Reconstructing feedback representations in ventral visual pathway with a generative adversarial autoencoder

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Abstract

While vision evokes a dense network of feedforward and feedback neural processes in the brain, visual processes are primarily modeled with feedforward hierarchical neural networks, leaving the computational role of feedback processes poorly understood. Here, we developed a generative autoencoder neural network model and adversarially trained it on a categorically diverse data set of images. We hypothesized that the feedback processes in the ventral visual pathway can be represented by reconstruction of the visual information performed by the generative model. We compared representational similarity of the activity patterns in the proposed model with temporal (magnetoencephalography) and spatial (functional magnetic resonance imaging) visual brain responses. The proposed generative model identified two segregated neural dynamics in the visual brain. A temporal hierarchy of processes transforming low level visual information into high level semantics in the

feedforward sweep, and a temporally later dynamics of inverse processes reconstructing low level visual information from a high level latent representation in the feedback sweep. Our results append to previous studies on neural feedback processes by presenting a new insight into the algorithmic function and the information carried by the feedback processes in the ventral visual pathway.

Author summary

It has been shown that the ventral visual cortex consists of a dense network of regions with feedforward and feedback connections. The feedforward path processes visual inputs along a hierarchy of cortical areas that starts in early visual cortex (an area tuned to low level features e.g. edges/corners) and ends in inferior temporal cortex (an area that responds to higher level categorical contents e.g. faces/objects). Alternatively, the feedback connections modulate neuronal responses in this hierarchy by broadcasting information from higher to lower areas. In recent years, deep neural network models which are trained on object recognition tasks achieved human-level performance and showed similar activation patterns to the visual brain. In this work, we developed a generative neural network model that consists of encoding and decoding sub-networks. By comparing this computational model with the human brain temporal (magnetoencephalography) and spatial (functional magnetic resonance imaging) response patterns, we found that the encoder processes resemble the brain feedforward processing dynamics and the decoder shares similarity with the brain feedback processing dynamics. These results provide an algorithmic insight into the spatiotemporal dynamics of feedforward and feedback processes in biological vision.

Introduction

In just a couple of hundred milliseconds, our brain interprets the visual scene around us [1–5], identifies faces [6, 7], recognizes objects [8–13], and localizes them [14–18]. Decades of cognitive neuroscience research has demonstrated that the brain accomplishes these complicated tasks through a cascade of hierarchical processes in the ventral visual stream starting in the early visual cortex (EVC) and culminating in the inferior temporal (IT) cortex.

While the feedforward recruitment of this hierarchy explains the core neural response patterns underlying visual recognition [19–21], it is unable to account for behavioural and neural dynamics observed in years of psychophysical, neurophysiological, and magneto/electrophysiological experiments [12, 22–25]. Indeed, variable timing of neural responses to visual stimuli beyond 200ms has been frequently associated with accumulation of sensory evidence through recurrent processes in the visual brain. However, the precise computational role of neural recurrent/feedback processes remains poorly understood at the system level. In particular, the algorithmic function of feedback processes and the type of information sent back along the visual hierarchy is still unknown.

To address this question, we develop a generative model which is adversarially trained on a diverse set of image categories. The model consists of two sub-networks: (i) An encoder sub-network receives a given visual stimulus, processes it in a hierarchy of neural layers to eventually produce a latent representation (code) of the visual input and (ii) a decoder sub-network which receives the latent representation and aims to reproduce the visual input from the information encoded in the latent representation.

This generative model enables us to not only investigate the encoding process of visual representations along the hierarchy of the encoder sub-network layers but also provides us an insight into the reverse process i.e. reconstructing the representations along the decoder sub-network layers. We hypothesize that the

visual information in the encoder sub-network in our computational model 29
mimics the feedforward pathway in the ventral visual stream and the decoder 30
sub-network which performs the reverse function may reveal the representations 31
along the feedback pathway. To test this hypothesis, after training the proposed 32
model, we compare the representations along its layers with 33
magnetoencephalography (MEG) and functional magnetic resonance imaging 34
(fMRI) data acquired from fifteen human participants in a visual recognition 35
experiment [13]. 36

