

Decoding Visual Stimuli from Neural Responses

Niru Maheswaranathan, Benjamin Naecker, Hannah Payne

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Abstract

A central question in neuroscience is how populations of neurons encode information about the external world and how that information is transformed to drive behavior. Here we apply machine learning approaches to shed light on these questions. Using data recorded from two brain areas (V4, a visual processing area, and the frontal eye field, which controls saccadic eye movements) in an awake behaving macaque monkey, we trained learning algorithms to decode information about a visual stimulus or the location of a planned eye movement. The algorithms were quite successful, indicating that both sensory information and motor plans may be read out effectively from multi-electrode recordings. Furthermore, by performing feature selection, we are able to investigate which channels encoded the most information about the stimulus.

Background

Early studies of information processing in the brain characterized the response of individual neurons to sensory inputs. Advances in both recording and computing technologies now allow for examination of how populations of neurons encode such information. Machine learning algorithms ranging from support vector machines to Gaussian process factor analysis have been applied effectively to the analysis of neural data [2, 3, 6]. An important practical application of such algorithms is in the deployment of brain machine interfaces (BMI), in which neural signals are decoded to drive electronic devices and artificial limbs. While early BMI efforts required that the human brain learn what mental states drove certain actions, modern BMI decodes the normal activity of the brain. Other applications of machine learning to neuroscience include analysis of functional brain imaging data, such as for lie detection [1] or for decoding a visual scene [4]. In addition, neuroscientists can also apply machine learning to determine which features of neural activity carry the most information about a stimulus or behavior, in order to gain insight into how the brain efficiently encodes information.

Our data was recorded from visual cortical areas of an awake behaving macaque monkey. We focused on visual areas because the areas are generally well-understood, and because stimuli are well-defined which provides for relatively easy incorporation into machine learning methods. Visual processing begins in the retina, where precise patterns of output signals ("spikes") encode relatively simple visual features, such as luminance and contrast. This information is then transferred to the visual cortex, where it radiates out to many areas responsible for processing specific types of visual information. Area V4 is one such area, known to be selective for simple features, such as orientation and basic shape, and modulated by top-down attentional control [5]. In addition to recordings from area V4, we also analyzed data from an area of the frontal cortex known as the frontal eye field (FEF), an area involved in both attentional control and the planning of precise, rapid eye movements known as saccades [7]. Figure 1a

shows where these areas are in the brain. Our data is courtesy of Nick Steinmetz, from the Tirin Moore lab here at Stanford.

The activity in V4 and FEF was recorded with a linear array electrode, which is able to record from 16 channels simultaneously in an awake behaving monkey. For data recorded from V4, the monkey maintained fixation at the center of a computer screen, on which an oriented grating appeared in the region of space for which that particular part of V4 was most sensitive (Figure 1b). During recordings from FEF, the monkey maintained central fixation ("Target On") while a target in one of six trained locations appeared for a short time, and then disappeared ("Target Off"). The monkey then maintained fixation until they were given a signal to act ("Go-Cue"), at which time the monkey made a controlled eye movement ("Saccade") to the previous location of the target (Figure 1c). Example recordings for the V4 and FEF data are shown in Figure 1d and 1e, respectively. These show the firing rates recorded from two randomly selected channels as a function of time. Note the subtle differences between the two channels, which makes it difficult to analyze such data.

We trained a series of algorithms to predict from the spiking neural data either the orientation of the grating (for data from V4) or the endpoint of the saccade trajectory (for data from FEF). We also performed a series of model analyses to explore the robustness of our trained algorithms. Our results indicate that support vector machines consistently outperform other algorithms. In addition, we found that despite having 16 separate channels of recordings, a small number of them usually proved far more informative than the remainder. A final interesting result is that on trials for which our algorithms incorrectly predicted the endpoint of the saccade, the animal's reaction time was significantly longer than on trials that the algorithm correctly predicted, suggesting that the neural activity on these trials was more noisy or somehow sub-optimal than on correct trials.

