speculated that the synchronization of oscillatory activity observed in that study was related to allocation of processing resources to the sensorimotor system for maintenance of the lever press. The task also required that processing resources be allocated to the visual system for attending to a visual display screen in anticipation of expected visual stimuli to which they had previously been repeatedly exposed. We therefore hypothesized that synchronized oscillatory activity would also carry top-down causal influences from higher- to lowerlevel areas in the visual system [13].

We report here the results from a preliminary analysis designed to test for top-down influences in synchronized population activity in the visual cortex of the macaque

Y. Chen (<u>vchen@bme.ufl.edu</u>) and M. Ding (<u>mding@bme.ufl.edu</u>) are with the J. Crayton Pruitt Family Department of Biomedical Engineering, University of Florida, Gainesville FL 32611 USA. monkey. The same methodology used to discover causal influences carried by beta frequency oscillations in the sensorimotor system [12] was used here. We now describe that methodology and its application to the question of cortical top-down causal influences in visual expectation.

II. COMPUTING CORTICAL NETWORKS

A. Subjects, Task, and Recording

Local Field Potentials (LFPs) were recorded and digitized at 200 Hz from 15 bipolar platinum microelectrodes chronically implanted at distributed sites across the lateral convexity of the right hemisphere of an adult male rhesus macaque monkey (contralateral to the dominant hand). The locations of the implanted electrode sites were transcribed to maps of the lateral cortical surface at the time of surgery. Experiments were performed by Dr. Richard Nakamura at the Laboratory of Neuropsychology at the National Institute of Mental Health, and animal care was in accordance with institution guidelines at the time. The monkey was highly trained to perform a visual pattern discrimination task in multiple experimental sessions. On each trial the monkey depressed a hand lever, and kept it pressed during a randominterval (0.12 to 2.2 s) wait period, after which one of four different patterned visual stimuli were presented for 100 ms. Experimental details are available in [14].

B. Multivariate Autoregressive Spectral Analysis

LFPs were subjected to spectral analysis using a Multivariate Autoregressive (MVAR) model that was estimated from the LFP time series in a 110-ms (22 point) analysis window (from 90 ms prior until 20ms after stimulus onset). A model order of 10 (50 ms) was used as a tradeoff between sufficient spectral resolution and overparameterization. The analyzed LFP data from all trials were treated as realizations of a common stochastic process, and used to estimate the model coefficients for that process.

The *p* channels of LFP recordings at time *t* are denoted by $\mathbf{X}_t = (x_{1t}, x_{2t}, \ldots, x_{pt})^T$, where T stands for matrix transposition. The MVAR model of order *m* describes the data as:

$$\sum_{k=0}^{m} A_k X_{t-k} = E_t$$
 (1)

where \mathbf{E}_t is a temporally uncorrelated residual error with covariance matrix $\boldsymbol{\Sigma}$, and \mathbf{A}_k are $p \times p$ coefficient matrices.

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S. L. Bressler is with the Center for Complex Systems and Brain Sciences, Florida Atlantic University, Boca Raton FL 33431 USA. Correspondence to <u>bressler@fau.edu</u>, tel 1-561-297-2322, fax: 1-561-297-3634.

C. G. Richter (<u>richter@ccs.fau.edu</u>) is also with the Center for Complex Systems and Brain Sciences, Florida Atlantic University, Boca Raton FL 33431 USA.

The coefficient matrices were obtained by solving the multivariate Yule–Walker equations (of size mp^2) using the Levinson, Wiggins, and Robinson algorithm [15]. From the coefficient matrices, the transfer function of the system was computed as:

$$H(f) = \left(\sum_{k=0}^{m} A_{k} e^{-2\pi i k f}\right)^{-1}$$
(2)

The spectral matrix was then derived from the transfer function and noise covariance matrix as:

$$S(f) = H(f)\Sigma H^{*}(f)$$
⁽³⁾

where the asterisk denotes matrix transposition and complex conjugation.

