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Predicting Perceptual Suppression from Local Field Potential in Visual Cortex

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Abstract— **Generalized flash suppression (GFS, Wilke et al. 2003) in which a salient visual stimulus can be rendered invisible despite continuous retinal input has provided a powerful means to study neural processes directly related to perception. However, the mechanisms underlying such perceptual suppression remain poorly understood. Here we asked how reliably the population responses could determine the perceptual states and what the roles of different areas in visual cortex played during suppression. Three monkeys were trained to perform the GFS task. Multi-channel neural activities in visual cortical areas V1, V2 and V4 were simultaneously recorded. Linear regression analysis on the time-frequency distributions of local field potential (LFP) recordings between two perceptual states (visible *vs.* invisible) showed that the significant power difference existed between the two perceptual states at the beta frequency band of 10-30 Hz. Linear discriminant analysis (LDA) classifiers were implemented to decipher perceptual states. Our results showed that LFP recordings provided significantly better prediction than the chance level, and the beta band signal provided better prediction than the broad band in all the three visual cortical areas. Broad band signal provided more accurate prediction in V4 than in V2 and V1, while the beta band signal provided consistently good predictions in V1, V2 and V4. Furthermore, multi-channel recordings were more informative than single electrode recordings in V1, V2 and V4, while in V1 and V4 the benefit of decoding population activity was significant. Channel-wise correlations limited the benefits of population activity. These results indicated that considerable information was retained in the beta band of the local field potential. The benefits of population activity were explored and the different roles of different visual cortical areas during perceptual suppression were investigated.**

I. INTRODUCTION

While salient stimuli are physically presented for the duration of the experimental trial, they may be rendered subjectively invisible. Such perceptual suppression illustrates that our conscious perception is not simply a faithful representation of the external world, but is also affected by internal neural processes in the brain. Previous research suggests that stimulus conditions that disturb early feature representations may bring about visual invisibility (Macknik et al., 1998), and deficits in visual attention can induce invisibility too (Mack and Rock, 1998). Visual illusions provide a helpful means to dissociate the external world representation and internal brain processes, and thus, have been studied to investigate the neural underpinnings of perception. However, the essential questions, such as how perceptual suppression arises from neural activities in different areas of visual cortex, still remain a matter of debate.

To address these questions, we first need to identify how the physical variables are encoded on which a perceptual decision is based. Many studies have been done to investigate whether it is possible to decode perceptual states and how reliably the perceptual state can be inferred (Haynes et al., 2005a, 2005b, Mehring et al., 2003, Hung et al., 2005). LFP low frequency analysis showed perception-related modulations in primary visual cortex V1 (Gail et al., 2004), while recordings from V1, V2 and V4 showed correlations with perception suppression, particularly in V4 (Leopold et al., 1996). Further study needs to be undertaken to clarify this discrepancy.

In the present study, we examined neural recordings from behaving monkeys performing a GFS task (Wilke et al., 2003), in which a salient monocular stimulus could be rendered subjectively invisible after a sudden presentation of random-moving dots appearing as a surrounding pattern. We explored the predictability of local field potential, investigated how well population activity could determine perceptual states, and investigated the roles of specific visual cortical areas, V1, V2 and V4 during subjective suppression.

II. MATERIALS AND METHODS

A. Materials

We will describe the GFS experiment briefly since detailed description was given previously (Wilke et al., 2003, 2006). The GFS experimental paradigm of this study is outlined in Fig. 1. Briefly, after the stimulus indicated by a red disk was presented, small random-moving dots appeared as the surroundings. With the immediate appearance of the surroundings, the red disk can be rendered invisible. If the stimulus disappeared from perception, the monkey was trained to release a lever; otherwise, monkey was to hold the lever. Since here the stimulus to the corresponding two perceptual states 'visible' and 'invisible' is physically identical, the visibility is dissociated from the external world. The neural recordings were sorted according to monkey response and the corresponding perceptual state was labeled to indicate visibility. Large fractions of unambiguous catch trials were interleaved to ensure the accuracy of the monkey responses.

Three adult Macaca mulatta monkeys participated in the experiment. While monkeys performed the task, neural activities were recorded by multiple microelectrodes which

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were inserted into V1, V2 and V4 through the dura mater. Detailed information about the surgery and training was described (Wilke et al., 2006). Stimuli were displayed on two 21-inch monitors through a mirror stereoscope. A small yellow spot (0.15˚) in the middle of screen served as a fixation spot and remained visible during trials. Stimulus size ranged between 0.6˚ to 3.2˚. Neural activities were recorded and local field potential was obtained after amplification and filtering between 1 and 500 Hz (Wilke et al., 2003).

