# Endogenous pre-stimulus activity modulates category tuning in ventral temporal cortex and influences perceptual behavior

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## Abstract

**Perception of sensory inputs is modulated by shifts in endogenous ongoing brain activity. Specifically, previous studies have tied endogenous pre-stimulus neural activity to behavior in sensory tasks. However, it remains unclear whether the endogenous activity modulates neural coding and category tuning in visual processing, and if this modulation of tuning provides a neural pathway for behavioral modulation. To address these questions, we collected intracranial electroencephalography (iEEG) data from category-sensitive areas in ventral temporal cortex (VTC) in 32 patients. A statistical model was designed to decode the category of the stimulus and quantify the influence of pre-stimulus activity on post-stimulus category tuning in single trials. The results showed that conditioning on pre-stimulus activity improved the classification accuracy, indicating that category-selectivity was modulated by pre-stimulus activity in VTC. Furthermore, the aspect of the pre-stimulus activity that modulated category tuning correlated with reaction time in a 1-back task. The spatial and temporal specificity of this pre-stimulus modulation showed characteristics that distinguish it from global fluctuations in cognitive state or slow fluctuations in resting-state. Taken together, these results demonstrate that endogenous activity modulates category tuning. This modulation provides a potential neural basis for perceptual variation arising from shifts in endogenous ongoing activity.**

**Keywords:** intracranial electroencephalography (iEEG); visual perception; neural coding; endogenous activity; ventral temporal cortex (VTC); classification

## Background

The neural responses to stimuli can be extremely variable. Part of the trial-by-trial variance in neural response can be attributed to the ongoing endogenous activity (Arieli, Sterkin, Grinvald, & Aertsen, 1996). Previous studies has linked the endogenous activity to global cognitive states, such as attention or arousal, as well as infra-slow resting-state fluctuations (Fox, Snyder, Zacks, & Raichle, 2006; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). There have been a number of studies showing the correlation between endogenous activity and post-stimulus neural response. It has been shown that the amplitude, variance, and patterns in the post-stimulus neural response are shaped by the endogenous ongoing activity (Arieli et al., 1996; Kisley & Gerstein, 1999; Başar, 1980; Henriksson, Khaligh-Razavi, Kay, & Kriegeskorte, 2015). It has also been shown that endogenous activity can also explain the variance in behavior across a number of perceptual domains including vision and audition (Busch, Dubois, & VanRullen, 2009; Ress, Backus, & Heeger, 2000; Kayser, McNair, & Kayser, 2016). Taken together, these results suggest a possible link between the endogenous activity and sensory perception of stimuli, in that the spontaneous activity can potentiate category recognition via modulating the post-stimulus activity. However, it is unknown if the endogenous activity modulates the neural differentiation between conditions to influence perception. In other words, it remains unknown if there is an interaction between endogenous pre-stimulus activity and neural tuning.

In this study, we used direct iEEG recording from category selective regions in a large cohort of human subjects to probe the relationship between endogenous activity and category tuning, as well as behavioral perception. Specifically, we directly tested and verified two main hypotheses. First, the pre-stimulus activity modulates the degree of category tuning in response to visual stimuli; second, the same aspect in pre-stimulus activity that modulates tuning also correlates with behavioral perception. We further evaluated the spatial and temporal specificity of the pre-stimulus modulation. The results suggest that the pre-stimulus modulation effect is a reflection of local processes, and the majority of the modulation effect are transient, with a small fraction of all channels showing trial-by-trial auto-correlation in the pre-stimulus modulation.

## Methods

A total of 32 epileptic patients with iEEG electrodes implanted participated in this study. The patients were shown images from six different visual categories (human bodies, human faces, English words, houses, tools, scrambled non-objects), and they performed a 1-back repeat detection task. From the 32 patients, we located 230 channels in VTC that demonstrated category-selectivity to one of the six categories.