Coherence spectral estimates were derived from the spectral matrix for all site pairs, k and l, as:

$$C_{kl}(f) = \left| S_{kl}(f)^2 \right| \left| \left[S_{kk}(f) S_{ll}(f) \right] \right|$$
(4)

where $S_{lk}(f)$ is the cross spectrum of the pair, and $S_{ll}(f)$ and $S_{kk}(f)$ are the individual power spectra.

C. Granger Causality Spectral Analysis

Bivariate autoregressive models were obtained for all site pairs, k and l, according to the procedure above, and Granger causality spectral estimates were computed according to Geweke's [16], [17] formulation as:

$$I_{k \to l}(f) = \frac{\left(\sum_{kk} - \frac{\sum_{lk}^{2}}{\sum_{ll}}\right) \left|H_{lk}(f)\right|^{2}}{\left|S_{ll}(f)\right|}$$
(5)

and

$$I_{l \to k}(f) = \frac{\left(\sum_{ll} - \frac{\sum_{kl}}{\sum_{kk}}\right) \left|H_{kl}(f)\right|^{2}}{\left|S_{kk}(f)\right|}$$
(6)

where Σ_{kk} , Σ_{ll} , Σ_{lk} , and Σ_{kl} are elements of Σ , and S_{kk} and S_{ll} are power spectra of sites *k* and *l*, respectively.

D. Cortical Network Analysis

The focus of our analysis was on peaks in the pairwise spectra produced by spectral coherence and Granger causality analyses. Peaks in the coherence spectra were taken as being indicative of resonant, rhythmic population activity that was phase-synchronized between cortical populations in relation to cognitive function [18]-[21]. Peaks in the Granger causality spectra indicated that this coherent oscillatory activity served to carry causal influences between cortical populations, either unidirectionally or bidirectionally.

III. MAPPING COHERENT CORTICAL NETWORKS

Coherence spectra were derived for all pairwise combinations of the 15 sites from an MVAR model, using the LFP time series in the prestimulus analysis window of 10,178 trials from 18 recording sessions to estimate the model coefficients.

Fig. 1 shows an example of a coherence spectrum from a pair of sites in the visual cortex, one in the Posterior Temporal cortex and the other in the foveal region of the Striate cortex. This spectrum displays a prominent peak in the low beta (13-20 Hz) frequency range. The largest coherence peaks were generally found to be in either the low (13-20 Hz) or high (20-30 Hz) beta frequency range, whereas smaller peaks were also observed in the gamma frequency range (30-50 Hz) in some cases. Coherence was only considered in the range from 9 to 50 Hz, the lower end corresponding to one full cycle of oscillation in the 110-ms analysis window.



Fig. 1. Representative coherence spectrum between Posterior Temporal site 6 and Striate site 1. A prominent peak is observed in the low beta (13-20 Hz) frequency range.

Those site pairs having peaks in their coherence spectra greater than a threshold level of 0.01 were plotted on maps in which coherence values are represented by the thickness of the lines connecting the recording sites (Figs. 2-4).



Fig. 2. Map of site pairs having peaks in the low beta (13-20 Hz) frequency range of their coherence spectra that exceed 0.01 in magnitude. The line thickness corresponds to coherence magnitude. The peak coherence frequency in Hz is indicated by the gray scale.



Fig. 3. Map of site pairs having peaks in the high beta (20-30 Hz) frequency range of their coherence spectra that exceed 0.01 in magnitude. The line thickness corresponds to coherence magnitude. The peak coherence frequency in Hz is indicated by the gray scale.



Fig. 4. Map of site pairs having peaks in the gamma (30-50 Hz) frequency range of their coherence spectra that exceed 0.01 in magnitude. The line thickness corresponds to coherence magnitude. The peak coherence frequency in Hz is indicated by the gray scale.

