bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

The development of transformation tolerant visual representations differs between the human brain and convolutional neural networks

Yaoda Xu[1] and Maryam Vaziri-Pashkam[2]

[1]Yale University, [2]National Institute of Mental Health

Corresponding Author: Yaoda Xu, Department of Psychology, Yale University, New Haven, CT 06520. Phone: 203-843-6718. Email: xucogneuro@gmail.com

Keywords: Visual object representation, tolerance, fMRI, convolutional neural networks, representational similarity

Acknowledgement: We thank Martin Schrimpf for help implementing CORnet-S, JohnMark Tayler for extracting the features from the three Resnet-50 models trained with the stylized images, and Thomas O'Connell, Brian Scholl, JohnMark Taylor and Nick Turk-Brown for helpful discussions and feedback on the results. This research was supported by National Institute of Health Grants (1R01EY030854 and 1R01EY022355) to Y.X.

Author contributions: The fMRI data used here were from two prior publications (Vaziri-Pashkam & Xu, 2019; Vaziri-Pashkam et al., 2019), with MV-P and YX designing the fMRI experiments and MV-P collecting and analyzing the fMRI data. YX conceptualized the present study and performed all the analyses reported here. YX wrote the manuscript with comments from MV-P.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Abstract

Existing single cell neural recording findings predict that, as information ascends the visual processing hierarchy in the primate brain, the relative similarity among the objects would be increasingly preserved across identity-preserving image transformations. Here we confirm this prediction and show that object category representational structure becomes increasingly invariant across position and size changes as information ascends the human ventral visual processing pathway. Such a representation, however, is not found in 14 different convolutional neural networks (CNNs) trained for object categorization that varied in architecture, depth and the presence/absence of recurrent processing. CNNs thus do not appear to form or maintain brain-like transformation-tolerant object identity representations at higher levels of visual processing despite the fact that CNNs may classify objects under various transformations. This limitation could potentially contribute to the large number of training data required to train CNNs and their limited ability to generalize to objects not included in training.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Introduction

We can easily recognize a car no matter where it appears in the visual environment, how far it is from us, and which way it is facing. The ability to extract object identity information among changes of non-identity information and form transformation-tolerant object representation allows us to rapidly recognize an object under different viewing conditions in the real world. This ability has been hailed as one of the hallmarks of primate high-level vision (DiCarlo & Cox, 2007; DiCarlo et al., 2012; Tacchetti et al., 2018). From a computational prospective, rectifying object representations with respect to all transformations or, equivalently, if the representations themselves were transformation invariant, reduces the complexity of learning by requiring much fewer training examples and improves generalization to objects and categories not included in training (Tacchetti et al., 2018).

Recent hierarchical convolutional neural networks (CNNs) have achieved human-like object categorization performance and are able to identify objects across a variety of identity preserving (sometimes quite challenging) image transformations (Yamins & Dicarlo, 2016; Kheradpisheh et al., 2016; Rajalingham, et al., 2018; Kriegeskorte, 2015; Serre, 2019). This has led to the thinking that CNNs likely form transformation-tolerant object representations in their final stages of visual processing similar to those seen in the primate brain (Hong et al., 2016; Yamins & Dicarlo, 2016; Tacchetti et al., 2018). CNNs incorporate the known architectures of the primate early visual areas and then repeat this design motif multiple times. Although the detailed neural mechanisms governing high-level primate vision remain largely unknow, CNNs' success in object categorization under image transformations has generated the excitement that perhaps the algorithms essential to high-level primate vision would automatically emerge in CNNs to provide us with a shortcut to understand and model high-level vision. While CNNs are capable of associating the same label to an object undergoing different transformations, CNNs could succeed by simply grouping all instances of an object encountered during training under the same

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

label without necessarily forming transformation-tolerant object representations like those found in high-level primate vision. Indeed, CNNs can achieve a near perfect classification accuracy even when image labels were randomly shuffled (Zhang et al. 2016), demonstrating their ability to memorize associations between images and random class labels. While this is one way to solve the invariance problem, this type of representation requires a large number of training data and has a limited ability to generalize to objects not included in training. Coincidentally, these two limitations have been argued to be the two major drawbacks associated with the current CNNs (Serre, 2019), raising the possibility that current CNNs may not actually form brain-like transformation-tolerant object representations in their final stages of visual processing.

