Cortical feedback to superficial layers of V1 contains predictive scene information.

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Abstract:

A central characteristic of brain function is the ability to merge sensory input with internal representations of the world, but relatively little is known about cortical feedback channels that facilitate internal representations. We blocked feedforward input to subsections of human primary visual cortex by occluding one quarter of the visual field while participants viewed 384 real-world scenes. Using high-resolution 7T fMRI, we show that superficial layers of V1 exhibit predictive response properties unique from those associated with V1 feedforward processing. Our findings suggest that feedback to superficial layers of V1 provides neurons with contextual information not available via feedforward input.

Keywords: Cortical feedback; V1; Layer-specific fMRI

Introduction

Local brain areas compare sensory input with internal representations of the world through contextual processing involving feedforward and feedback connections (Gilbert & Li, 2013). Many experiments have furthered our understanding of the features that modulate early sensory areas through feedforward channels, but relatively little is known about the feature space that drives cortical feedback channels. Accessing and describing these internal feedback information channels will provide information about the structure of internal representations and is central to fully understanding neural computations (Petro & Muckli, 2016).

To study feedback, one must disentangle feedforward and non-feedforward sources of input to an area, which involves independent stimulation or inactivation of feedback and feedforward pathways. This can be achieved by pairing single- or multiunit recordings with electrical stimulation, pharmacological intervention, cooling or optogenetics (Muckli & Petro, 2013; Petro et al. 2014), but these methodologies are generally too invasive for studying the healthy human brain. A non-invasive strategy to measure feedback is to homogenize feedforward input using visual occlusion while recording with functional MRI. Feedback influences wide-spread dendritic activity but does not necessarily lead to spiking activity in cells1. Functional MRI is therefore particularly powerful for studying feedback because it is sensitive to energy-consumption associated with dendritic spatially-specific activity (Logothetis, 2005).

Here, we asked whether feedforward sensory input and predictive feedback signals could be read out from different layers of cortex, and what types of information these two inputs to early visual cortical neurons contain. By utilizing an occlusion paradigm in combination with recordings from high-resolution fMRI, we compared depth-specific V1 responses to sensory- and prediction-based computational models and to high-level scene category information.

Methods

We blocked feedforward input to subsections of human retinotopic visual cortex by occluding one quarter of the visual field (Muckli et al. 2015; Smith & Muckli, 2010). One participant viewed 384 real-world scenes (192 occluded and 192 non-occluded scenes) in 5 scanning sessions while we recorded V1 responses using high-resolution 7T fMRI. Data were acquired using a multi-band accelerated 2D Gradient Echo EPI sequence (resolution: 0.80mm isotropic; number of slices: 56; slice spacing: 0mm; TR: 2000ms; TE: 25ms; multi-band factor: 2; iPAT factor: 3; flip angle: 75º).

For each V1 voxel, we calculated a population receptive field (Dumoulin & Wandell, 2008) and defined voxel-specific feedforward and feedback models with varying levels of computational complexity (Figure 1). Model information included contrast energy and spatial coherence (Weibull model; Groen et al. 2013), orientation and spatial frequency (Gist model; Oliva & Torralba, 2001), and high-level category information