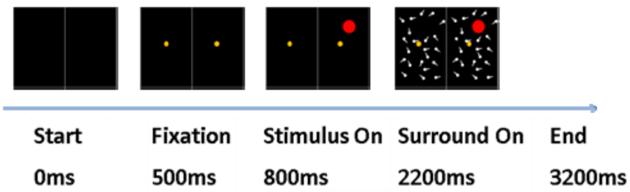

Figure 1. Experimental paradigm of GFS. Monocularly presented stimulus and dioptic surround condition.

B. Methods

Time-frequency analysis: Short-time Fourier transform (STFT) has been used to obtain the time-frequency distribution of a signal by representing the time resolution of the frequency spectrum. It is assumed that the signal is stationary within a short window in which the Fourier transform is performed. By sliding the window along time course, the signal can be represented in both time and frequency domain. We used a 32-point Hanning window that moved every 2 points along time-varying signal after LFP was down-sampled to 200 Hz. For a given channel, STFT was performed on individual trials, and then averaged across trials to obtain the time-frequency distribution. As a result, a set of time-frequency distributions were obtained over all of the channels. The procedure was separately done for each of the two perceptual states.

Regression analysis: Linear regression is used for prediction by modeling and analysis of numerical data consisting of a dependent variable (also called response variable) and independent variables (also called predictors). The R^2 value indicates the prediction ability of the model. The dependent variable y in regression equation 1 is modeled as a function of the independent variables X and error term ε

$$y = X\beta + \varepsilon \quad (1)$$

The parameters β and ε are to be determined by the least squares best fit of response variable y on the observed data, X. The method of least squares is a technique of fitting data and the best fit is reached when the sum of squared residuals has its least value.

R^2 is a measure of the global fit of the model. Specifically, R^2 is one minus the ratio of the error sum of squares to the total sum of squares and the range is from 0 to 1. A R^2 value close to 1 implies that the regression model provides perfect predictions while 0 indicates no linear relationship between the response and predictors.

To apply linear regression, the predictors X were from the time-frequency distributions of multi-channel recordings, and y was to be set up by the labels of the corresponding true perceptual states '*visible*' or '*invisible*', indicated by monkey behavioral responses. A linear regression model was then set up where R^2 and p values for the model could be obtained to evaluate the prediction ability. Then, based on the time-frequency distribution of R^2 or p values, the frequency band and time period associated with perceptual suppression was determined, which provided information for the following decoding analysis.

Decoding: Two perceptual states, 'visible' and 'invisible', are analyzed, while the stimuli are identical. The predictive value of the neural signal is assessed by comparing the predicted perceptual states, which is inferred from neural activities, with the perceptual states labels indicated by monkey responses.

We used the Fisher linear discriminant analysis (Duba et al., 2000) to decode perceptual states due to its excellent performance, as well as its high efficiency. Since the stimuli are identical, the perceptual discrimination is separated from external world, and the classifier is applied upon neural activities to decipher perceptual states.

Linear discriminant analysis requires the projection of data from n dimensions onto a line. Among the n-dimension samples X, n_1 is in the subset D_1, and n_2 in the subset D_2. Two subsets are obtained, since there are two perceptual states. We separate different patterns by finding the orientation in which the projected samples are well separated. This is done by maximizing the difference between the subset mean m_i to be large relative to some measure of standard deviations as Eq .2 indicates:

$$w = S_w^{-1}(m_1 - m_2) \quad (2)$$

Where

$$S_w = S_1 + S_2 \quad (3)$$

$$S_i = \sum_{x \in Di} (x - m_i)(x - m_i)^T \quad (4)$$

T denotes transposition. Thus, we obtained $\boldsymbol{w}$ for Fisher's linear discinimant. The optimal decision boundary is given by the equation as below:

$$w^T x + w_0 = 0 \quad (5)$$

Since in the present study, psychophysical testing determined approximately a 50% disappearance probability, the constant w_0 is defined as:

$$w_0 = -0.5 * (w^T m_1 + w^T m_2) \quad (6)$$

To avoid over-fitting, leave-one-out cross-validation will be applied. Data is divided into two subsets: one subset is used to train a LDA classifier and the other for testing the classifier. The testing subset contains one trial and the training subset contains the remaining trials. Classifiers are trained on the training subset and the obtained optimal decision criteria will be implemented on the test subset. The prediction result will then be obtained for this test subset. This procedure will be repeated so that all the trials are tested and classified based on models learned from the other trials. The prediction results for all the trials can be taken together to give an averaged prediction result.

Permutation approach: To test the influence of correlations among simultaneous recordings, we eliminate the correlations by a permutation approach. Considering two channels of recordings with many trials, randomly pairing data for channel 1 with data for channel 2 from a different trial leads to the channel-wise correlations to be removed.