At the neuronal level, a defining signature of transformation-tolerant object representation is a neuron's ability to maintain its relative selectivity (rank-order) for different objects across transformations even though the absolute neuronal responses might rescale with each state of a transformation (Schwartz et al., 1983; Tovee et al., 1994; Ito et al., 1995; DiCarlo & Manusell, 2003; Brincat & Connor, 2004; DiCarlo and Cox, 2007; Li et al., 2009; Murty & Arun, 2017). Such a neuronal response profile would predict that, as tolerance increases, objects and categories should be arranged in increasingly similar order across an identity-preserving image transformation such that two similar objects or categories at one state of a transformation should also be similar at another state of the transformation. This signature of tolerance at the representational structure level, however, has never been tested.

Here we took advantage of existing human fMRI data sets and tested object representational structure invariance across changes in position and size in higher levels of visual processing in the human brain and its development across the human ventral visual processing hierarchy. To increase signal to noise ratio (SNR), we examined the averaged response from multiple exemplars of an object category rather than the response of a single exemplar. The results from the human brain were then compared with those from 14 different CNNs

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

trained to perform object categorization with varying architecture, depth and the presence/absence of recurrent processing. This allowed us to directly test whether a similar representational scheme existed in both the human brain and CNNs. We found that while the relative similarity among object categories becomes more invariant across changes in position and size during information processing in human ventral visual regions, the development of such invariance, however, was not found in CNNs trained for object categorization. CNNs thus do not appear to form transformation-tolerant object representation like the human brain does in higher levels of visual processing.

Results

In two fMRI experiments, human participants viewed blocks of sequentially presented object images. Each image block contained different exemplars from the same object category. A total of eight real-world object categories were used, including bodies, cars, cats, chairs, elephants, faces, houses, and scissors (Vaziri-Pashkam & Xu, 2019; see Figure 1a). These object images were shown in two types of transformations: position (top vs bottom) and size (small vs large) (Figure 1b). To ensure that object identity representation in lower brain regions would reflect the representation of identity and not low-level differences among the images of the different categories, both experiments used controlled images with the spectrum, histogram, and intensity of the images normalized and equalized across the different categories (Willenbockel et al., 2010).

We examined fMRI responses from independently defined human early visual areas V1 to V4 and higher visual object processing regions LOT and VOT (Figure 1c). Reponses in LOT and VOT have been shown to correlate with successful visual object detection and identification (Grill-Spector et al. 2000; Williams et al., 2007) and their lesions have been linked to visual object agnosia (Goodale et al.,1991; Farah, 2004). These two regions have been argued to be the homologue of the macaque IT (Orban et al., 2004). For a given brain region, fMRI response patterns were extracted for each category for each type of transformations. Within each state of a given transformation (e.g., the upper

