Brain2GAN; Reconstructing perceived faces from the primate brain via StyleGAN3

Abstract

Neural coding characterizes the relationship between stimuli and their corresponding neural responses. The usage of synthesized yet photorealistic reality by generative adversarial networks (GANs) allows for superior control over these data: the underlying feature representations that account for the semantics in synthesized data are known a priori and their relationship is perfect rather than approximated post-hoc by feature extraction models. We exploit this property in neural decoding of multi-unit activity responses that we recorded from the primate brain upon presentation with synthesized face images in a passive fixation experiment. The face reconstructions we acquired from brain activity were astonishingly similar to the originally perceived face stimuli. This provides strong evidence that the neural face manifold and the disentangled w-latent space conditioned on StyleGAN3 (rather than the z-latent space of arbitrary GANs or other feature representations we encountered so far) share how they represent the high-level semantics of the high-dimensional space of faces.

1 Introduction

The field of neural coding aims at deciphering the neural code to characterize how the brain recognizes the statistical invariances of structured yet complex naturalistic environments. *Neural encoding* seeks to find how properties of external phenomena are stored in the brain by modeling the stimulus-response transformation (van Gerven, 2017). Vice versa, *neural decoding* aims to find what information about the original stimulus is present in and can be retrieved from the measured brain activity by modeling the response-stimulus transformation (Haynes & Rees, 2006; Kamitani & Tong, 2005). In particular, reconstruction is concerned with re-creating the literal stimulus image from brain activity. In both cases, it is common to factorize the direct transformation into two by invoking an in-between feature space (Figure 1). Not only does this favor data efficiency as neural data is scarce but it also allows one to test alternative hypotheses about the relevant stimulus features that are stored in and can be retrieved from the brain.

Figure 1: **Neural coding.** The transformation between sensory stimuli and brain responses via an intermediate feature space. Neural encoding is factorized into a nonlinear "analysis" and a linear "encoding" mapping. Neural decoding is factorized into a linear "decoding" and a nonlinear "synthesis" mapping.

The brain can effectively represent an infinite amount of visual phenomena to interpret and act upon the environment. Although such neural representations are constructed from experience, novel yet plausible situations that respect the statistics of the natural environment can also be mentally simulated or *imagined* (Dijkstra et al., 2019). From a machine learning perspective, generative models achieve the same objective: they capture the probability density that underlies a (very large) set of observations and can be used to synthesize new instances which appear to be from the original data distribution yet are suitably different from the observed instances. Particularly, generative adversarial networks (GANs) (Goodfellow et al., 2014) are among the most impressive generative models to date which can synthesize novel yet realistic-looking images (e.g., natural images and images of human faces, bedrooms, cars and cats (Brock et al., 2018; Karras et al., 2017; 2019; 2021) from randomly-sampled latent vectors. A GAN consists of two neural networks: a generator network that synthesizes images from randomly-sampled latent vectors and a discriminator network that distinguishes synthesized from real images. During training, these networks are pitted against each other until the generated data are indistinguishable from the real data. The bijective latent-to-image relationship of the generator can be exploited in neural decoding to disambiguate the synthesized images as visual content is specified by their underlying latent code (Kriegeskorte, 2015) and perform *analysis by synthesis* (Yuille & Kersten, 2006).

The current work follows the experimental paradigm proposed by Dado et al. (2022): face stimuli were synthesized from randomly-sampled latent vectors using the generator network of a GAN and presented to a macaque with cortical implants in a passive fixation task. A decoder model could then be fit to predict latents from recorded brain activity using the *ground-truth* latent representations that were originally used for synthesis. Note that this latent-image relationship is always perfect. As such, this method circumvents the bottleneck of information loss that results from *approximate* inversion of the (unidirectional) generator in order to retrospectively obtain latents from images. Reconstructions of the perceived stimuli were created by feeding the predicted latents to the generator. First, we show that neural decoding of brain activity via the less entangled w-latent space of the StyleGAN3 model (Karras et al., 2021) led to reconstructions strikingly similar to the perceived stimuli. Second, the largest contribution to the decoding performance of higher-level semantics is explained by the inferior temporal (IT) cortex which is located at the end of the visual ventral pathway for visual object recognition. Third, we found that reconstructing faces from brain activity to which we applied linear operations looked similar to the faces we obtained by applying the same operations to the latents which further indicates overlap in structure between the neural face manifold and the GAN latent space.