The map of low beta coherence (Fig. 2) shows the greatest values involving Striate (sites 1-3), Prestriate (sites 4,5), and Posterior Temporal (site 6) areas. Some additional pairs are

seen in Frontal cortex.

The map of high beta coherence (Fig. 3) shows the largest values involving Somatosensory (site 9), Motor (site 8), and Posterior Parietal (sites 10,11) areas. The coherent network in this sensorimotor region has previously been described [12]. What is novel in Fig. 3 is that the Posterior Parietal sites (10,11) are not only involved in the sensorimotor network, but are also coherent with Prestriate site 4 and foveal Striate site 1. This finding suggests that these Posterior Parietal sites are providing some mediating function between the sensorimotor and visual systems. In fact, these sites are in the superior parietal lobule, which is known to have dual somatosensory and visual functionality [22].

The gamma coherence map (Fig. 4) shows mostly longrange coupling between visual cortical areas (Striate sites 1,3 and Prestriate site 4) with Frontal cortical sites, including Motor site 8.

IV. SEGREGATED VISUAL CORTICAL NETWORKS

The posterior cortical portions of the coherent low and high beta networks from Figs. 2 and 3 are illustrated together in Fig. 5 in an expanded format. The spatial pattern of high beta coherences suggests a dorsal oscillatory network coupling lower-level visual cortical sites (Prestriate site 4 and foveal Striate site 1) with higher-level Posterior Parietal sites 10 and 11, as well as Somatosensory site 9. It is most likely that the visual-somatosensory coherences were mediated by the Posterior Parietal sites. This possibility will be tested using partial coherence analysis [23].

The spatial pattern of low beta coherences suggests a ventral oscillatory network coupling lower-level visual cortical sites (Striate sites 1, 2, and 3 and Prestriate sites 4 and 5) with higher-level Posterior Temporal site 6. To a large degree, the dorsal and ventral oscillatory networks (light and dark shaded lines in Fig. 5) are spatially segregated, suggesting that they may relate to the segregated functional properties long known to exist for the dorsal and ventral visual systems [24]-[27]. It is interesting to note that the faster cycle speed represented by the dorsal high beta, as compared to the ventral low beta, oscillations may correspond to the overall faster processing times through the dorsal system [28]-[30].



Fig. 5. Composite map of posterior cortex showing site pairs having peaks in the low or high beta range of their coherence spectra that exceed 0.01 in magnitude. The arrow thickness corresponds to the coherence magnitude. The peak coherence frequency in Hz is indicated by the gray scale.

V. MAPPING GRANGER CAUSAL NETWORKS

Granger causal spectra were also computed bidirectionally for all pairwise combinations of the 15 sites. Fig. 6 shows an example of the bidirectional Granger causal spectra for the same pair of visual cortical sites (Posterior Temporal site 6 and foveal Striate site 1) as in Fig. 1. This figure shows a clear-cut example of the situation where a peak in coherence has a corresponding Granger causal peak in one direction, but not the other. In this case, a low beta top-down Granger causal influence (from Posterior Temporal site 6 to Striate site 1) is above threshold, but the bottom-up influence in the opposite direction is not.



Fig. 6. Representative Granger causal spectra between posterior temporal site 6 and striate site 1. An above-threshold peak is observed in the low beta (13-20 Hz) frequency range in the top-down direction (6 \rightarrow 1), whereas no peak is observed above the 0.01 threshold value in the bottom-up direction (1 \rightarrow 6).

As with coherence, pairs of sites having peaks in their Granger causal spectra greater than 0.01 were plotted on cortical maps (Figs. 7-9). The thickness of the arrows between recording sites represents the strength of Granger causal influence, and the direction of their tapering indicates

the direction of causal influence.



Fig. 7. Map of site pairs having peaks in the low beta (13-20 Hz) frequency range of their Granger causality spectra that exceed 0.01 in magnitude. The arrow thickness corresponds to the Granger causality magnitude, and the direction of tapering of the arrow corresponds to the direction of Granger causal influence. The peak Granger causality frequency in Hz is indicated by the gray scale.