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Figure 1

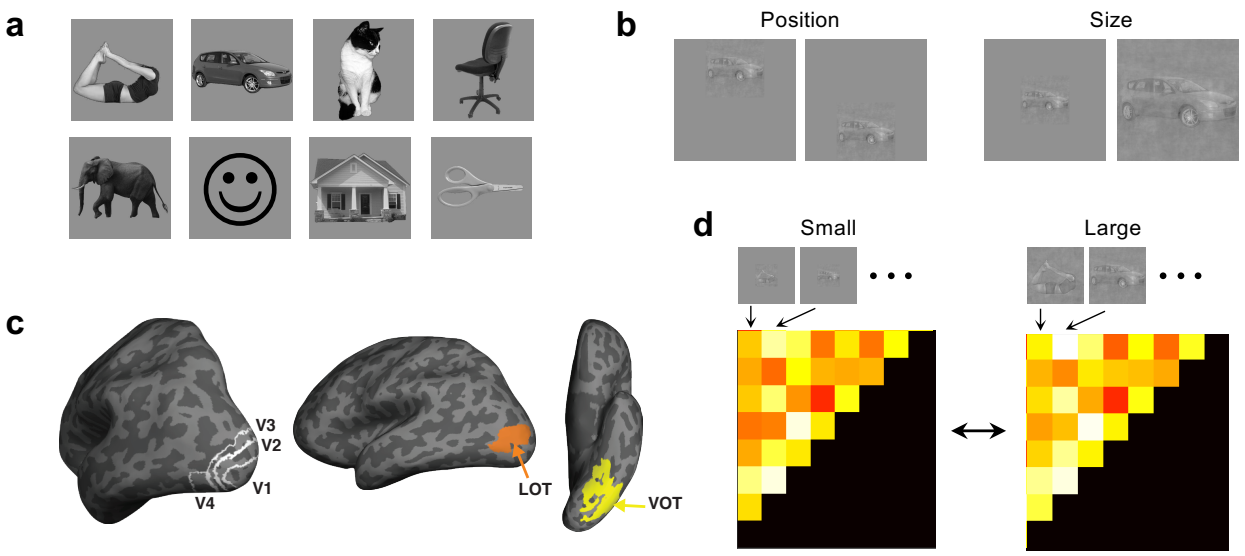


Figure 1. **a.** The eight real-world object categories used. **b.** The two types of nonidentity transformations examined: position (top vs bottom) and size (small vs large). To ensure that object identity representation in lower brain regions would reflect the representation of identity and not low-level differences among the images of the different categories, both experiments used controlled images with the spectrum, histogram, and intensity of the images normalized and equalized across the different category. **c.** The brain regions examined. They included topographically defined early visual areas V1 to V4 and functionally defined higher object processing regions LOT and VOT. **d.** The representational similarity analysis used to compare the representational structural between the two states of a nonidentity transformation (using size transformation as an example). In this approach, for a given brain region or a sampled CNN layer, a representation dissimilarity matrix was first formed by computing all the pairwise Euclidean distances of fMRI response patterns or the CNN output for all the object categories in one state of the transformation. The off-diagonal elements of this matrix were then used to form a representational dissimilarity vector. These dissimilarity vectors were correlated between the two states of the transformation to assess the similarity between the two.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

position), we calculated pairwise Euclidean distances of the z-normalized fMRI response patterns for all the object categories to construct a category representational dissimilarity matrix (RDM, Kriegeskorte & Kievit, 2013, see Figure 1d). We then correlated these RDMs between the two states of each transformation using Spearman rank correlation. These correlations were corrected by the reliability of each brain region before the results were compared across brain regions (see Methods).

For both position and size transformations, RDM correlation across the two states of each transformation linearly increased from lower to higher visual regions (the averaged linear correlation coefficients were .40 and .61, respectively for position and size, and both were greater than 0, $t(6) = 2.42$, $p = 0.026$ for position, and $t(6) = 4.11$, $p = 0.003$ for size; all t-tests were one-tailed as the effects were tested for a specific direction). Additionally, correlations were higher between the average of LOT and VOT than the average of V1 to V3 for both position and size ($t(6) = 2.59$, $p = 0.021$ for position; and $t(6) = 3.41$, $p = 0.007$ for size; the difference between LOT and VOT and those among V1 to V3 were not significant, all $Fs < 1.31$, $ps > .29$; see Figure 2a). Thus, for both position and size transformation, object representational structure becomes increasingly invariant from lower to higher ventral visual regions. These results remain the same whether z-normalized Euclidean distance measure or correlation measure was used, and remained qualitatively similar even when Pearson correlation, rather than Spearman rank correlation, was applied (see Supplemental Figure 1).