1.1 EARLIER WORK

Visual experience is partially determined by the selective responses of neuronal populations along the visual ventral "what" pathway (Ungerleider & Mishkin, 1982). That is, the receptive fields of neurons in early cortical regions are selective for simple features (e.g., local edge orientations (Hubel & Wiesel, 1962)) whereas those of neurons in deeper regions respond to more complex patterns of features (Gross et al., 1972; Hung et al., 2005). Previous work has shown how the features extracted by deep convolutional neural networks predict neural responses in the ventral visual stream to perceived naturalistic stimuli in the human brain (Yamins et al., 2014; Cadieu et al., 2014; Khaligh-Razavi & Kriegeskorte, 2014; Güçlü & van Gerven, 2015; Yamins & DiCarlo, 2016; Cichy et al., 2016; Eickenberg et al., 2017) as well as in the primate brain (Freiwald & Tsao, 2010; Chang & Tsao, 2017). In turn, such deep convnets have also been deployed for decoding of neural responses during visual perception, imagery and dreaming (Horikawa & Kamitani, 2017b;a; St-Yves & Naselaris, 2018; Shen et al., 2019b;a; Güçlütürk et al., 2017; VanRullen & Reddy, 2019; Dado et al., 2022).

2 METHODS

2.1 IMPLEMENTATION DETAILS

We used the original PyTorch implementation of StyleGAN3 (Karras et al., 2021). For the perceptual similarity metric, we used the MXNet implementation of Alexnet and the keras implementation of VggFace. All analyses were carried out in Python 3.8 on the internal cluster.

Figure 2: **StyleGAN3 generator architecture.** The generator takes a 512-dim. latent vector as input and transforms it into a 1024^2 resolution RGB image. We collected a dataset of 4000 training set images and 100 test set images. For the passive fixation experiment, the images were resized to 500^2 resolution.

2.2 DATA

2.2.1 STIMULI

We synthesized photorealistic face images of 1024^2 resolution from (512-dim.) z-latent vectors with the generator network of StyleGAN3 (Karras et al., 2020) (Figure 2) which is pretrained on the high-quality Flickr-Faces-HQ (FFHQ) dataset (Karras et al., 2019). The z-latents were randomly sampled from the standard Gaussian that was truncated at 0.7 so that the sampled values are ensured to fall within this specified range which benefits the quality of the faces. Crucially, StyleGAN3 maps the z-latent space via an 8-layer MLP to an intermediate (512-dim.) w-latent space for feature disentanglement. The w-latents then get integrated in the generator network via adaptive instance normalization. The training set consisted of 4000 synthesized face images that were each presented once to cover a large stimulus space to fit a general model. The test set consisted of 100 images that were averaged over twenty repetitions.

2.2.2 FEATURES

For the main analysis, the z- and w-latent space of StyleGAN3 were both used as the in-between feature space. In addition, we also extracted the intermediate layer activations to our face stimuli from Alexnet for object recognition (Krizhevsky, 2014), the vgg16 implementation of VggFace for face recognition (Parkhi et al., 2015) and the discriminator network of StyleGAN3. We fit multiple encoding models to see how well their feature representations can explain the recorded responses. Because the features from VGGFace and the discriminator were very large ($\sim 10^6$), we performed downsampling, as done in (Eickenberg et al., 2017). I.e., for each channel in the activation, the feature map was spatially smoothed with a Gaussian filter and subsampled such that the total number of output features was lower than 50,000 per image. The kernel size was set to be equal to the downsampling factor.

2.2.3 RESPONSES

We recorded multi-unit activity (Super & Roelfsema, 2005) with 15 chronically implanted electrode arrays (64 channels each) in one macaque (male, 7 years old) upon presentation with the synthesized face images in a passive fixation experiment (Figure 3). Neural responses were recorded in V1 (7 arrays), V4 (4 arrays) and IT (4 arrays) leading to a total of 960 channels. For each trial, we averaged the early response of each channel using the following time-windows: 25-125 ms for V1, 50-150 ms for V4 and 75-175 ms for IT. The data was normalized as in (Bashivan et al., 2019) such that for each channel, the mean was subtracted from all the responses which were then divided by the standard deviation. All procedures complied with the NIH Guide for Care and Use of Laboratory Animals and were approved by the local institutional animal care and use committee.

Figure 3: **The passive fixation task.** The monkey was fixating a red dot with gray background for 300 ms followed by a fast sequence four face images (500^2 pixels): 200 ms stimulus presentation and 200 ms inter-trial interval. The stimuli were slightly shifted to the lower right such that the fovea corresponded with pixel (150, 150). The monkey was rewarded with juice if fixation was kept for the whole sequence.