Our model identified two separate dynamics of representational similarities 37
with MEG temporal data. The first one is consistent with the temporal 38
hierarchy of processes transforming low level visual information into high level 39
semantics in the feedforward sweep, and the second one reveals a temporally 40
subsequent dynamics of inverse processes reconstructing low level visual 41
information from a high level latent representation in the feedback sweep. 42
Further, comparison of encoder and decoder representations with two fMRI 43
regions of interests, namely EVC and IT, revealed a growing categorical 44
representation along the encoder layer (feedforward sweep) similar to IT and a 45
progression in detail visual representations along the decoder layers (feedback 46
sweep) akin to EVC. 47

Results 48

Construction of a generative model performing image 49 reconstruction 50

Previous work revealed that deep convolutional neural networks (DNNs) trained 51
on image classification develop hierarchical representations similar to the 52
cascade of processes along ventral visual pathway [3, 26–33]. However, 53
neuroscience evidence suggests top-down modulations of neural responses which 54
occur after some delay through abundant number of feedback connections in 55

visual cortex are critical to resolving visual recognition in the brain [12, 23, 24]. 56

Therefore, these feedforward deep neural network models do not fully represent 57

the complex visual processes in the ventral visual pathway. Here, we investigate 58

whether a deep generative model trained to compress and reconstruct images 59

could reveal similar representations as feedforward and feedback processes in the 60

ventral visual pathway. With this aim, we developed a deep generative 61

autoencoder neural network model using adversarial autoencoder (AAE) 62

framework [34]. AAE is a generative adversarial network (GAN) [35] where the 63

generator has an autoencoder architecture. Figure 1 depicts our proposed model 64

architecture. The autoencoder generator consists of two main components: 1) 65

an encoder which receives the visual stimuli and performs a cascade of simple 66

operations such as convolution, pooling, and normalization to map the visual 67

input to a latent feature vector (LV); 2) a decoder which receives the latent 68

vector and performs a cascade of simple deconvolution, upsampling and 69

normalization operations to reconstruct the input visual stimuli from 70

information encoded in the latent space. The model is trained with two 71

objectives - a reconstruction loss criterion, and an adversarial criterion. The 72

dual objectives training turns the autoencoder into a generative model whose 73

latent space learns data distribution properties that enables generative process 74

and avoids overfitting to the reconstruction objective. We hypothesize that the 75

encoder sub-network models the feedforward pathway of processes in ventral 76

visual stream, while the decoder sub-network models the reconstruction of visual 77

features in the feedback pathway. 78

To train our model, we assembled a super category data set (see Materials 79

and methods section for details). The super category data set includes 1,980,000 80

images from four equally distributed categories of (1) Faces, (2) Animates, (3) 81

Objects, and (4) Scenes. The rational behind assembling and using this data set 82

is two-fold: (1) ecologically, the human brain learns to develop high-level 83

category representations across multiple recognition tasks (e.g. faces, animals, 84

objects, scenes, etc.); Indeed, years of neuroscience research have identified a cascade of brain regions along ventral visual stream starting in early visual cortex (EVC) which processes low level visual features and eventually resolves visual categories at the end of the hierarchy in inferior temporal cortex (IT). (2) In this study, we compare model representations with brain imaging data (fMRI and MEG) from a visual recognition experiment [13]. We maintained consistency with the four categories from the stimulus set utilized in the brain imaging experiment which includes 156 images. Please note that this stimulus set was not used for training the model. After training the model on super category data set for over 800 epochs when the adversarial and reconstruction losses reached their local minima on the training set (Figure 2A), we determined how well our model performed on the 156 image set (as a testing dataset). Figure 2B illustrates this image set and the corresponding reconstructed images. The model performed the reconstruction on the training dataset with 0.109 ± 0.006 mean absolute error (MAE) and on the 156 image set with 0.119 ± 0.003 MAE between the input image and the corresponding reconstructed image. We computed the upper-bound performance of the model by sampling random pairs of images from the training and testing sets performing MAE between the different image pairs. On the training set, we observed a MAE of 0.53 ± 0.014 between the random image pairs and 0.62 ± 0.017 on the random pairs from the testing set. These results show that the model not only have converged to an optimum but also generalizes well to the testing set.