We next examined whether CNNs exhibit a similar pattern in RDM correlation across the two states of each transformation from lower to higher layers. The 14 CNNs we examined included both shallower networks, such as Alexnet, VGG16 and VGG 19, and deeper networks, such as Googlenet, Inception-v3, Resnet-50 and Resnet-101 (Supplemental Table 1). We also included a recurrent network, Cornet-S, that has been shown to capture the recurrent processing in macaque IT cortex with a shallower structure and have

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Figure 2

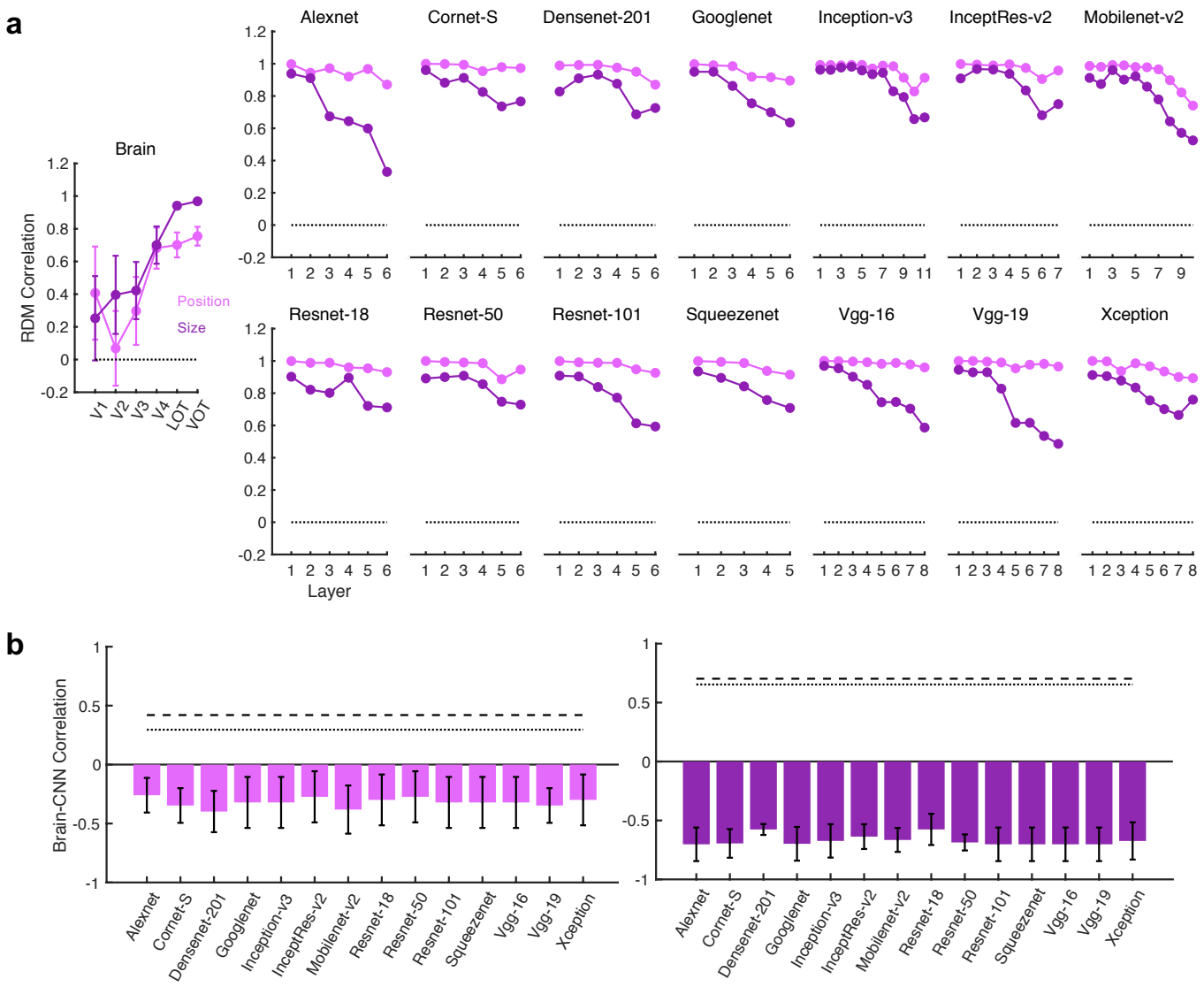


Figure 2. Evaluating object representational structure tolerance during the course of visual processing in the human brain and 14 different CNNs. **a.** Correlating the object representational structures across the two states of position and size transformations within each human ventral brain regions and each sampled layer of the 14 different CNNs using Spearman rank correlation. Results from the brain regions were corrected by the reliability of each region (see Methods). **b.** Response profile correlation between the brain and each CNN plotted against the upper and lower bound of the noise ceiling of the brain response reliability across human participants. While object representational structure becomes increasingly invariant from lower to higher levels of visual processing in the human brain, it becomes more variant from lower to higher CNN layers, with all CNN response profiles showing negative correlation with that of the brain.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

been argued to be the current best model of the primate ventral visual processing regions (Kubilius et al., 2019; Kar et al., 2019). All CNNs were pretrained with ImageNet images (Deng et al., 2009). Following a previous study (O'Connor et al., 2018), we sampled from 6 to 11 mostly pooling layers of each CNN (see Supplemental Table 1 for the specific CNN layers sampled). We extracted the response from each sampled CNN layer for each exemplar of a category and then averaged the responses from the different exemplars to generate a category response for each state of a given transformation, similar to how an fMRI category response was extracted.

Despite differences in the exact architecture, depth, and presence/absence of recurrent processing, all CNNs exhibited overall similar trajectories for a given transformation. For position change, all CNNs showed overall high RDM correlation to position change but with a downward trend from lower to higher layers (Figure 2a). Given the heavy use of convolution in CNN architecture to capture translational invariance (LeCun, 1989), the high RDM correlation to position change is expected; however, the downward trend across layers is not. This downward trend became much more prominent for size change, going from 1 to dropping below .8 from lower to higher layers across all