We considered the pre-stimulus activity $X_{pre}$ as proxy for the endogenous activity; and we used post-stimulus activity $X_{post}$ to extract category coding information. A generalized linear model (GLM) (1) was used as a classifier to decode the category information from $X_{post}$, conditioning on $X_{pre}$ in each of the category-selective electrode.

$$p(y|X_{post}, X_{pre}) = f(X_{post}{}^T\beta_{post} - X_{pre}{}^T\beta_{pre}) \tag{1}$$

The model was fitted in a two-step block-wise manner. In the first step, we force $\beta_{pre} = 0$ and only searched for optimal $\beta^*_{post}$ in the post-stimulus activity that best discriminates between categories. This would result in a trial-by-trial neural metric, ${X_{post}}^T \beta_{post}$, which quantified the post-stimulus category selectivity. In the second step, we fixed the optimal $\beta^*_{post}$ and optimized the model with respect to $\beta_{pre}$. This allowed the category classification to be made conditioning on the pre-stimulus activity, and critically, provided a neural metric ${X_{pre}}^T \beta_{pre}$ in pre-stimulus activity that quantified the amount of influence from pre-stimulus activity on the post-stimulus category selectivity on a trial-by-trial basis. We defined $MI \equiv {X_{pre}}^T \beta_{pre}$ as the pre-stimulus modulation index (MI).

## Results

First, we examined whether conditioning on the pre-stimulus activity changes the classification accuracy. As shown in Table 1, we found that the inclusion of pre-stimulus activity improved the classification accuracy for all visual categories. This result confirmed that, at a functional level, conditioning on pre-stimulus activity improves trial-by-trial category tuning.

Table 1: Sensitivity index ($d'$) for category classification with evoked response before and after conditioning on pre-stimulus activity (p-value for paired t-test)

| Category | Evoked | Evoked + Pre-stim | p-value |
|---|---|---|---|
| bodies | 1.1051 | 1.2391 | $0.038$ |
| faces | 1.3957 | 1.5072 | $< 10^{-5}$ |
| words | 0.9594 | 1.0951 | $< 10^{-5}$ |
| tools | 0.6994 | 0.8016 | $0.0078$ |
| houses | 1.0585 | 1.2046 | $< 10^{-5}$ |
| non-objects | 0.8477 | 1.0442 | $< 10^{-5}$ |

Second, we tested if the same aspect of pre-stimulus activity that modulates post-stimulus category tuning also correlates to behavioral perception. To assess this we divided the trials into two groups purely by the magnitude of the trial-by-trial pre-stimulus modulation index, and compared the behavioral reaction time (RT) in the 1-back task. We found that there is a significant difference in RT between high and low pre-stimulus MI trials (mean $\text{RT}_{\text{high MI}} = 660.4$ ms, mean $\text{RT}_{\text{low MI}} = 676.8$ ms, $p < 0.05$, permutation test).

To evaluate the spatial specificity of the effect, we computed the mean cross-channel correlation between different category-selective channels in each subject. We found that the maximum mean within-subject cross-channel correlation $r^2$ is only 0.035, and in almost all subjects, this correlation is very close to 0. This suggests that this critical component in the pre-stimulus is not part of a global effect, such as fluctuations in attention or arousal, but instead is local to cortex.

To evaluate the temporal specificity of the modulation effect, we computed the auto-correlation in pre-stimulus MI in consecutive trials for each channel. While in the large majority of the channels the effect is transient (no significant auto-correlation detected), in 41 out of 230 channels, we found significant auto-correlation ($p < 0.05$, uncorrected). Therefore, in some cortical regions the pre-stimulus effect may be related to infra-slow fluctuations often seen in resting-state studies.

To sum up, we found that pre-stimulus activity influences the degree of category tuning in response to visual stimuli. The same aspects in pre-stimulus activity that influences post-stimulus category tuning also correlates with perceptual behavior performance. This modulation provides a potential neural basis for perceptual variation arising from shifts in endogenous ongoing activity. Furthermore, the pre-stimulus modulation effect is a reflection of local processes. The majority of the pre-stimulus modulation effect is transient, but a small fraction of the category-selective channels show trial-by-trial auto-correlation.


## Acknowledgments

This work was supported by the National Institute on Drug Abuse under award R90DA023420 (to YL), the National Institute of Mental Health under award R01MH107797 and R21MH103592 (to ASG), and the National Science Foundation under award 1734907 (to ASG and MG).


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