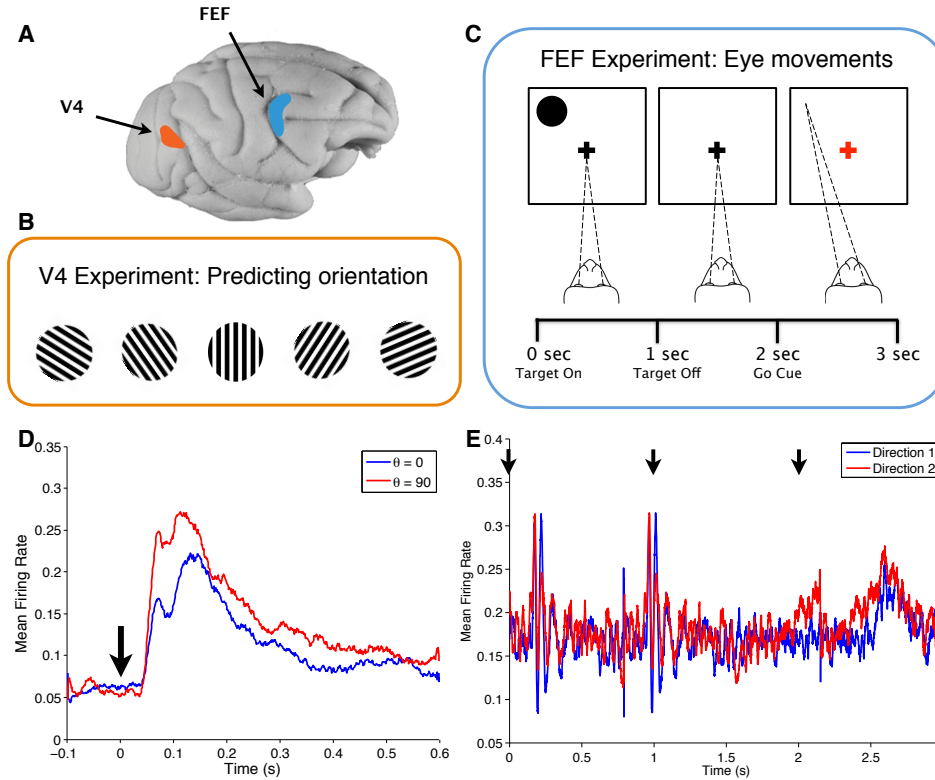


Figure 1: Experimental setup - see text for description.

V4 Experiment

First, we looked at neural recordings from visual area V4. We pre-processed the data by computing the average firing rate of the neurons recorded from a given channel over the 0.5 s stimulus presentation. This left us with a data set of 16 features (corresponding to each channel) and around 1400 examples. We randomly chose ten percent of these to be testing examples, and used the rest as training examples. We first trained three different machine learning algorithms to predict what orientation stimulus was shown to the monkey based on of the activity in V4. For our support vector machine (SVM) implementation, we used a radial basis function (RBF) gaussian kernel with parameters chosen via grid search and cross-validation. The results of the grid search are shown in Figure 2b. Figure 2a shows comparison of the accuracy of these algorithms across three separate days of recording. We see that the generalized linear model (GLM) performs poorly, while multinomial logistic regression (MLR) and the SVM perform reasonably well. Since there are eight possible stimulus orientations, chance accuracy corresponds to 12.5%. The large change in accuracy over different days suggests that the electrode placement has a significant impact on learning algorithm performance. The electrode is removed and re-inserted into the monkey's brain each

day. Thus, poor electrode placement is the most likely reason for the varying accuracy.

Figure 2d shows that as we vary the number of training examples, the learning algorithm (MLR) performance increases and saturates around 80%. Here, 138 examples of data were randomly selected for testing, and the number of selected training examples was varied. This indicates that having more training data would not drastically improve performance. We also performed feature selection to determine which channels were most important for the learning algorithm. Figure 2c shows these results. All pairwise combinations of two channels (for the third day of recording, since it performed the best as shown in Fig. 2a) were removed from the data set and the accuracy of a MLR model was computed. Color indicates the accuracy with the given channels removed. We see that channels 13 and 14 have the largest impact on performance, reducing accuracy by around 10% individually and around 20% when both are removed. The linear array electrode used for recording is inserted depth-wise, perpendicular to cortex. Therefore, channels 13 and 14 are most likely picking up signals from the deeper layers of cortex (layers 4-5). It would be interesting to test exactly why these channels are the most useful, and if this is a robust phenomenon.