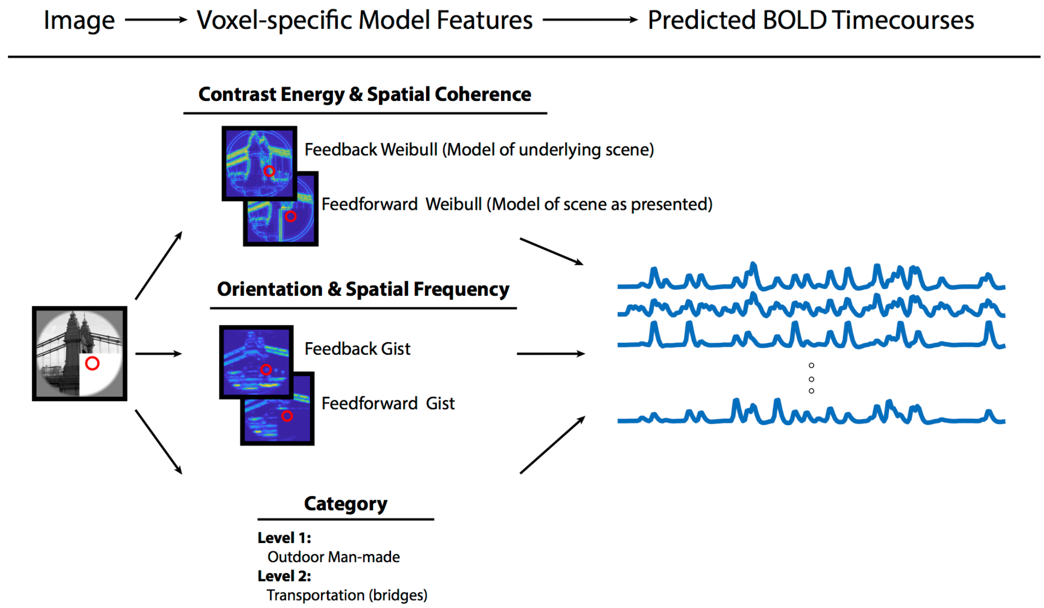

Figure 1: Voxel-specific feature time courses. The process of creating feature-based predicted time courses is shown for one voxel (the population receptive field of this example voxel is shown in red). Each stimulus image was decomposed into feedforward and feedback Weibull and Gist feature maps. Feedforward maps were based on the image as it was presented, with the occlusion in place. Feedback maps treated the image as if it had not been occluded and were based on possible predictive voxel responses.

(SUN database hierarchy; Xiao et al. 2010). V1 neurons in the lower-right scene quadrant received meaningful input during non-occluded scene presentations, but not during occluded scene presentations. Therefore, feedforward models were defined as responses related to scenes as they were *presented*. Feedback models were defined as responses related to scenes as they would be *predicted* (i.e. responding as if the scene was not occluded).

Responses from each model were convolved with a hemodynamic response function to create model time courses. We fitted model time courses to fMRI data and calculated the unique variance explained by models in an independent dataset (containing left-out scene stimuli) using semi-partial correlation statistics. We defined a voxel's tuning to feedforward and feedback signals as the ratio of unique variance explained by sensory feedforward and predictive feedback models.

Results

Results from cortical depth-specific analyses are shown in Figure 2. For six evenly-spaced cortical depths in Occluded V1 (between 10% and 90% of the total cortical thickness), we show the unique information provided by each model to voxel predictions. All layers show more information for feedforward models than for feedback models, and Gist is the more informative of the two feedforward models. This makes sense given V1's prominent orientation and spatial frequency sensitivity. Importantly though, feedforward models do not account for all information encoding in V1 voxels. All feedback models display unique information, and the amount of feedback information increases from deep to superficial layers. Further, category information adds substantial information to both Occluded and Non-Occluded models. In Occluded regions, there are equivalent amounts of category information and predictive low-level information in the deepest layer of cortex. However, category information rises more than the other two feedback models through middle and superficial layers. The right side of Figure 2 shows probability density of voxel tuning to feedforward and feedback models, separated by cortical depth. Voxels in deep layers of cortex are more likely to be heavily tuned to feedforward signals. However, tuning shifts toward feedback signals in superficial layers, where many feedback connections terminate in cortex (Larkum, 2013).

Discussion

Superficial layers of V1 exhibit predictive (and higher-level) response properties unique from the orientation and spatial frequency properties typically associated with V1 feedforward processing. Our findings suggest that feedback connections terminating in superficial