III. RESULTS

Three monkeys were trained to perform the generalized flash suppression task (Fig. 1). During each session, neural activities of the monkeys were simultaneously recorded by multi-electrodes from V1, V2 and V4, using typically 4 to 7 electrodes. The signal recorded from each electrode was processed to yield LFP recordings.

A. Time-frequency distribution

Since neural activities are variable in time and LFP signal covers a broad frequency range, our first step is to identify the time period of suppression and the relevant frequency bands which are directly associated with suppression. STFT was used to provide information about how the spectral content of the signal evolved with time, which explored a combined time-frequency representation of the signal. The distributions corresponding to the two perceptual states were obtained separately. Linear regression was applied to set up a linear model to investigate the difference between time-frequency distributions of the two states from all of the channels. The R^2 values for the model in the three visual cortical areas V1, V2 and V4 were shown with the same scale in Fig. 2 (Left). From Fig. 2, the main difference between the two perceptual states appeared in the beta frequency band of 10-30 Hz between 500 ms and 800 ms time period after surround onset. The beta band signal stood out consistently in all the three visual cortical areas V1, V2 and V4, especially in V4. High frequency band (>40Hz) conveyed some information about perceptual states too, especially in V1 and V2, although not so significant as the beta band. The power within the beta band signal of the two perceptual states was extracted and the time course of the ensemble activity of the two conditions was shown in Fig. 2 (right). The divergence between the two conditions 'visible' and 'invisible' after surrounding onset were visually quite obvious in V1, V2 and V4, particular in V4.

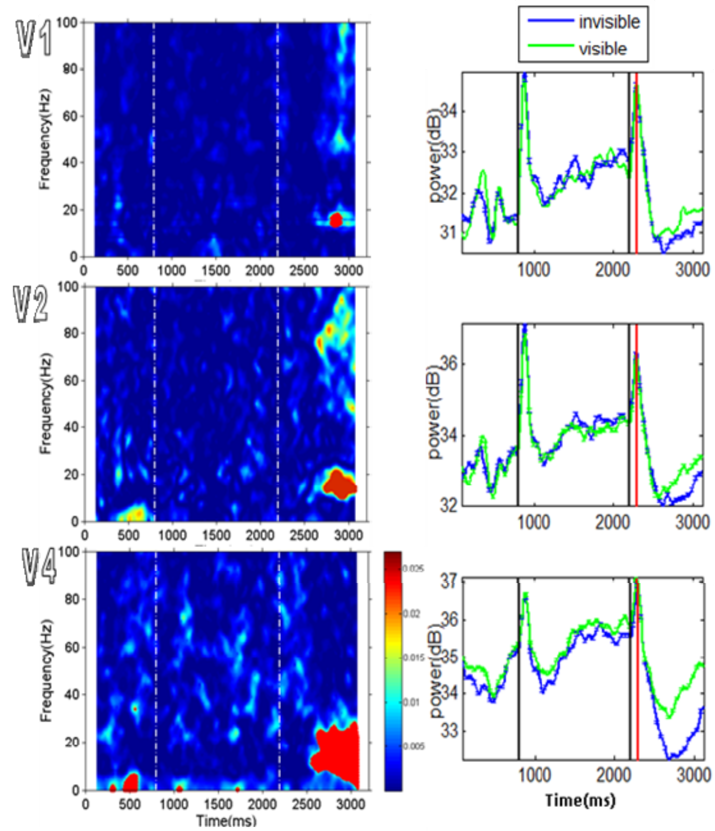

Figure 2. Right: R^2 distribution for V1, V2 and V4 in the same scale. White dash dot lines indicate stimulus onset (800 ms) and surround onset (2200 ms). Significance ($p < 0.05$) was shaded in red. Left: Ensemble activity of beta band for 'visible' (green) and 'invisible' (blue) for V1, V2 and V4. Two vertical black lines indicate stimulus onset and surrounding onset. The red lines indicate the peak after surrounding onset.

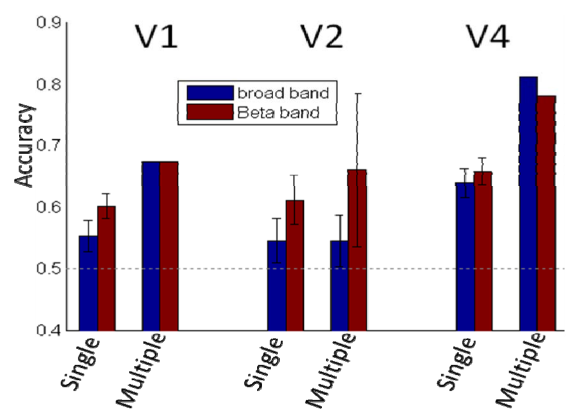

Figure 3. Prediction accuracy of broad band *vs.* beta band from single electrode recordings and multi-electrode recordings in V1, V2 and V4. Gray line indicates chance level 0.5.