2.3 MODELS

We used linear mapping to evaluate our claim that the feature- and neural representation effectively encode the same stimulus properties, as is standard in the field. A more complex nonlinear transformation would not be valid to support this claim since this could theoretically map anything to anything. We used regularization for encoding due to the high dimensionality of the feature space.

2.3.1 DECODING

Multiple linear regression was used to model how the individual units within feature representations y (e.g., w-latents) are linearly dependent on brain activity $\mathbf{x}$:

$$\mathcal{L} = \frac{1}{2} \sum_i \left(y_i - \mathbf{w}^T \mathbf{x}_i \right)^2 \tag{1}$$

where i ranges over samples. This was implemented by prepending a dense layer to the generator architecture to transform brain responses into feature representations which were then run through the generator as usual. This response-feature layer was fit with ordinary least squares while the remainder of the network was kept fixed. Note that no truncation was applied for the reconstruction from predicted features/latents.

2.3.2 ENCODING

Kernel ridge regression was used to model how every recording site in the visual cortex is linearly dependent on the stimulus features. In contrast to decoding, encoding required regularization to avoid overfitting since we predicted from feature space $\mathbf{x}_i \rightarrow \phi(\mathbf{x}_i)$ where $\phi()$ is the feature extraction model. Hence we used ridge regression where the norm of $\mathbf{w}$ is penalized to define encoding models by a weighted sum of $\phi(\mathbf{x})$:

$$\mathcal{L} = \frac{1}{2} \sum_i \left(y_i - \mathbf{w}^T \phi(\mathbf{x}_i) \right)^2 + \frac{1}{2} \lambda ||\mathbf{w}||^2 \tag{2}$$

where $\mathbf{x} = (\mathbf{x}_1, \mathbf{x}_2, ..., \mathbf{x}_N)^T \in \mathbb{R}^{N \times d}$, $y = (y_1, y_2, ..., y_N)^T \in \mathbb{R}^{N \times q}$, N the number of stimulus-response pairs, d the number of pixels, q the number of neural recording sites and $\lambda \geq 0$ the regularization parameter. We then solved for $\mathbf{w}$ by applying the "kernel trick" (Welling, 2013):

$$\mathbf{w} = (\lambda \mathbf{I}_m + \Phi \Phi^T)^{-1} \Phi y \tag{3}$$

where $\Phi = (\phi(x_1), \phi(x_2), ..., \phi(x_N)) \in \mathbb{R}^{N \times m}$ (i.e., the design matrix) where m is the number of feature elements and $Y_i = (y_1^{(i)}, y_2^{(i)}, ..., y_N^{(i)}) \in \mathbb{R}^{N \times 1}$. This means that $\mathbf{w}$ must lie in the space induced by the training data even when $m \gg N$. The optimal λ is determined with grid search, as in (Güçlü & van Gerven, 2014). The grid is obtained by dividing the domain of λ in n values and evaluate model performance at every value. This hyperparameter domain is controlled by the capacity of the model, i.e., the effective degrees of freedom dof of the ridge regression fit from $[1, N]$:

$$\text{dof}(\lambda_i) = \sum_{j=1}^{N} \frac{s_j^2}{s_j^2 + \lambda_i} \tag{4}$$

where s are the non-zero singular values of the design matrix Φ as obtained by singular value decomposition. We can solve for each λ_i with Newton's method. Now that the grid of lambda values is defined, we can search for the optimal λ_i that minimizes the generalized cross validation error ϵ between target t and prediction y:

$$\epsilon = \sum_{j=1}^{N} \left(\frac{t-y}{1 - \frac{\text{dof}(\lambda_i)}{N}} \right)^2. \tag{5}$$

2.4 EVALUATION

Decoding performance was evaluated by six metrics that compared the stimuli from the held-out test set with their reconstructions from brain activity: latent similarity, Alexnet perceptual similarity, VGGFace perceptual similarity, latent correlation, pixel correlation and structural similarity index (SSIM). For *latent similarity*, we considered the cosine similarity per latent dimension between predicted and ground-truth latent vectors:

$$\text{Latent cos similarity} = \frac{\hat{z}_i \cdot z_i}{\sqrt{\sum_{i=1}^{512}(\hat{z}_i)^2}\sqrt{\sum_{i=1}^{512}(z_i)^2}}$$

where $\hat{z}$ and z are the 512-dimensional predicted and ground-truth latent vectors, respectively. For *perceptual similarity*, we compute the cosine similarity between deeper layer activations (rather than pixel space which is the model input) extracted by deep neural networks. Specifically, we fed the stimuli and reconstructions to the feature extraction models Alexnet (Krizhevsky, 2014) pretrained on object recognition and VGGFace (vgg16) (Parkhi et al., 2015) pretrained on face recognition and extracted the activations of their last convolutional layer. We then considered the cosine similarity per activation unit:

$$\text{Perceptual cos similarity} = \frac{f(\hat{x})_i \cdot f(x)_i}{\sqrt{\sum_{i=1}^{n}(f(x)_i)^2}\sqrt{\sum_{i=1}^{n}(f(\hat{x})_i)^2}}$$

where x and $\hat{x}$ are the 224×224 RGB (image dimensionality that the models expects) visual stimuli and their reconstructions, respectively, n is the number of activation elements, and $f(.)$ is the image-activation transformation. *Latent and pixel correlation* measure the standard linear (Pearson product-moment) correlation coefficient between the latent dimensions of the predicted and ground-truth latent vectors and the luminance pixel values of stimuli and their reconstructions, respectively. *SSIM* looks at similarity between stimuli and their reconstructions in terms of luminance, contrast and structure (Wang et al., 2004).

Furthermore, we also tested for *attribute similarity* (Dado et al., 2022) between stimuli and their reconstructions using the intrinsic semantic vectors of the generator which we accessed using closed-form factorization ("SeFa") (Shen & Zhou, 2021). In short, the unsupervised SeFa algorithm decomposes the pre-trained weights of the generator into 512 different latent semantics (of 512 dimensions each) which can be used for editing the synthesized images in w-space. This is also a means to understand what each latent semantic encodes: if a face becomes younger or older when traversing the latent in the negative or positive direction of the latent semantic, we can conclude post-hoc that it encodes the attribute "age". In our case, we used it to score each stimulus and reconstruction by taking the inner product between their w-latent and latent semantic and check for similarity.

3 RESULTS

3.1 NEURAL DECODING

We performed neural decoding via the original z-latent space and the less entangled w-latent space of StyleGAN3 and found that the latter resulted in a major improvement of decoding performance, see Figure 4 and Table 1 for qualitative and quantitative results, respectively. The qualitative results are from decoding via the w-latent space only (and not from z-latent space). Perceptually, there is high resemblance between stimuli and their reconstructions in terms of many facial attributes, such as gender, age, pose, haircut, lighting, hair color, skin tone, smile and eyeglasses.

Figure 4: **Qualitative results:** The 100 test set stimuli and their reconstructions from brain activity.

The contribution of each brain region to the overall reconstruction performance was determined by occluding the recordings from the other two sites. Concretely, the two site responses were replaced with the average response of all but the corresponding response such that only the site of interest remained. Alternatively, one could evaluate region contribution by training three different decoders on neural data subsets, but the current occlusion method made it more interpretable how a region contributed to the same decoder's performance. As such, we found that this is for the largest part determined by IT-responses which is the most downstream site we recorded from.

We validated our results with a permutation test as follows: for a thousand times, we sampled a hundred random latents from the same distribution as our original test set and generated their corresponding face images. Per iteration, we checked whether these random latents and faces were closer to the ground-truth latent and faces than our predicted latents and faces. We found that our predicted latents from brain activity and corresponding faces were always closer to the original stimuli for both z- and w-latents and all six metrics, yielding statistical significance ($p < 0.001$).

Table 1: **Quantitative results.** The upper block decoded the z-latent whereas the lower block decoded the w-latent from brain activity. Decoding performance is quantified in terms of six metrics: latent cosine similarity, latent correlation (Student's t-test), perceptual cosine similarity using Alexnet and VGGFace, pixel-wise correlation (Student's t-test) and structural similarity index (SSIM) in pixel space between stimuli and their reconstructions ($mean \pm std.error$). The rows display performance when using either the recordings from "all" recording sites or only from a specific brain area. The latter is achieved by occluding the recordings from the other two brain regions in the test set. Neural decoding from all brain regions into the w-latent resulted in the overall highest reconstruction performance.