Fig. 8. Map of site pairs having peaks in the high beta (20-30 Hz) range of their Granger causality spectra that exceed 0.01 in magnitude. The arrow thickness corresponds to the Granger causality magnitude, and the direction of tapering of the arrow corresponds to the direction of Granger causal influence. The peak Granger causality frequency in Hz is indicated by the gray scale.



Fig. 9. Map of site pairs having peaks in the gamma (30-50 Hz) range of their Granger causality spectra that exceed 0.01 in magnitude. The arrow thickness corresponds to the Granger causality magnitude, and the direction of tapering of the arrow corresponds to the direction of Granger causal influence. The peak Granger causality frequency in Hz is indicated by the gray scale.

The maps of low beta (Fig. 7), high beta (Fig. 8), and gamma (Fig. 9) Granger causality largely mirrored the corresponding coherence maps in the three frequency ranges. Of the 16 pairs having above-threshold coherence peaks in the low beta range, 8 also had above-threshold Granger causality peaks in either direction; of the 22 coherent pairs in the high beta range, 16 also had Granger causality in either direction; and of the 9 coherent pairs in the gamma range, 5 also had Granger causality in either direction. It was relatively rare for a pair to have an above-threshold Granger causality peak without also having above-threshold coherence peak (1 pair in the low beta range, 3 in high beta, and 4 in gamma).

Granger causality in the beta range was predominantly unidirectional: of the 9 above-threshold Granger causality peak values in the low beta map, 7 were unidirectional and only 2 were bidirectional; and of the 19 in the high beta map, 16 were unidirectional and only 3 were bidirectional. However, of the 9 above-threshold Granger causality peak values in the gamma map, 4 were unidirectional and 5 were bidirectional.

VI. TOP-DOWN INFLUENCES IN VISUAL CORTEX

The posterior cortical portions of the low and high beta Granger causal networks from Figs. 7 and 8 are illustrated together in Fig. 10 in an expanded format. The spatial pattern and directionality of high beta Granger causal influences suggests a dorsal network exerting top-down influences from higher-level Posterior Parietal sites 10 and 11 (and Somatosensory site 9) to lower-level visual cortical sites (Prestriate site 4 and foveal Striate site 1). It is possible that the top-down Granger causal influence from somatosensory cortex may have been mediated by the Posterior Parietal sites. This possibility will be tested using conditional Granger causality analysis [31].



Fig. 10. Composite map of posterior cortex showing site pairs having peaks in the low or high beta range of their Granger causal spectra that exceed 0.01 in magnitude. The arrow thickness corresponds to the Granger causality magnitude, and the direction of tapering of the arrow corresponds to the direction of Granger causal influence. The peak Granger causality frequency in Hz is indicated by the gray scale.

To investigate the functional role of top-down Granger causal influences in the visual cortex in relation to visual expectation, we are currently testing the hypothesis that topdown Granger causal influences represent top-down modulatory influences from higher levels of the visual hierarchy onto lower levels. It has been proposed that such top-down modulatory influences could serve to control the throughput gain of neuronal assemblies in the lower-level areas [32]-[34]. We hypothesized that top-down modulatory gain control would produce greater or lesser efficacy in the response of visual cortical neurons to an expected visual stimulus, and that this efficacy would be observable in the early portion of the Visual Evoked Potential (VEP). We further postulated that, if top-down modulatory effects are detectable using Granger causality, then the magnitude of the VEP would correspond to the magnitude of the top-down Granger causality value.