Representational similarity of the generative model to early and late brain regions in the ventral visual stream

We first determined the encoder/decoder representational similarities with early and late brain regions along the ventral visual cortex. For this, we chose early visual cortex (EVC) and inferior temporal cortex (IT) defined anatomically based on [36] and employed the representational similarity analysis (RSA)

Fig 1. Computational model architecture. The model is a generative adversarial network. The generator is an autoencoder consisting of five convolutional blocks (E1-E5) and one fully connected layer (E6) in the encoder and one fully connected layer (D1) followed by five deconvolutional blocks in the decoder (D2-D6). Each convolutional block encompasses batch normalization, convolution, nonlinear activation function, and pooling operations. Alternatively, each deconvolutional block encompasses batch normalization, deconvolution, nonlinear activation function, and upsampling operations. The discriminator consists of two fully connected layers. The training Data set consists of 1,980,000 images organized into four super-ordinate categories: (i) Faces, (ii) Animates, (iii) Objects, (iv) Scenes. **LV** denotes the latent vector generated by the encoder and **DL** is a one-hot data set label (one of the four mentioned training data sets). Both vectors are concatenated and fed to the discriminator, while only the latent vector is fed to the decoder.

method [37,38] as the integrative framework for model-brain comparisons. 113

For each region of interest (ROI), we extracted the fMRI response patterns to 114
each image, vectorized it and computed condition-specific pairwise distances (1- 115
Pearson's R) to create a 156 x 156 representational dissimilarity matrix (RDM) 116
per participant. We also fed the images to the generator and extracted 117
layer-specific activations for each image condition. Then by computing the 118
pairwise distances (1-Pearson's R) of image evoked layer activation patterns, we 119
created layer-specific RDMs (see Figure 3 and Materials and methods section for 120
details). We then compared subject-specific ROI RDMs with the model layer 121

Fig 2. Computational model performance. (A) Adversarial and Reconstruction loss over epochs. (B) 156 image set and their corresponding reconstructed image by the model.

RDMs by computing Spearman's correlations (Figure 3ADE). Figure 4A and B show subject averaged RDMS and their corresponding 2-dimensional multidimensional scaling (MDS) visualizations of EVC and IT, respectively. As expected EVC shows a random pattern across categories, whereas IT demonstrates clear categorical distinctions. Figure 4C-D compares the encoder and decoder layers correlations with EVC and IT RDMs.

The EVC representational correlations across layers of the encoder (and

inverse order of the decoders) demonstrate a decreasing trend, while IT
representational correlations across model layers progressively increase. Notably,
early processing layers of the model (E1/D6) and late processing layers (E6/D1)
show similar correlations both for EVC and IT. However, middle layers
correlations are significantly different when comparing encoder and decoder in
both ROIs (N=15; two-sided ttests; false discovery rate corrected at $P < 0.05$).
Further, the correlations of EVC is stronger with the decoder than encoder
whereas the correlations of IT is higher for the encoder than the decoder. This
indicates the reconstructing processes are more similar to detail representations
in EVC than IT.

The generative model unfolds the temporal dynamics of brain feedforward and feedback representations

The visual information traverses a hierarchy of regions in the visual cortex and
evolves over time rapidly. While the structure of our proposed model does not
directly delineate the human brain temporally, it has a clear sequential structure
which temporally unfolds the feedforward and feedback sequences in the visual
cortex. That is, information flows layer to layer and evolves from image low
level features to higher level latent concepts (feedforward sweep) and then from
this high level latent code sequentially the image level information is
reconstructed (feedback sweep). To test the hypothesis that the proposed model
indeed temporally mirrors ventral visual stream dynamics, we compared the
representations of time-resolved MEG data acquired in a visual recognition
experiment with the layer representations in the encoder and decoder
sub-networks. From each participant's data, we first extracted the MEG sensor
measurements for each image condition from -200ms to 1000ms (with 1 ms
resolution) relative to image onset. Then we computed dissimilarities (SVM
classifiers decoding performances, see Materials and methods section for details)
between evoked MEG pattern vectors of each pair of images and created time