		Lat. sim.	Lat. corr.	Alexnet sim.	VGGFace sim.	Pixel corr.	SSIM
z	All	0.0818 ± 0.0044	0.0817 ± 0.0045	0.2502 ± 0.0023	0.1789 ± 0.0013	$0.4331 \pm 5.6e{-}5$	0.3811
	V1	0.0405 ± 0.0046	0.0397 ± 0.0046	0.1982 ± 0.0022	0.1430 ± 0.0012	0.2887 ± 0.0001	0.2640
	V4	0.0332 ± 0.0046	0.0323 ± 0.0046	0.2088 ± 0.0022	0.1485 ± 0.0012	$0.2430 \pm 6.1e{-}5$	0.2211
	IT	0.0452 ± 0.0044	0.0446 ± 0.0044	0.2137 ± 0.0022	0.1498 ± 0.0012	$0.3105 \pm 7.1e{-}5$	0.2794
w	All	$\mathbf{0.4579 \pm 0.0019}$	$\mathbf{0.2908 \pm 0.0047}$	$\mathbf{0.2855 \pm 0.0029}$	$\mathbf{0.2391 \pm 0.0017}$	$\mathbf{0.6055 \pm 6.7e\text{-}5}$	**0.5547**
	V1	0.3792 ± 0.0022	0.1478 ± 0.0047	0.1509 ± 0.0023	0.1151 ± 0.0012	0.2958 ± 0.0001	0.2256
	V4	0.3783 ± 0.0023	0.1450 ± 0.0049	0.1535 ± 0.0024	0.1137 ± 0.0012	$0.2530 \pm 8.2e{-}5$	0.1665
	IT	0.4009 ± 0.0021	0.1828 ± 0.0051	0.1906 ± 0.0026	0.1451 ± 0.0014	$0.4119 \pm 8.5e{-}5$	0.3275

Figure 5: **Neural decoding performance in time**. The development of decoding performance (Y-axis) in terms of all six metrics based on the recorded response data in V1, V4, IT and all brain regions and over the full time course of 300 ms (X-axis). Stimulus onset happened at 100 ms. For visualization purposes, a sigmoid was fit to these data points and the shaded areas denote the predefined time windows we used for our original analysis.

3.2 NEURAL DECODING IN TIME

Neural decoding performance was assessed in time (Figure 5). Rather than taking the average response over the whole predefined windows for V1, V4 and IT, we took the average response over a 10 ms time window that was slided without overlap over the full time course of 300 ms. This resulted in thirty responses over time per stimulus. As expected, performance climbed and peaked first for (early) V1, then (intermediate) V4 and lastly (deep) IT. We also observed that IT outperformed the other two regions.

3.3 NEURAL DECODING OF FACIAL ATTRIBUTES

We used attribute similarity to quantify how well particular facial attributes were predicted from brain activity using the 512 latent semantics found by SeFa (Figure 6). After sorting the latent semantics based on attribute similarity, we edited an arbitrary test set example with the highest performing latent semantic ($r = 0.8217$) to qualitatively visualize which facial attributes it encoded (e.g., pose and age, Figure 6C). The 512 latent semantics are known to be hierarchically organized (Shen & Zhou, 2021) and we also find this hierarchy in predictive performance where the highest and lowest correlations are at the earliest and latest latent semantics, respectively. Face editing revealed that the earliest latent semantics encode clear and well-known facial attributes (e.g., gender, age, skin color, lighting and pose) whereas it is unclear what attributes are encoded by the later ones since editing did not result in clear perceptual changes.

3.4 NEURAL ENCODING

Neural encoding predicted the brain activity from the eight (feature) layers from Alexnet, Vgg16 and the StyleGAN3 discriminator (i.e., $3 \times 8 = 24$ encoding models in total). Encoding performance was assessed by correlating the predicted and recorded responses (Student's t-test) after which the model layer with the highest performance was assigned to each recording site on the brain (Figure 7A). In line with a body of literature (Yamins et al., 2014; Cadieu et al., 2014; Khaligh-Razavi & Kriegeskorte, 2014; Güçlü & van Gerven, 2015; Yamins & DiCarlo, 2016; Cichy et al., 2016; Eickenberg et al., 2017), our results show a complexity gradient from early to deeper brain areas. That is, V1 (early region) encodes more simple features (e.g., edges and contrasts) from early model layers whereas IT (deeper region) encodes more complex features (e.g., entire objects) from deeper model layers. The performance of the encoding models was good overall (Figure 7B).