Up to this point, all of our analyses focused on using

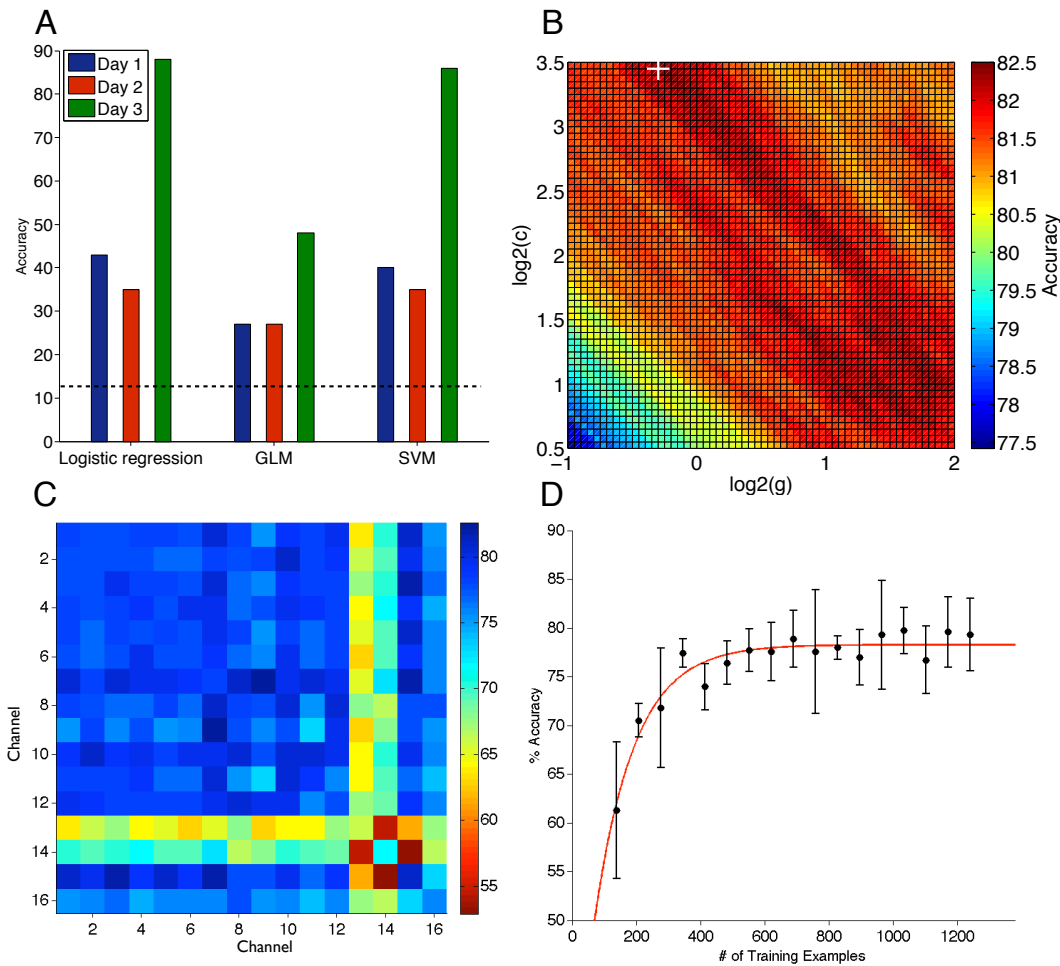


Figure 2: (a) Accuracy of each model. (b) Feature selection. Red line indicates accuracy with all features included. (c) Parameter search for radial basis function SVM. (d) Accuracy vs. # of training examples.

features generated by averaging over the entire stimulus presentation (0.5 s). We wondered if by splitting the half a second period into distinct bins, each of which is an independent feature, we could improve the algorithms' performance. However, such an analysis is subject to overfitting. Figure 3a and 3b show the training (dashed lines) and generalization (solid lines) error as the number of bins was increased (again with 10% of the data randomly selected for testing) for MLR and SVM algorithms, respectively. We see that the training accuracy quickly rises

to 100%, while the generalization error drops off rather quickly. This means that we are overfitting the training data when splitting the recordings into discrete time bins, which suggests that there is not much additional information contained by the temporal structure of the firing rates. However, for the SVM (Figure 3b), it appears that splitting the data into a few bins (<10) may help performance, although it is difficult to say for sure given our error bounds.

