How well do deep neural networks trained on object recognition characterize the mouse visual system?

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Abstract

Recent work on modeling neural responses in the primate visual system has benefited from deep neural networks trained on large-scale object recognition, and found a hierarchical correspondence between layers of the artificial neural network and brain areas along the ventral visual stream. However, we neither know whether such task-optimized networks enable equally good models of the rodent visual system, nor if a similar hierarchical correspondence exists. Here, we address these questions in the mouse visual system by extracting features at several layers of a convolutional neural network (CNN) trained on ImageNet to predict the responses of thousands of neurons in four visual areas (V1, LM, AL, RL) to natural images. We found that the CNN features outperform classical subunit energy models, but found no evidence for an order of the areas we recorded via a correspondence to the hierarchy of CNN layers. Moreover, the same CNN but with random weights provided an equivalently useful feature space for predicting neural responses. Our results suggest that object recognition as a high-level task does not provide more discriminative features to characterize the mouse visual system than a random network. Unlike in the primate, training on ethologically relevant visually guided behaviors – beyond static object recognition – may be needed to unveil the functional organization of the mouse visual cortex.

1 Introduction

Visual object recognition is a fundamental and difficult task performed by the primate brain via a hierarchy of visual areas (the ventral stream) that progressively untangles object identity information, gaining invariance to a wide range of object-preserving visual transformations [1,2]. Fueled by the advances of deep learning, recent work on modeling neural responses in sensory brain areas builds upon hierarchical convolutional neural networks (CNNs) trained to solve complex tasks like object recognition [3]. Interestingly, these models have not only achieved unprecedented performance in predicting neural responses in several brain areas of macaques and humans [4-7], but they also revealed a hierarchical correspondence between the layers of the CNNs and areas of the ventral stream [4-6]: the higher the area in the ventral stream, the higher the CNN layer that explained it best. The same approach also provided a quantitative signature of a previously unclear hierarchical organization of A1 and A2 in the human auditory cortex [7]. These discoveries about the primate have sparked a still unresolved question: to what extent is visual object processing also hierarchically organized in the mouse visual cortex and how well can the mouse visual system be modeled using goal-driven deep neural networks trained on static object classification? This question is important since mice are increasingly used to study vision due to the plethora of available experimental techniques such as the ability to genetically identify and manipulate neural circuits that are not easily available in primates. Recent work suggests that rats

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are capable of complex visual discrimination tasks [8] and recordings from extrastriate areas show a gradual increase in the ability of neurons in higher visual areas to support discrimination of visual objects [9, 10].

Here, we set out to study how well the mouse visual system can be characterized by goal-driven deep neural networks. We extracted features from the hidden layers of a standard CNN (VGG16, [11]) trained on object categorization, to predict responses of thousands of neurons in four mouse visual areas (V1, LM, AL, RL) to static natural images. We found that VGG16 yields powerful features for predicting neural activity, outperforming a Gabor filter bank energy model in these four visual areas. However, VGG16 does not significantly outperform a feature space produced by a network with an identical architecture but random weights. In contrast to previous work in primates, our data provide no evidence so far for a hierarchical correspondence between the deep network layers and the visual areas we recorded.

2 Model Architecture

Our network (Fig.[1]) follows the work of [5, 13]. It consists of four main network components: a core that provides nonlinear features of input images, a readout that maps those features to each neuron’s responses, a shifter that predicts receptive field shifts from pupil position, and a modulator that provides a gain factor for each neuron based on running speed and pupil dilation of the mouse.

For the core we use VGG16 [11] up to one of the first eight convolutional layers. We chose VGG16 due to its simple feed-forward architecture, competitive object classification performance, and increasing popularity to characterize rodent visual areas [10, 13]. The collection of output feature maps of a VGG16 layer – the shared feature space – was then fed into a spatial transformer readout for each neuron (Fig.[1B], see [12] for details). This readout learns one \((x, y)\) location for each neuron (its receptive field location, RF) [12] and extracts a feature vector at this location from multiple downsampled versions (scales) of the feature maps. The output of the readout is a linear combination of the concatenated feature vectors. We regularized the feature weights with an \(L_1\) penalty to encourage sparsity.

Shifter and modulator are multi-layer perceptrons (MLP) with one hidden layer. The shifter takes the tracked pupil position in camera coordinates and predicts a global receptive field shift \((\Delta x, \Delta y)\) in monitor coordinates. The modulator uses the mouse’s running speed, its pupil diameter, and the derivative to predict a gain for each neuron by which the neuron’s predicted response is multiplied. A soft-thresholding nonlinearity turns the result into a non-negative spike rate prediction (Fig.[1]). All components of the model are trained jointly end-to-end to minimize the difference between predicted and observed neural responses using Adam with a learning rate of \(1e^{-4}\), a batch size of 125 and early stopping.