3.5 WALKING THE NEURAL FACE MANIFOLD VIA W-LATENT SPACE

Manifold hypothesis states that real-world data instances can be viewed as points in high-dimensional space that are concentrated on manifolds which (locally) resemble Euclidean space. Linear changes in the (low-dimensional) GAN latent landscape directly translate to the corresponding (high-dimensional) pixel space and thus approximate local manifolds (Shao et al., 2018). That is, visual data that look perceptually similar in terms of certain features are also closely positioned in latent space. In accordance, spherical interpolation between two distinct latent vectors results in

Figure 6: **Attribute similarity.** In total, we computed 512 attribute scores by taking the inner product between a w-latent underlying a face and a latent semantic as obtained by SeFa. Attribute similarity is then defined as the correlation (Student's t-test) between attribute scores of stimuli and those of their reconstructions. **A.** Histograms of 512 correlations is skewed to the right. The vertical dashed line denotes the median. **B.** The 512 latent semantics (x-axis) and their correlation coefficients (r) are sorted from high to low (significant denoted in blue). **C.** The six latent semantics with the highest attribute similarity are taken and the attribute scores of predicted (x-axis) and ground-truth w-latent (y-axis) are displayed together with the correlation coefficient slope. **D.** To reveal what facial attributes a latent semantic encodes, we traveled in the semantic direction by face editing; the latent semantic was subtracted of or added to an arbitrary w-latent and reconstructed the corresponding face image. For instance, when the first semantic boundary in **C.** is subtracted from a w-latent, the corresponding face changes pose to the left and becomes younger whereas its pose changes to the right and gets older when this semantic is added.

Figure 7: **A.** Layer assignment across all brain channels and the visual areas V1, V4 and IT. **B.** Performance of all 24 encoding models (x-axis) in terms of correlation (Student's t-test, y-axis) between all predicted and recorded brain responses.

Figure 8: In both A. and B., linear operations are applied to ground-truth w-latents (row 1), w-latents decoded from brain activity (row 2), recorded responses which we then decoded into a w-latent (row 3) and encoded responses (using our kernel ridge encoder) from ground-truth w-latents which we then decoded back into a w-latent (using our linear decoder). This figure shows the resulting faces generated from the w-latents. **A.** Linear interpolation between two w-latents from the test set. **B.** Vector arithmetic with the average w-latent of specific facial attributes. To obtain the average w-latent we averaged as many relevant samples as possible from the test set.

an ordered set of latents where contained semantics in the corresponding images vary gradually with latent code. Note that we used spherical rather than regular linear interpolation to account for the spherical geometry of the latent space (i.e., multimodal Gaussian distribution). The latent space also obeys simple arithmetic operations (Mikolov et al., 2013). We found that the generated faces from latents after application of spherical interpolation (Figure 8A) and vector arithmetic (Figure 8B) on brain responses were perceptually similar as when applied directly to the w-latents. This indicates that the functional neural face manifold and the w-latent space are organized similarly such that brain responses can be spherically/linearly modified to obtain the brain responses to unseen faces.

4 DISCUSSION

We showed that neural decoding of brain activity during visual perception via the intermediate w-latent space conditioned on StyleGAN3 resulted in image reconstructions that strongly resemble the originally-perceived stimuli, making it the state-of-the-art in neural decoding. Although it is safe to assume that the brain represents the visual stimuli it is presented with, it has been largely unsolved *how* it represents them as there are virtually infinite candidate representations possible to encode the same image. The goal of this study was to find the correct representation. Our results demonstrate that StyleGAN3 features/latents are linearly related to brain responses such that latent and response must encode the same real-world phenomena similarly. This indicates that StyleGAN3 successfully disentangled the neural face manifold (DiCarlo & Cox, 2007) rather than the conventional z-latent space of arbitrary GANs or any other feature representation we encountered so far. Note that Style-GAN3 has never been optimized on neural data. The StyleGAN3-brain correspondence can shed light on what drives the organization of (neural) information processing in vision. For instance, the analogy between adversarial training of StyleGAN3 and predictive coding where the brain is continuously generating and updating its mental model of the world to minimize prediction errors. To conclude, unsupervised generative modeling can be used to study biological vision which in turn supports the development of better computational models thereof and other (clinical) applications.

5 ETHICS STATEMENT

In conjunction with the evolving field of neural decoding grows the concern regarding mental privacy. Because we think it is likely that access to subjective experience will be possible in the foreseeable future, we want to emphasize that it is important to at all times strictly follow the ethical rules and regulations regarding data extraction, storage and protection. It should never be possible to invade subjective contents of the mind.

6 REPRODUCIBILITY STATEMENT

Upon publication, we will make our data publicly available together with the code and a detailed description on how to recreate our results to ensure transparency and reproducibility.

REFERENCES

Pouya Bashivan, Kohitij Kar, and James J DiCarlo. Neural population control via deep image synthesis. *Science*, 364(6439), 2019.

Andrew Brock, Jeff Donahue, and Karen Simonyan. Large scale gan training for high fidelity natural image synthesis. *arXiv preprint arXiv:1809.11096*, 2018.