B. Decoding

As shown in Fig. 2, the time-frequency distribution of R^2 values indicated a time period and frequency band related to perceptual suppression. Thus, features in the time window, 500 ms to 800 ms after surround onset and the frequency beta band were extracted to decipher perceptual states.

LFP broad band signal and beta band signal allowed for the possibility of predicting suppression significantly greater than chance level (*0.5*) for all the three visual cortical areas V1, V2 and V4 (Fig. 3) ($p<0.05$). LFP beta band signal yielded better prediction in V1, V2 and V4, while in V1 the different performance from broad band signal was significant. The results revealed that LFP recordings contained information associated with perceptual suppression, and the beta band signal was more informative, especially in V1. Furthermore, more accurate prediction was observed in V4 than in V2 and V1 for broad band signal ($p<0.05$), indicating that V4 was more involved in suppression.

On the basis of simultaneous multi-channel LFP recordings, it can be said that neural activities from multiple channels yielded more accurate prediction in V1, V2 and V4, while in V1 and V4, the improvement was significant (*p<0.05*). LFP multi-channel analysis allowed for >80% accuracy in prediction of suppression in V4.

C. Correlation effect

Correlation among multiple channels of simultaneously recorded LFP can be relatively high. To test the influence of correlations, we compared prediction accuracy of simultaneously recorded LFP beta band to that obtained by a permutation approach, which shuffled trial order (correlation absent). The effect of correlations was shown in Fig. 4 where the two curves diverged as the number of channels increased. The results suggested that channel-wise correlations limited the benefits of averaging across populations, thus decreased the accuracy of perceptual discrimination.

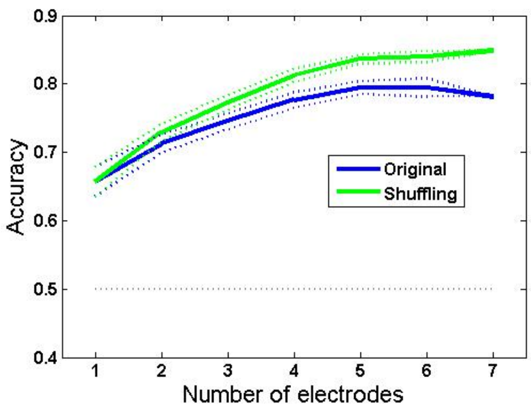

Figure 4. Prediction accuracy of simultaneously recorded (blue) and shuffled (green) beta band signal in the function of number of electrodes in V4. Error bar: standard error.

IV. Discussion

The aim of this study is to investigate how accurate perceptual states can be inferred from neural activities. Low-to-medium frequency LFP data showed perception-related modulations in V1 (Gail et al., 2004), while in V4 it showed strong modulations in the firing rate during perceptual suppression (Leopold et al., 1996). Furthermore, consistent and sustained modulation of V1, V2 and V4 occurred at lower frequency bands (Wilke et al., 2006). In the present study, we demonstrated that the beta band signal was more related to perceptual suppression. LFP broad band signal in V4 provided more accurate prediction than in V2 and V1, while the beta band provides comparably good prediction in V1, V2 and V4. Broad band prediction results indicated that V4 may be more involved in perceptual suppression, while beta band signal conveyed sufficient information related to perceptual suppression even in early visual cortical areas. Additionally, high frequency band signal also carried information related to perceptual suppression, especially in V1 and V2. LFP recordings, whether broad band, beta band or gamma band, all provided a more accurate prediction than the chance level. This indicated that LFP recordings carried some information associated with perceptual suppression. Meanwhile, different prediction performance was observed with different bands signal in the cortex. The different prediction performance between broad band and beta band signal among V1, V2 and V4 shed light on the debate whether different visual cortical areas were involved in vision.

Furthermore, the multi-channel recordings can be used to predict perceptual states with higher accuracy than single electrode recordings. The improvement observed in multi-channel recordings indicated that neural activities from different electrodes may carry complementary information about perceptual states and a number of neurons may jointly contribute to the perceptual decision. Here significantly better prediction was observed in V1 and V4. In V2, fewer electrodes were implanted and this may explain that benefit from population activity in V2 is not as obvious as that gained in V1 and V4. The effect of channel-wise correlations was examined with simultaneous multi-electrode recordings and the results revealed that the channel-wise correlations limited the benefit of population activity and thus decreased prediction performance. The results suggested that the commonly used surrogate for the true information in the population (Hung et al., 2005) should be revised upon recording simultaneously from many neurons. Further studies are necessary to explore the population coding.

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