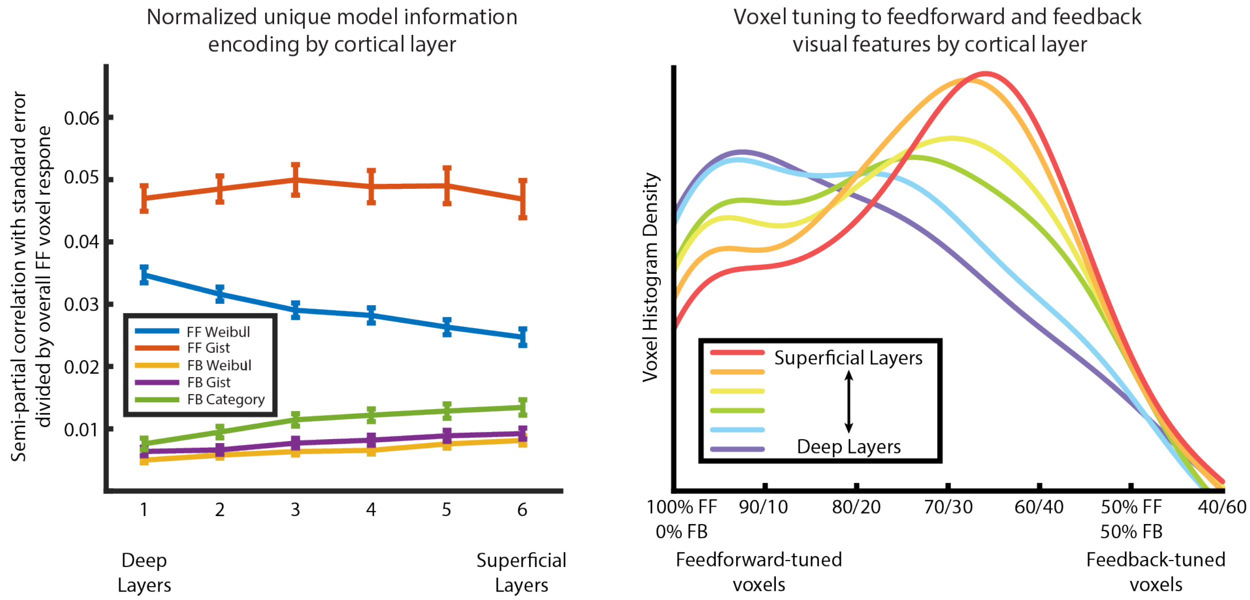

Figure 2: [Left side] Unique model information is displayed as the average of all voxel-model semi-partial correlations with standard error at 6 cortical depths [10%, 26%, 42%, 58%, 74%, 90%], with Layer 1 being labeled as the deepest layer and Layer 6 as the most superficial. Layers are normalized by their mean image response to all Non-Occluded images. [Right side] Voxel tuning histograms are shown for each cortical depth separately. Tuning was calculated by contrasting the unique information encoding of feedforward models to that of feedback models for each voxel. Probability density functions were defined for each cortical depth ROI using kernel density estimation.

layers provide V1 neurons with contextual information not available via localized feedforward input. Importantly, the separation of these models requires occlusion. Under non-occluded circumstances, the presented and predicted features are identical, making feedforward and feedback signals inseparable. It is therefore an exciting future consideration to devise occlusion methods for different sensory modalities, where similar effects might be uncovered.

While superficial layers of cortex have increased tuning to predictive feedback signals, their activity is still predominantly explained by feedforward features. This was shown by increased correlations on the left side of Figure 2, and the 70-30 tuning split (feedforward to feedback) on the right side of the figure. How can we reconcile this relatively small feedback tuning in superficial layers with its putative impact on cortical processing?

A promising theory points to the segregated arrival of feedback and feedforward inputs to the apical and basal dendrites of cortical layer 5 pyramidal neurons. This theory posits that in addition to feedforward action on basal dendrites in middle to deep layers of cortex, pyramidal neuron activity is affected by feedback inputs arriving to apical tuft dendrites in superficial layer 1, which trigger Ca^{2+} spikes. Through a mechanism known as backpropagation-activated Ca^{2+} spike firing (BAC firing), these Ca^{2+} spikes can convert a single somatic output spike into a 10ms burst containing 2–4 spikes (Larkum et al., 1999), meaning that feedback inputs might have a substantially greater role in determining the firing of pyramidal neurons than would be expected by their metabolic consumption (Larkum, 2013). Modeling work has recently explored segregated dendrite morphology for neuronal units, and these efforts corroborate the computational benefits theorized in the current study (Spoerer et al. 2017; Guerguiey et al. 2017).

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