the CNNs (in a number of CNNs the correlation dropped below .4), while the same correlation went from .2 to close to 1 from lower to higher brain regions (Figure 2a). Direct correlation of the response profiles (using Spearman rank correlation) revealed negative correlations between the brain and CNNs that were all significantly below the lower bound of the noise ceiling of the brain response across human participants (for position, $ts > 2.62$, $ps < .020$; for size, $ts > 8.41$, $ps < .001$; all t tests were one tailed as only testing for correlation below the lower bound of the noise ceiling was meaningful here; see Figure 2b). Thus, for position and size transformations, the object representational structure became *more variant* from lower to higher CNN layers, the opposite of what was seen in the human brain. Despite CNNs' success in classifying objects under identity preserving image transformations, how CNNs represent the relative similarity among the different objects appears to differ from that of the human

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

brain. The built-in CNN architecture at the earlier layers likely gives it a boost in forming similar object representational structures in early stages of processing compared to visual processing in the brain. However, such a strong invariant representation in CNNs is gradually lost during the course of processing, such that the representations formed at final stages of CNN processing no longer appear to contain object representational structures invariant to these transformations.

Although CNNs are believed to explicitly represent object shapes in the higher layers (Kriegeskorte, 2015; LeCun et al., 2015; Kubilius et al., 2016), emerging evidence suggests that CNNs may mostly use local texture patches to achieve successful object classification (Ballester & de Araújo, 2016, Gatys et al., 2017; Geirhos et al., 2019). However, when Resnet-50 was trained with stylized ImageNet images in which the original texture of every single image was replaced with the style of a randomly chosen painting, object classification performance significantly improved, relied more on shape than texture cues, and became more robust to noise and image distortions (Geirhos et al., 2019). When we compared the representations formed in Resnet-50 pretrained with ImageNet images with those from Resnet-50 pretrained with stylized ImageNet Images under three different training protocols (Geirhos et al., 2019), however, we found overall remarkably similar results in the RDM correlations across the two states of each transformation and all were different from what was seen in the human brain (Supplementary Figure 2). The inability of Resnet-50 to exhibit brain-like invariance in object representational structure across transformations suggests that there are likely fundamental differences between the two that cannot be easily overcome by this type of training.