Fig 3. Representational similarity analysis to compare fMRI, MEG and model representations. (A) fMRI response patterns were extracted from each ROI and pairwise condition-specific dissimilarities (1-Pearson's R) were computed to create one fMRI RDM per ROI and participant (see Materials and methods section for detail). (B) RDMs for the generative model were computed at each convolutional/deconvolutional block after feeding 156 images to the computational model. (C) MEG data consists of time-series data with 306 channels and 1200 time points (milliseconds) per trial. For each condition, we extracted a vector of size 306 at each time point as the activity pattern to compute the RDMs using SVM classifiers decoding accuracies (see Materials and methods section for detail). (D) Using RDMs from MEG and fMRI ROIs, we compared (Spearman's R) them with the RDMs from the computational model to investigate the spatio-temporal correspondences between the human brain and the computational model. (E) Correlations between time-resolved MEG RDMs and computational model RDMs result in a subject-specific signal for each layer across time, which we then average them over subjects.

resolved representational dissimilarity matrices (RDMs) for each individual. We
also fed the images to the generator and extracted layer-specific activations for
each image condition. Then by computing the pairwise distances (1-Pearson's R)
of image evoked layer activation patterns, we created layer-specific RDMs (see

Fig 4. Spatial representational comparisons (A) Neural representations in early visual cortex (EVC). The subject-averaged EVC RDM matrix, and its 2D multidimensional scaling visualization. (B) Neural representations in inferior temporal area (IT). The subject-averaged IT RDM matrix, and its 2D multidimensional scaling visualization. (C) Encoder, decoder and LV layer RDMs are correlated (Spearman's R) with subject-specific EVC RDMs. The averaged correlations over subjects with standard error of the mean are depicted. (D) Encoder, decoder and LV layer RDMs are correlated (Spearman's R) with subject-specific IT RDMs. The averaged correlations over subjects with standard error of the mean are depicted. The color coded (*) above each panel in C-D indicates that the correlation of the corresponding layer is significantly above zero. The black (*) indicates the correlations of the corresponding encoder and decoder layers are significantly different (N=15; two-sided ttests; false discovery rate corrected at $P < 0.05$).

Figure 3 and Materials and methods section for details). Then we correlated
layer-specific model RDMs with time-resolved subject specific MEG RDMs
(Spearman's R) resulting in correlation time series for each layer of the model.
Figure 5A-B show the subject averaged correlation time series for layers of
encoder and decoder sub-networks, respectively. Our results showed that all
layers of the proposed model were representationally similar to human brain

activity patterns, indicating that the model captures evolution of brain visual representations over time (N=15; permutation tests; cluster definition threshold $P < 0.05$; cluster significance threshold $P < 0.01$). Next, we investigated whether the hierarchy of the layered architecture unfolds the temporal dynamics of encoding (feedforward) and decoding (feedback) visual processes in the brain. Specifically, we examined the relationship between hierarchy of model layers and the peak latency of the correlation time series (Figure 5C). Consistent with previous works [29], the first peak latency of correlation time courses relating MEG and the encoder representations increased with the hierarchy of the encoder layers (Spearman's $R = 0.78$, $P < 0.0001$). The inspection of peak latencies in the decoder time series depicted in Figure 5B revealed a progressively increasing pattern from D1 to D6 (Spearman's $R = 0.84$, $P < 0.0001$). That is, the peak latency in D1 occurs at 151ms and over the decoder layers progressively the peak latency increases, the peak latency of D6 occurs at 204ms. Given that the decoder later layers are reconstructing the visual stimuli and thus closer to image level feature space, these temporal dynamics may explain the temporal dynamics of feedback information sent down the ventral stream. We further identified a salient second peak in layers E1 to E5 which their peak latencies negatively correlated with layers order in the Encoder (Spearman's $R = -0.57$, $P < 0.0001$) and they are significantly later than the corresponding layers in the decoder (all peak latency analyses are based on permutation based bootstrapping; N=15; two-sided hypothesis tests; $P < 0.0001$; Bonferroni corrected). Again confirming a later dynamics of representational similarities between these layers and the brain, possibly indicating a second sweep of visual information processing.