FEF Experiment

We next examined neural data from the frontal eye field (FEF) in macaque monkeys. We examined neural firing rates aligned with the four phases: Target On, Target Off, Go Cue, and Saccade (Figure 1c). The total experiment

lasted three seconds, therefore there was some overlap between Go Cue and Saccade-aligned periods.

We applied several machine learning algorithms to decode the desired target location from neural data. Features were the average firing rate during each of these four periods across all 16 electrodes. Using these fea-

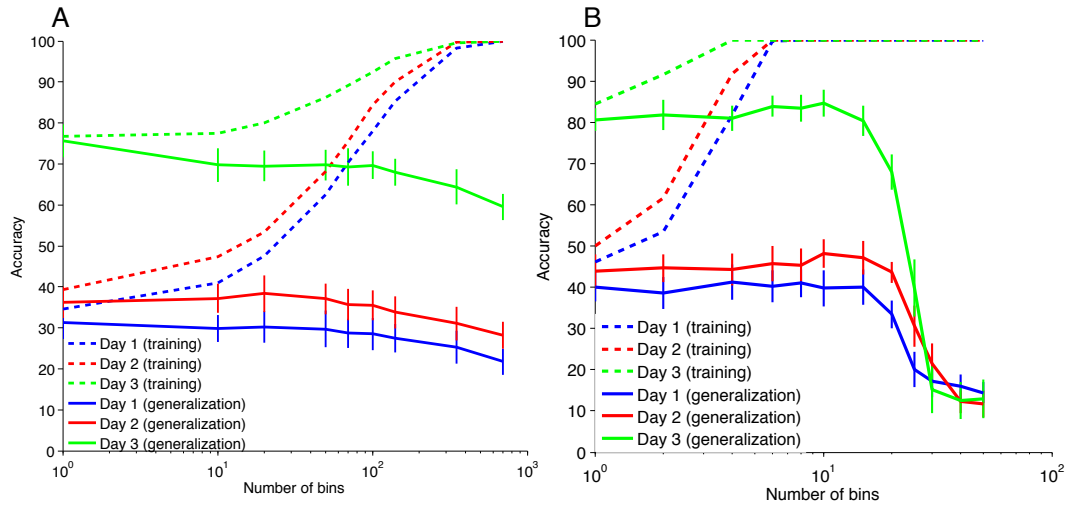


Figure 3: Generalization/training error vs. bin size for MLR (a) and SVM (b)

tures, the best accuracy was 74% using a support vector machine with a Gaussian radial basis function (Figure 4a). Since there are six possible targets, chance accuracy would be 16.7%. SVM performed far better than both logistic regression (47% accuracy) and a generalized linear model (56 % accuracy). To optimize the SVM, a parameter search was used to find the best kernel width (g) and slack parameter (c) (Figure 4c).

Interestingly, the monkey's reaction times were slower on trials that were incorrectly classified by the learning algorithm (Figure 5c). This difference was significant for both SVM ($p = .014$, one-tailed t-test) and logistic regression ($p = .0049$). The fact that slow trials were harder to classify could indicate that the neural trajectories on these trials were less reliable than those with fast reaction times - if the monkey was not as confident in making the saccade, this could be reflected in the neural response.

To investigate which phases of the experiment contained the most information about the target location, we excluded each of the four phases in turn from the analysis. Not surprisingly, removing Target On impaired performance the most, reducing accuracy from 76% to 66%. Removing Saccade-aligned information had the next highest impact, followed by Go Cue and Target Off. Interestingly, even though excluding Target Off data had very little impact in the algorithms performance, the monkey clearly still remembered the target location during this period, indicating that the memory was likely stored elsewhere than FEF, and that FEF may play a larger role in detecting the location of a new target, and later in initiating a saccade to the desired location.