To further document potential processing differences between object categories and single objects, instead of object categories, we examined CNN representational structure for eight single object images (one from each of the 8 categories used in the fMRI experiments) undergoing the same four types of transformations. Additionally, we tested CNN representations for both the

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

controlled images (as in the fMRI experiments) and the original images. We obtained virtually the same results; if anything, the decrease in invariance was more drastic for the single objects than for the object categories reported earlier (Supplementary Figure 3). The lack of invariance in representational structures at higher levels of CNN visual processing thus applies to both object categories and single objects.

Besides position and size, we also tested two non-Euclidian transformations involving a change in image statistics (original vs controlled images) and the spatial frequency (SF) content of an image (high vs low SF) (see Supplementary Results). We again found an increase in tolerance in object representational structure across these two transformations from lower to higher human visual regions, but not from lower to higher CNN layers (Supplementary Figures 4 to 7).

Discussion

Existing single cell neural recording findings predict that, as information ascends the visual processing hierarchy in the primate brain, the relative similarity among the objects would be increasingly preserved across identity-preserving image transformations. Interestingly, this key prediction has never been directly tested at the population representational structure level. Here we confirm this prediction and show that object category representational structure becomes increasingly invariant across position and size changes as information ascends the human ventral visual processing pathway. Such a representation, however, is not found in 14 different CNNs trained for object categorization. Similar performance was observed for both shallow and deep CNNs (e.g., Alexnet vs Googlenet), and the recurrent CNN did not perform better than the other CNNs. Training a CNN with stylized images did not improve performance either. CNNs thus do not appear to form or maintain brain-like transformation-tolerant object identity representations during the course of visual processing despite the fact that CNNs are largely successful in classifying objects under various transformations.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Although we examined object category responses averaged over multiple exemplars rather than responses to each object in an effort to increase SNR, previous research has shown similar category and exemplar response profiles in macaque IT and human lateral occipital cortex with more robust responses for categories than individual exemplars due to an increase in SNR (Hung et al., 2005; Cichy et al., 2011). Rajalingham, et al. (2018) recently reported better behavior-CNN correspondence at the category but not at the individual exemplar level. Thus, comparing the representational structure at the category level, rather than at the exemplar level, should have increased our chance of finding a close brain-CNN correspondence. In a recent study, for the same sets of real-world categories used here, we showed that the object representational structures formed in lower CNN layers could fully capture those formed in lower human visual processing regions (Xu & Vaziri-Pashkam, 2020). Despite this close brain-CNN correspondence at lower levels of visual processing, the present study shows that none of the CNNs examined here exhibits the same transformation-tolerant object representation in the human brain at higher levels of visual processing. Importantly, our CNN results did not depend on the usage of object categories, as we showed that the lack of invariance in representational structures at higher levels of CNN visual processing applies to both object categories and single objects.