In the next step, we investigated the representational relationships among the encoder and the decoder layers of the model. To this end, we first computed the pairwise correlations between all encoder and decoder layer RDMs. The matrix depicted in Figure 5E summarizes these pairwise correlations and reveals which

representations across model layers are similar or dissimilar. Figure 5F visualizes these relationships with multi dimensional scaling (MDS) method. Visual inspection of this matrix manifests firstly the dissimilarity of latent layer representation from encoder and decoder layers, secondly similarity of late layer of encoder (E6) and early layer of the decoder (D1); and also similarity of early layer of decoder (E1) and late layer of the decoder (D6), thirdly the dissimilarity of middle layers of encoder and decoder indicating the difference in the representations of encoding (feedforward) and decoding (feedback) processes.

To obtain a more clear picture of brain-model temporal dynamics relationships across encoder and decoder sub-networks, we compared the correlation time courses corresponding to the encoder and decoder layers with the same level of processing in Figure 6A. The correlation time course of latent layer is depicted separately. Figure 6B depicts the corresponding model layers RDMs and their 2-dimensional MDS visualizations. As demonstrated in Figure 5, firstly the low level feature processing layer of encoder (E1) and decoder (D6) follow a notably similar dynamics. Further, the high level feature processing layers of encoder (E6 and E5) also depict a similar temporal dynamics with high level feature processing layers of the decoder (D1 and D2, respectively). However, the dynamics are explicitly different when middle level layers are compared (i.e. E2 vs.D5, E3 vs. D4, E4 vs. D3). This is also evident from comparison of the MDS visualizations of RDMs in each row. The peak latencies of the correlation time courses are marked with color-coded arrows. Consistent with Figure 5C, the peak latencies of low and high level processing layers coincide around the same time, whereas the peaks of mid-level feature processing layers of the decoder occurs between the first and second peaks of the corresponding encoder time courses.

Together, comparison of MEG temporal representations with the encoder and decoder sub-networks of our proposed model segregated the brain representational dynamics that transforms the low level visual features to high

level categorical semantics and the inverse functional processes that reconstructs
low level features from the high level code. These two identified dynamics of
processing can be associated with feedforward and feedback sweeps along ventral
visual stream.

Discussion

Using a generative model, we dissected the dynamics of processes in the ventral
visual pathway into two temporally distinct stages: the initial sweep depicts
neural representational similarity with the hierarchy of representations along the
encoder sub-network which transforms visual features into a latent
representation (feedforward sweep); and the subsequent sweep shows neural
representational similarity with the decoder sub-network which layer by layer
reconstructs visual details from the latent representational code (feedback
sweep).

As demonstrated in Figure 5A-C, the temporal representational similarities
of the encoder sub-network replicates previous findings showing hierarchical
representational similarities between the visual brain and the feedforward DNNs
that are trained on object recognition tasks [21, 26, 27, 29, 32, 39]. Specifically, it
has been demonstrated that object recognition DNNs develop internal
representations that are hierarchically similar to brain representations in early
visual cortex [39], area V4 (a mid-level region), and IT cortex (a high level
categorical region) along ventral visual pathway in primates [21, 26] and
humans [27, 29, 32]. Unlike the object recognition DNNs, the encoder
sub-network in our model is trained in an unsupervised manner, i.e., the
information regarding image classes (e.g. a car, a basketball) were not provided
to this network during training. This is a critical finding, as it shows supervision
is not required for the development of this hierarchical architecture observed in
DNNs and the brain. Further, comparing the representational dynamics of the

Fig 5. Temporal representational comparisons. (A) Encoder and MEG representational comparison. We correlated the encoder layer RDMs with subject-specific time-resolved MEG RDMs resulting in fifteen correlation time courses. We then averaged these time courses over participants. (B) Decoder and MEG representational comparison. Correlation of the decoder layer RDMs and time-resolved MEG RDMs. The color-coded lines below the curves show the time points when the correlations are significantly above zero ($N=15$; permutation tests; cluster definition threshold $P < 0.01$; cluster threshold $P < 0.05$). (C) Peak latency for encoder and decoder. The encoder have significantly earlier peak latency across all layers ($P = 0.014$). Error bars are expressed in standard error of the mean. (D) The architecture of the models with layers's label corresponding to (C). (E) The visualization of relationships between model layers representations. The matrix of RDM correlations between encoder and decoder layers is depicted. Each matrix entry compares two RDMs indexed by corresponding row and column in terms of Pearson's R. (F) The multidimensional scaling visualization of the RDMs relationships.