3 Experiments

Neural data. We recorded responses of excitatory neurons in areas V1, LM, AL, and RL (layer 2/3) from two scans from one mouse and a third scan from a second mouse with a large-field-of-view
two-photon mesoscope (see [14] for details). We selected cells based on a classifier for somata on the
segmented cell masks and deconvolved their fluorescence traces, yielding 7393, 4674, 4680, 5797
neurons from areas V1, LM, AL, and RL, respectively. We further monitored pupil position, dilation,
and absolute running speed of the animal. The aquisition frame rate was 6.7 Hz.

Visual stimuli. Stimuli consisted of 5100 images taken
from ImageNet, cropped to 16:9 and converted to gray-
scale. The screen was 55 × 31 cm at a distance of 15 cm,
covering roughly 120° × 90°. In each scan, we showed
5000 of these images once (training and validation set)
and the remaining 100 images 10 times each (test set).
Each image was presented for 500 ms followed by a blank
screen lasting between 300 ms and 500 ms. For each
neuron, we extract the accumulated activity between 50 ms
and 550 ms after stimulus onset using a Hamming window.

4 Results

We fitted one model (that of Fig[1], see [12] for training
details) for each combination of scan, brain area, VGG16
layer (out of the first eight), random initialization (out of
three seeds), and input resolution. We considered several
resolutions of the input images because the right scale at
which VGG16 layers extract relevant features that best
match the representation in the brain is unknown. Opti-
mizing the scale for each layer was critical, since the
non-correspondence between a single layer and a brain area (in
terms of best correlation performance) strongly depends
on the input resolution (e.g. see Fig[3]A for V1 data). For
further analyses (Fig[3]B & 4), we pick for each case the
best performing input scale in the validation set.

No hierarchical correspondence. Previous results in
primates [3] show that a brain area higher in the hierarchy
is better matched (i.e. has a peak in prediction performance)
by a higher network layer. In contrast, when comparing the
average performance across cells and scans for each con-
volutional layer and brain area, we find no clear evidence
for a hierarchy (Fig[3]B) since there is no clear ordering of
the brain areas.

VGG16 outperforms classical models. We then investigate whether the lack of an evident hierar-
chy was due to an overall poor performance of our model. Thus, we first revise how much of the
explainable stimulus-driven variability the VGG16-based model captures. To this end we calculate
the oracle correlation (the conditional mean of n − 1 responses without the model) [12] obtaining
an upper bound of the achievable performance. Then we evaluate the test correlation of our model
restricted to visual input information (no shifter and no modulator), against the oracle (Fig[3]B) and
find that VGG16 features explain a substantial fraction of the oracle for the for areas (70–78%) and
average performance across cells and scans for each con-

Second, we consider a subunit energy model with Gabor quadrature pairs as a baseline due to its
competitive predictive performance of macaque V1 responses [3]. We replace the core from Fig[4]
with a Gabor filter bank (GFB) consisting of a large number of Gabor filters with different orientations,

sizes and spatial frequencies arranged in quadrature pairs, and followed by a squaring nonlinearity [5].
We find that for all areas and scans, the VGG16 core outperformed the GFB (Fig[4]B).

Core with random weights performs similarly. The results so far show that VGG16 provides
a powerful feature space to predict responses, which may suggest that static object recognition
could be a useful high-level goal to describe the function of the mouse visual system. However,
we were surprised that most VGG layers led to similar performance. To understand this result
better, we also evaluated a core with a similar architecture but random weights. This random core
performed similarly well as its pre-trained counterpart (Fig [4c]), suggesting that training on static
object recognition as a high-level goal is not necessary to achieve state-of-the-art performance in
predicting neural responses in those four visual areas. Instead, a sufficiently large collection of
random features followed by rectification provides a similarly powerful feature space.

5 Discussion

In contrast to similar work in the primate, we find no match between the hierarchy of mouse visual
cortical areas and the layers of CNNs trained on object categorization. Although VGG16 achieves
state-of-the-art performance, it is matched by random weights. There are two important implications
of our results: First, our work is in line with previous work in machine learning that shows the power
of random features [15]. Therefore, we argue that models based on random features should always
be reported as baselines in studies on neural system identification. Second, optimizing the network
for static object recognition alone as a high-level goal does not appear to be the right approximation
to describe representations and the visual hierarchy in the mouse cortex. Although our results do
not exclude a potential object processing hierarchy in the mouse visual system, they suggest that
training with more ethologically relevant visually guided tasks for the mouse could be a more fruitful
goal-driven approach to characterize the mouse visual system [16]. For instance, an approach with
dynamic stimuli such as those found during prey capture tasks [17] could yield more meaningful
features to unveil the functional organization of the mouse visual system.

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