With its vast computing power, CNNs likely associate different instances of an object via a brute force approach (i.e., by simply grouping all instances of an object encountered under the same object label) without preserving the relationships among the objects across transformations and forming (or maintaining) transformation-tolerant object representations. This may contribute to some of the brain-CNN discrepancies reported in prior studies, such as CNNs' ability to fully capture lower, but not higher, levels of visual representational structures of real-world objects as reported in our recent study (Xu & Vaziri-Pashkam, 2020), their ability to explain only about 50% of the response variance of macaque V4 and IT (Cadieu et al., 2014; Yamins et al., 2014; Kar et al. 2019; Bashivan et al., 2019; Bao et al., 2020), their usage of different features in object

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

recognition (Ballester & de Araujo, 2016, Ulman et al., 2016; Gatys et al., 2017; Baker et al., 2018; Geirhos et al., 2019), and their susceptibility to the negative impact of adversarial images (Serre, 2019). While some have regarded CNNs as the current best models of the primate visual system (Khaligh-Razavi & Kriegeskorte, 2014; Güçlü & van Gerven, 2015; Cichy et al., 2016; Eickenberg et al., 2017; Cichy & Kaiser, 2019; Kubilius et al., 2019), the present results show that current CNNs likely differ from the primate visual brain in important ways, especially for high-level vision. Thus repeating the design motif of the primate early visual areas in CNN architecture may not be sufficient to automatically recover the algorithms used by primate high-level vision and such a shortcut as is may be limited in helping us fully understand and model high-level primate vision.

The formation of transformation-tolerant object representations in the primate brain has been argued to be critical in facilitating information processing and learning by reducing the number of training examples needed while at the same time increasing the generalizability from the trained images to new instances of an object and a category (Tacchetti et al., 2018). Even if CNNs were to use a fundamentally different, but equally viable, computational algorithm to solve the object recognition problem compared to the primate brain, implementing transformation tolerant visual representation in their visual processing may nevertheless help overcome the two major drawbacks currently associated with the CNNs: a requirement of large training examples and a limitation in generalizability to objects not included in training (Serre, 2019). That being said, making CNNs more brain like has its own practical advantages: as long as CNNs “see” the world differently from the human brain, they will make mistakes that are against human prediction and intuition. If CNNs are to aid or replace human performance, they need to capture the nature of human vision and then improve upon it. This will ensure the safety and reliability of the devices powered by CNNs, such as in self-driving cars, and, ultimately, our trust in using such an information processing system. Thus, in addition to benchmarking object recognition performance, it may be beneficial for future CNN architectures and/or

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

training regimes to explicitly improve transformation-tolerant object representations at higher levels of CNN visual processing. For example, preserving the similarity structure among the objects across transformations could be incorporated as a routine in CNN training. Doing so may push forward the next leap in model development and make CNNs not only better models for object recognition but also better models of the primate brain.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Materials and Methods

fMRI Experimental Details

Details of the fMRI experiments have been described in a previously published study (Vaziri-Pashkam & Xu, 2019). They are summarized here for the readers' convenience.

Seven healthy human participants with normal or corrected to normal visual acuity, all right-handed, and aged between 18-35 took part in both the position and size experiments. Each experiment was performed in a separate session lasting between 1.5 and 2 hours. Each participant also completed two additional sessions for topographic mapping and functional localizers. MRI data were collected using a Siemens MAGNETOM Trio, A Tim System 3T scanner, with a 32-channel receiver array head coil. For all the fMRI scans, a T2*-weighted gradient echo pulse sequence with TR of 2 sec and voxel size of 3 mm x 3 mm x 3 mm was used. FMRI data were analyzed using FreeSurfer (surfer.nmr.mgh.harvard.edu), FsFast (Dale et al., 1999) and in-house MATLAB codes. FMRI data preprocessing included 3D motion correction, slice timing correction and linear and quadratic trend removal. Following standard practice, a general linear model was then applied to the fMRI data to extract beta weights as response estimates.