Fig 6. Comparisons of encoder and decoder representational dynamics. (A) Comparison of correlation time series of the encoder and decoder layers with the same level of processing. The color-coded lines below the curves show the timepoints when the correlations are significantly above zero ($N=15$; permutation tests; cluster definition threshold $P < 0.01$; cluster threshold $P < 0.05$). (B) The model RDMs and their corresponding MDS visualizations.

decoder sub-network and the visual brain revealed a temporally subsequent
hierarchy of processing (Figure 5B-C) which progressively builds visual detail

from the latent representation. This indicates that beyond feedforward sweep, 254
 brain visual processes demonstrate similarities with the reconstruction function 255
 implemented in the decoder sub-network. This finding contributes to unraveling 256
 the algorithmic functional role of feedback processes in the visual cortex. 257
 Finally, representational comparison of two brain regions at the beginning and 258
 end of ventral visual pathway, EVC and IT, with the encoder and decoder 259
 subnetworks (Figure 6) revealed the encoding processes in the feedforward sweep 260
 develops a categorical representations similar to IT and the reconstructing 261
 processes in feedback sweep evolves into detail representations similar to EVC. 262

Materials and methods 263

Our study consists of two components: (i) The computational model and (ii) the 264
 MEG/fMRI data from human participants, both of which are analyzed and 265
 compared in the result section. We focus on the ventral visual pathway, hence, 266
 we acquire both human brain and computational model neuronal activations on 267
 visual centric tasks. In this section, we will describe the computational model, 268
 SP (Super Category) image dataset, and MEG/fMRI data acquisition and 269
 analysis. 270

Neuroimaging experiments 271

The fMRI and MEG data used in this study has been published in [13] 272
 previously and is publicly available at <http://twinsetfusion.csail.mit.edu/>. In 273
 this section, we briefly describe the experiment design, data acquisition and 274
 analysis. 275

Participants 276

Brain data were acquired from fifteen right-handed healthy participants with 277
 normal or corrected to normal vision in two separate experiments (MEG and 278

fMRI). Participants (9 females, 27.87 ± 5.17 years old) signed an informed consent form and were compensated for their participation. Both experiments were conducted in accordance with the Declaration of Helsinki and approved by the Institutional Review Board of Massachusetts Institute of Technology.

Stimulus set and experimental design

The stimulus set consists of 156 natural images of four distinct visual categories: (i) Faces, (ii) Animates (animals and people), (iii) Objects, (iv) Scenes [13]. The participants viewed images presented for 0.5 sec (with 2.5 sec inter stimulus interval (ISI) in fMRI sessions and 0.7 to 0.8 sec ISI in MEG session) at the center of the screen at 6° visual angle. Functional MRI data were acquired in two sessions (11-15 runs in total) and MEG data were acquired in one session of 25 runs. Images were presented once in each run and in random order. The participants were performing a vigilance task of oddball detection.

fMRI data acquisition and analysis

The fMRI experiment was conducted at the Athinoula A. Martinos Imaging Center at MIT, using a 3 T Siemens Trio scanner with 32-channel phased-array head coil. Each imaging session started with acquiring structural images using a standard T1-weighted sequence (176 sagittal slices, FOV = 256 mm², TR = 2530 ms, TE = 2.34 ms, flip angle = 9°) and then 5–8 runs of 305 volumes of functional data (11–15 runs across the two sessions). Gradient-echo EPI sequence was used for functional data acquisition (TR = 2000 ms, TE = 29 ms, flip angle = 90° , FOV read = 200 mm, FOV phase = 100%, bandwidth 2368 Hz/Px, gap = 20%, resolution = 3.1 mm isotropic, slices = 33, ascending interleaved acquisition). For preprocessing of fMRI data, we used SPM software. The preprocessing of functional data included slice-time correction, realignment and co-registration to the first session T1 structural scan, and normalization to the standard MNI space. For multivariate analysis, we did not smooth the data.