Charles F Cadieu, Ha Hong, Daniel LK Yamins, Nicolas Pinto, Diego Ardila, Ethan A Solomon, Najib J Majaj, and James J DiCarlo. Deep neural networks rival the representation of primate it cortex for core visual object recognition. *PLoS computational biology*, 10(12):e1003963, 2014.

Le Chang and Doris Y Tsao. The code for facial identity in the primate brain. *Cell*, 169(6):1013–1028, 2017.

Radoslaw Martin Cichy, Aditya Khosla, Dimitrios Pantazis, Antonio Torralba, and Aude Oliva. Comparison of deep neural networks to spatio-temporal cortical dynamics of human visual object recognition reveals hierarchical correspondence. *Scientific reports*, 6(1):1–13, 2016.

Thirza Dado, Yağmur Güçlütürk, Luca Ambrogioni, Gabriëlle Ras, Sander Bosch, Marcel van Gerven, and Umut Güçlü. Hyperrealistic neural decoding for reconstructing faces from fmri activations via the gan latent space. *Scientific reports*, 12(1):1–9, 2022.

James J DiCarlo and David D Cox. Untangling invariant object recognition. *Trends in cognitive sciences*, 11(8):333–341, 2007.

Nadine Dijkstra, S.E. Sander E. Bosch, and Marcel A.J. M.A.J. van Gerven. Shared neural mechanisms of visual perception and imagery. *Trends in Cognitive Sciences*, 23(5):423–434, 2019. ISSN 1879307X. doi: 10.1016/j.tics.2019.02.004. URL https://doi.org/10.1016/j.tics.2019.02.004.

Michael Eickenberg, Alexandre Gramfort, Gaël Varoquaux, and Bertrand Thirion. Seeing it all: Convolutional network layers map the function of the human visual system. *NeuroImage*, 152:184–194, 2017.

Winrich A Freiwald and Doris Y Tsao. Functional compartmentalization and viewpoint generalization within the macaque face-processing system. *Science*, 330(6005):845–851, 2010.

Ian Goodfellow, Jean Pouget-Abadie, Mehdi Mirza, Bing Xu, David Warde-Farley, Sherjil Ozair, Aaron Courville, and Yoshua Bengio. Generative adversarial nets. *Advances in neural information processing systems*, 27, 2014.

Charles G Gross, CE de Rocha-Miranda, and DB Bender. Visual properties of neurons in inferotemporal cortex of the macaque. *Journal of neurophysiology*, 35(1):96–111, 1972.

Umut Güçlü and Marcel AJ van Gerven. Unsupervised feature learning improves prediction of human brain activity in response to natural images. *PLoS computational biology*, 10(8):e1003724, 2014.

Umut Güçlü and Marcel AJ van Gerven. Deep neural networks reveal a gradient in the complexity of neural representations across the ventral stream. *Journal of Neuroscience*, 35(27):10005–10014, 2015.

Yağmur Güçlütürk, Umut Güçlü, Katja Seeliger, Sander Bosch, Rob van Lier, and Marcel A van Gerven. Reconstructing perceived faces from brain activations with deep adversarial neural decoding. *Advances in neural information processing systems*, 30, 2017.

John-Dylan Haynes and Geraint Rees. Decoding mental states from brain activity in humans. *Nature reviews neuroscience*, 7(7):523–534, 2006.

Tomoyasu Horikawa and Yukiyasu Kamitani. Generic decoding of seen and imagined objects using hierarchical visual features. *Nature communications*, 8(1):1–15, 2017a.

Tomoyasu Horikawa and Yukiyasu Kamitani. Hierarchical neural representation of dreamed objects revealed by brain decoding with deep neural network features. *Frontiers in computational neuroscience*, 11:4, 2017b.

David H Hubel and Torsten N Wiesel. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of physiology*, 160(1):106–154, 1962.

Chou P Hung, Gabriel Kreiman, Tomaso Poggio, and James J DiCarlo. Fast readout of object identity from macaque inferior temporal cortex. *Science*, 310(5749):863–866, 2005.

Yukiyasu Kamitani and Frank Tong. Decoding the visual and subjective contents of the human brain. *Nature neuroscience*, 8(5):679–685, 2005.

Tero Karras, Timo Aila, Samuli Laine, and Jaakko Lehtinen. Progressive growing of gans for improved quality, stability, and variation. *arXiv preprint arXiv:1710.10196*, 2017.

Tero Karras, Samuli Laine, and Timo Aila. A style-based generator architecture for generative adversarial networks. In *Proceedings of the IEEE/CVF Conference on Computer Vision and Pattern Recognition*, pp. 4401–4410, 2019.