With further improvement in recording and feature

selection, SVM should be a robust technique for decoding neural data, with applications in the field of neural prosthetics, for example to decode desired movement trajectories. Although machine learning algorithms do not directly probe biological mechanisms, they can reveal interesting features, such as increasing reaction time with variation in neural activity, which would not otherwise be apparent.

Conclusions

We have showed that it is possible to decode visual stimuli using multi-unit recordings from macaque cortex. Using feature selection, our algorithm gives evidence that information about a visual orientation is best encoded in deep cortical layers, and that information about present and future saccadic eye movements is encoded in the frontal eye field (FEF). Furthermore, for the V4 experiment, given the amount of data we had available, it appears as if training algorithms on the temporal structure of firing rates after stimulus does not improve performance. Finally, for the FEF experiment, we observe that the monkey's reaction time is correlated with our machine learning algorithm performance, suggesting that the motor regions responsible for coordinating saccadic eye movements depend on robust encoding in FEF.

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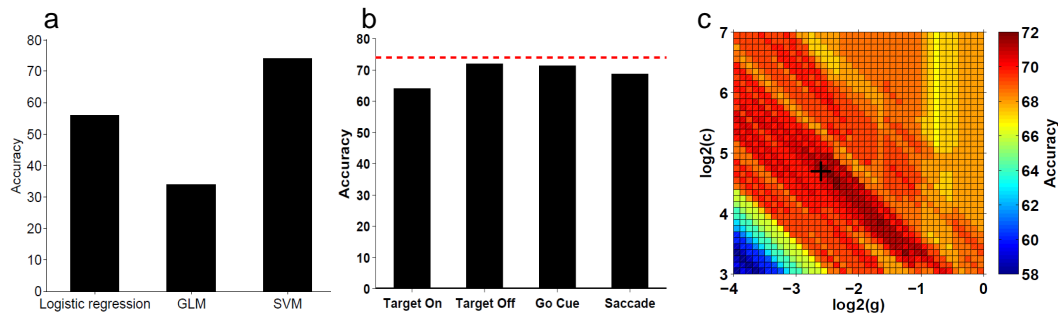


Figure 4: FEF results. (a) Accuracy of each model. (b) Feature selection. Red line indicates accuracy with all features included. (c) Parameter search for radial basis function SVM.

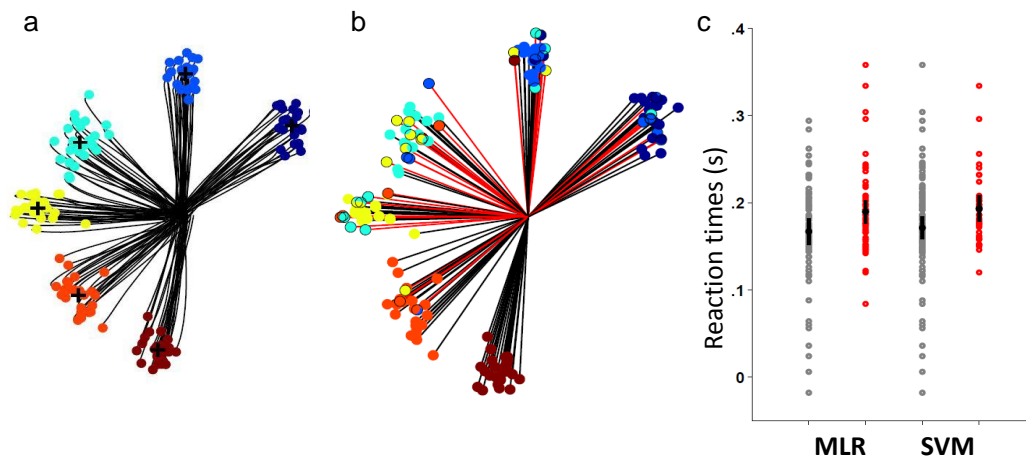


Figure 5: FEF results. (a) Actual saccade trajectories. (b) Target classifications predicted from neural data. (c) Reaction times slower on trials incorrectly classified by SVM.

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