We used general linear modeling (GLM) to estimate fMRI responses to the 156 stimuli. The events including stimuli conditions and nulls were modeled with event onsets and impulse response function. Further, the motion and run regressors were included in the GLM. Then we convolved the defined regressors with the hemodynamic response function and estimated the beta-values for each stimulus condition. Then by contrasting each image condition with the explicitly defined null condition, we obtained t-maps per image condition for each participant. For the current study, we investigated two anatomically defined [36] regions of interest (ROIs) along the ventral visual stream, early visual cortex (EVC) and inferior temporal cortex (IT).

We used multivariate analysis and computed pairwise dissimilarities between 156 image specific fMRI responses using 1-Pearson correlation distances and constructed a 156 x 156 representational dissimilarity matrix (RDM) per participant per ROI (EVC and IT). In detail, we extracted t-value patterns corresponding to each image condition from each region of interest, arranged them into vectors. Then we calculated the pairwise distances of the 156 image specific vector patterns. With this process, we obtained a 156 x156 RDM per ROI for each participant.

MEG data acquisition and analysis

The MEG experiment was conducted at the Athinoula A. Martinos Imaging Center at MIT, using a 306-channel Elekta neuromag TRIUX system with sampling rate of 1 kHz. The acquired data were filtered by a 0.03 to 330 Hz band-pass filter. We measured the participants' head position prior and during the recording with 5 coils attached to their head. We then applied a maxfilter for temporal source space separation and head movements correction [40,41]. For preprocessing of MEG data, we used Brainstorm software [40]. We extracted trials from -200 ms to 1000 ms with respect to image onset. We then removed the baseline mean and smoothed the data with a 30 HZ low-pass filter. For each

participant, we obtained 25 trials per image condition. We employed
 multivariate pattern analysis to compute the dissimilarity relations between
 image conditions [10–13, 29, 42, 43]. At each time point t , we arranged MEG
 sensor measurements of each image condition into pattern vectors of $306 \times N$
 dimension, where N denotes the number of trials per condition. We then
 randomly assigned the trials of each condition into 8 bins and subaveraged the
 trials within each bin to overcome computational complexity and reduce noise.
 Support vector machine classifiers were trained on the subaveraged MEG
 pattern vectors of each pair of images at each time point to discriminate the
 pairs. The performance of the classifier in discriminating each pair of images
 with leave-one-out cross validation procedure was used as the dissimilarity
 measure between the pairs to populate a 156×156 representational dissimilarity
 matrix (RDM) at each time point. The rows and columns of the RDM are
 indexed by the image conditions and each matrix element indicates the
 dissimilarity of the corresponding image conditions based on MEG
 measurements of the specific time point.

Computational Model Architecture and Training

Previous work revealed that deep convolutional neural networks trained on
 object recognition develop similar representations akin to the hierarchical
 processes along ventral visual stream [3, 26–32]. However, there are abundant
 number of feedback connections in ventral visual stream and therefore, these
 feedforward neural network models may not fully represent the complex visual
 processes in the ventral visual pathway.

Here, we aim to investigate whether a deep generative model trained to map
 images to a latent code and then reconstruct the images from the features
 encoded in the latent space can reveal similar representations as feedforward and
 feedback processes in the ventral visual pathway. With this aim, we developed a
 deep generative autoencoder neural network model using adversarial

autoencoder (AE) framework [34, 35].

AEs consist of two sub-networks: (i) The encoder takes a given data and outputs a lower representation of the data (latent code) and (ii) the decoder takes the latent code and aims to reproduce the input data. Alternatively, the GAN framework is a min-max adversarial game between two distinct neural networks: (i) The generator(G), aims at generating synthetic data by learning the distribution of the real data and (ii) the discriminator (D), aims at distinguishing the generator's fake data from real data. The generator uses a function $G(z)$ that maps samples z from the prior $p(z)$ (normal distribution) to the data space $p(x)$. $G(z)$ is trained to maximally confuse the discriminator into believing that samples it generates come from the data distribution. The solution to this game can be expressed as following [35]:

$$\min_G \max_D [\mathbb{E}_{x \sim p_{data}} [\log D(x)] + \mathbb{E}_{z \sim p_z} [\log (1 - D(G(z)))]] \quad (1)$$

We chose an AE architecture because we hypothesize that the encoder embodies similar neuronal characteristics as the image classification DNNs and thereby could resemble the human brain feedforward representations. Alternatively, we hypothesize that the decoder part of the AE architecture which generates the image from the latent space code would encompass the neuronal representations similar to feedback processes in the human visual brain.