Tero Karras, Samuli Laine, Miika Aittala, Janne Hellsten, Jaakko Lehtinen, and Timo Aila. Analyzing and improving the image quality of stylegan. In *Proceedings of the IEEE/CVF Conference on Computer Vision and Pattern Recognition*, pp. 8110–8119, 2020.

Tero Karras, Miika Aittala, Samuli Laine, Erik Härkönen, Janne Hellsten, Jaakko Lehtinen, and Timo Aila. Alias-free generative adversarial networks. *Advances in Neural Information Processing Systems*, 34, 2021.

Seyed-Mahdi Khaligh-Razavi and Nikolaus Kriegeskorte. Deep supervised, but not unsupervised, models may explain it cortical representation. *PLoS computational biology*, 10(11):e1003915, 2014.

Nikolaus Kriegeskorte. Deep neural networks: a new framework for modeling biological vision and brain information processing. *Annual review of vision science*, 1:417–446, 2015.

Alex Krizhevsky. One weird trick for parallelizing convolutional neural networks. *arXiv preprint arXiv:1404.5997*, 2014.

Tomas Mikolov, Ilya Sutskever, Kai Chen, Greg S Corrado, and Jeff Dean. Distributed representations of words and phrases and their compositionality. *Advances in neural information processing systems*, 26, 2013.

Omkar M. Parkhi, Andrea Vedaldi, and Andrew Zisserman. Deep face recognition. In Xianghua Xie, Mark W. Jones, and Gary K. L. Tam (eds.), *Proceedings of the British Machine Vision Conference (BMVC)*, pp. 41.1–41.12. BMVA Press, September 2015. ISBN 1-901725-53-7. doi: 10.5244/C.29.41. URL https://dx.doi.org/10.5244/C.29.41.

Hang Shao, Abhishek Kumar, and P Thomas Fletcher. The riemannian geometry of deep generative models. In *Proceedings of the IEEE Conference on Computer Vision and Pattern Recognition Workshops*, pp. 315–323, 2018.

Guohua Shen, Kshitij Dwivedi, Kei Majima, Tomoyasu Horikawa, and Yukiyasu Kamitani. End-to-end deep image reconstruction from human brain activity. *Frontiers in Computational Neuroscience*, pp. 21, 2019a.

Guohua Shen, Tomoyasu Horikawa, Kei Majima, and Yukiyasu Kamitani. Deep image reconstruction from human brain activity. *PLoS computational biology*, 15(1):e1006633, 2019b.

Yujun Shen and Bolei Zhou. Closed-form factorization of latent semantics in gans. In *Proceedings of the IEEE/CVF Conference on Computer Vision and Pattern Recognition*, pp. 1532–1540, 2021.

Ghislain St-Yves and Thomas Naselaris. Generative adversarial networks conditioned on brain activity reconstruct seen images. In *2018 IEEE international conference on systems, man, and cybernetics (SMC)*, pp. 1054–1061. IEEE, 2018.

Hans Super and Pieter R Roelfsema. Chronic multiunit recordings in behaving animals: advantages and limitations. *Progress in brain research*, 147:263–282, 2005.

L.G. Ungerleider and M. Mishkin. Two cortical visual systems. In *Analysis of visual behavior*, pp. 549–586–. MIT Press, Cambridge, MA, 1982.

Marcel AJ van Gerven. A primer on encoding models in sensory neuroscience. *Journal of Mathematical Psychology*, 76:172–183, 2017.

Rufin VanRullen and Leila Reddy. Reconstructing faces from fmri patterns using deep generative neural networks. *Communications biology*, 2(1):1–10, 2019.

Zhou Wang, Alan C Bovik, Hamid R Sheikh, and Eero P Simoncelli. Image quality assessment: from error visibility to structural similarity. *IEEE transactions on image processing*, 13(4):600–612, 2004.

Max Welling. Kernel ridge regression. *Max Welling's classnotes in machine learning*, pp. 1–3, 2013.

Daniel LK Yamins and James J DiCarlo. Using goal-driven deep learning models to understand sensory cortex. *Nature neuroscience*, 19(3):356–365, 2016.

Daniel LK Yamins, Ha Hong, Charles F Cadieu, Ethan A Solomon, Darren Seibert, and James J DiCarlo. Performance-optimized hierarchical models predict neural responses in higher visual cortex. *Proceedings of the national academy of sciences*, 111(23):8619–8624, 2014.

Alan Yuille and Daniel Kersten. Vision as bayesian inference: analysis by synthesis? *Trends in cognitive sciences*, 10(7):301–308, 2006.