To test these ideas, we first use a template matching procedure ([35], [36)] to estimate the early VEP amplitude at different low-level visual cortical sites, individually for each of the 10,178 trials. We then rank order the ensemble of trials according to VEP amplitude, and collect the sorted trials into 300-trial groups, starting with the smallest amplitudes and proceeding to the largest, each group sharing 150 trials with the previous one. Granger causality analysis is then performed on the LFPs from the ensemble of trials in each group during the prestimulus analysis window. Finally, we compute the correlation coefficient for the relation between group prestimulus Granger causality and group VEP amplitude. Overall, the procedure is very similar to that described in [11].

Two examples of results are shown in Figs. 11 and 12. In Fig. 11, the relation between the prestimulus top-down Granger causality from Posterior Temporal site 6 to foveal Striate site 1 and the VEP amplitude at Striate site 1 is shown. The significant positive correlation in this figure

indicates that the level of top-down prestimulus Granger causal influence from the Posterior Temporal site to the Striate site was highly predictive of the subsequent VEP amplitude at the latter location. This finding serves as preliminary confirmation of our hypothesis that top-down Granger causal influences represent a modulatory gain control mechanism in visual cortex. In this case, it appears that the effect of the top-down causal influence was to increase the throughput gain at Striate site 1.



Fig. 11. Scatter plot showing the relation between trial group average Visual Evoked Potential (VEP) amplitude and group peak Granger causality magnitude. The relation is shown for the topdown Granger causality magnitude from Posterior Temporal site 6 to Striate site 1, for which the Granger causality peak was in the low beta frequency range.

In Fig. 12, the relation between the prestimulus top-down Granger causality from Posterior Parietal site 11 to foveal Striate site 1 and the VEP amplitude at Striate site 1 is shown. The significant negative correlation in this figure is in stark contrast to the significant positive correlation in Fig. 11. The negative correlation also indicates that the level of top-down prestimulus Granger causal influence from the Posterior Temporal site to the Striate site was highly predictive of the subsequent VEP amplitude at the latter location. However, high levels of top-down Granger causal influence were predictive of *low* rather than high VEP amplitudes. Therefore, this finding may also provide confirmation of our hypothesis, but with the effect of the top-down influence being to *decrease* the throughput gain at Striate site 1, rather than increase it.



Fig. 12. Scatter plot showing the relation between trial group average Visual Evoked Potential (VEP) amplitude and group peak Granger causality magnitude. The relation is shown for the topdown Granger causality magnitude from Posterior Parietal site 11 to Striate site 1, for which the Granger causality peak was in the high beta frequency range.

VII. CONCLUSIONS

This study extends the findings presented in [12], where a coherent beta-frequency network of phase-synchronized neuronal assemblies was reported to carry Granger causal influences in a highly structured manner within the sensorimotor cortex of the macaque monkey.

The preliminary results presented here are consistent with the idea that top-down Granger causal influences reflect actual top-down modulatory effects, exerted in coherent oscillatory visual cortical networks, that may operate to modulate the throughput gain in lower-level cortical neuronal assemblies. It appears that high-level assemblies in both the dorsal and ventral visual systems may exert such top-down modulatory effects, the first in the high beta frequency range, and the second in the low beta range.

The difference observed in the sign of correlation of the top-down influences with striate VEP amplitude between the ventral and dorsal visual systems may have functional significance. First, the Posterior Temporal cortex is known to be involved in visual pattern recognition. Hence, it would appear reasonable that its top-down effect on the foveal Striate site should be facilitatory, because such an effect might enhance the fidelity of the subsequent poststimulus bottom-up input received by the Posterior Temporal cortex. Contrarily, the Posterior Parietal cortex has been found to exert a strong causal influence on the Motor cortex as part of the sensorimotor system's maintenance of the lever press by the hand [12]. It may be that this area exerts an attenuative effect on the foveal Striate site in order to reduce the fidelity of visual input, and thereby prevent interference with its sensorimotor function.

Although preliminary, these results suggest that Granger causality analysis of cortical LFPs may provide a means for measuring top-down modulatory influences in visual cortex. Such influences have long been postulated to serve a variety of important computational functions, but have previously proved to be very difficult to quantify.

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