Our generative autoencoder model architecture consists of a total of 13 layers: (i) the encoder consists of 6 layers; 5 convolutional layers and one fully-connected layer, (ii) the decoder consists of 6 layers; 5 deconvolutional layers and one fully-connected layer, and (iii) lastly one fully-connected layer representing the latent code layer. The latent code vector z captures high level representation of the data distribution. The discriminator architecture consists of a total of three fully connected layers (Figure 1B).

Super Category (SC) Dataset

In computer vision literature, deep neural network models are usually trained to optimize category specific recognition performance on large scale datasets. However, the human brain learns to develop high-level representations for categories across multiple recognition tasks (eg faces, objects, scenes, etc). Indeed, years of cognitive neuroscience has demonstrated brain regions which are functionally respond preferentially to one of these categories compared to others (eg. Fusiform gyrus, IT area, Parahipocampal cortex, ...). Therefore, to train our proposed model we put together a super category (SC) data set consisting of 1,980,00 images from four equally distributed distinct categories: (i) Animals, (ii) Objects, (iii) Scenes, and (iv) Faces. Images from the Faces category were acquired from the VGGFaces2 dataset [44], Objects and Animals categories were from the ImageNet dataset [45], and Scenes categories were from the Places356 dataset [46]. To make all classes equal, we have randomly sampled 495,000 images per class. During computational model training and testing, each image was preprocessed through a pipeline: (i) Images were resized to 224×224 , and (ii) normalized from 0 to 225 to -1 to 1 range values.

Lastly, the neuronal representations for the generative AE model were computed at each convolutional/deconvolutional block after feeding 156 images used in the neuroimaging experiments to the encoder of the computational model. Please note this image set was not used in training the model. We employed the vectorized model activity patterns of each convolutional/deconvolutional block to compute dissimilarity distances (1-Pearson's R) for each pair of images and create an RDM per model layer (Figure 3B).

Representational similarity analysis to relate the brain and model representations

We used representational similarity analysis (RSA) [37,38] to map MEG measurements, fMRI responses, and model activation patterns into a common space where they are directly comparable.

RSA transforms the stimulus-specific response patterns into a representational space by creating matrices summarizing pairwise distance relationships of the response patterns (i.e. defined as the correlational distance, or a classifier performance in discriminating two conditions). The matrix capturing these pairwise dissimilarity measures is called representational dissimilarity matrix (RDM).

To relate the spatio-temporal dynamics of neural representations in the human brain with our proposed model, we computed the similarity (in terms of Spearman's R) of fMRI ROI RDMs and time-resolved MEG RDMs with our computational model RDMs (Figure 3D).

Correlations between subject-specific time-resolved MEG RDMs and computational model layer RDMs result in a signal for each layer per participant across time (Figure 3F). While, correlations between subject-specific fMRI ROI RDMs and computational model layer RDMs result in subject-specific correlation values per layer (Figure 3E). To account for different levels of noise in brain ROIs, we estimated the noise ceiling in EVC and IT [47,48] and normalized the fMRI ROI and model correlations with the corresponding noise ceiling [49]. Then the correlation time series (for MEG/Model comparisons) or correlation values (for fMRI/Model comparisons) were averaged over participant and tested against zero for statistical significance.

Statistical tests

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We used nonparametric statistical test methods which make no assumptions on 438
the distribution of the data [50, 51]. For statistical inference on the correlation 439
time series, we used permutation-based cluster-size inference with null 440
hypothesis of zero. For statistical assessments of peak latencies, we 441
bootstrapped the subject-specific correlation time series for 1000 times to 442
estimate an empirical distribution over peak latencies [12, 29, 43]. 443

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