In the position experiment, we tested position tolerance and presented images either above or below the fixation (Figure 1b). We used cut-out grey-scaled images from eight real-world object categories (faces, bodies, houses, cats, elephants, cars, chairs, and scissors) and modified them to occupy roughly the same area on the screen (Figure 1a). For each object category, we selected ten exemplar images that varied in identity, pose and viewing angle to minimize the low-level similarities among them. Participants fixated at a central red dot throughout the experiment. Eye-movements were monitored in all the fMRI experiments to ensure proper fixation. During the experiment, blocks of images were shown. Each block contained a random sequential presentation of ten

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

exemplars from the same object category shown either all above or all below the fixation. To equal low-level image differences among the different categories, controlled images were shown. Controlled images were generated by equalizing contrast, luminance and spatial frequency of the images across all the categories using the shine toolbox (Willenbockel et al., 2010, see Figure 1b). All images subtended 2.9º x 2.9º and were shown at 1.56º above the fixation in half of the 16 blocks and the same distance below the fixation in the other half of the blocks. Each image was presented for 200 msec followed by a 600 msec blank interval between the images. Participants detected a one-back repetition of the exact same image. This task engaged participants' attention on the object shapes and ensured robust fMRI responses. Two image repetitions occurred randomly in each image block. Each experimental run contained 16 blocks, one for each of the 8 categories in each of the two image positions. The order of the eight object categories and the two positions were counterbalanced across runs and participants. Each block lasted 8 secs and followed by an 8-sec fixation period. There was an additional 8-sec fixation period at the beginning of the run. Each participant completed one scan session with 16 runs for this experiment, each lasting 4 mins 24 secs.

In the size experiment, we tested size tolerance and presented images either in a large size (5.77º x 5.77º) or small size (2.31º x 2.31º) centered at fixation (Figure 1b). As in the position experiment, controlled images were used here. Half of the 16 blocks contained small images and the other half, large images. Other details of the experiment were identical to that of the position experiment.

We examined responses from independent localized early visual areas V1 to V4 and higher visual processing regions LOT and VOT (Figure 1c). V1 to V4 were mapped with flashing checkerboards using standard techniques (Sereno et al., 1995). Following the detailed procedures described in Swisher et al. (2007) and by examining phase reversals in the polar angle maps, we identified areas V1 to V4 in the occipital cortex of each participant (see also Bettencourt & Xu,

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

2016) (Figure 1C). To identify LOT and VOT, following Kourtzi and Kanwisher (2000), participants viewed blocks of face, scene, object and scrambled object images. These two regions were then defined as a cluster of continuous voxels in the lateral and ventral occipital cortex, respectively, that responded more to the original than to the scrambled object images. LOT and VOT loosely correspond to the location of LO and pFs (Malach et al., 1995; Grill-Spector et al.,1998; Kourtzi & Kanwisher, 2000) but extend further into the temporal cortex in an effort to include as many object-selective voxels as possible in occipito-temporal regions.

To generate the fMRI response pattern for each ROI in a given run, we first convolved an 8-second stimulus presentation boxcar (corresponding to the length of each image block) with a hemodynamic response function to each condition; we then conducted a general linear model analysis to extract the beta weight for each condition in each voxel of that ROI. These voxel beta weights were used as the fMRI response pattern for that condition in that run. Following Tarhan and Konkle (2019), we selected the top 75 most reliable voxels in each ROI for further analyses. This was done by splitting the data into odd and even halves, averaging the data across the runs within each half, correlating the beta weights from all the conditions between the two halves for each voxel, and then selecting the top 75 voxels showing the highest correlation. This is akin to including the best units in monkey neurophysiological studies. For example, Cadieu et al. (2014) only selected a small subset of all recorded single units for their brain-CNN analysis. We obtained the fMRI response pattern for each condition from the 75 most reliable voxels in each ROI of each run. We then averaged the fMRI response patterns within each half of the runs and applied z-normalization to the averaged pattern for each condition in each ROI to remove amplitude differences between conditions and ROIs before further analyses were carried out (see more below).

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

CNN details

We included 14 CNNs in our analyses (see Supplemental Table 1). They included both shallower networks, such as Alexnet, VGG16 and VGG 19, and deeper networks, such as Googlenet, Inception-v3, Resnet-50 and Resnet-101. We also included a recurrent network, Cornet-S, that has been shown to capture the recurrent processing in macaque IT cortex with a shallower structure (Kubilius et al., 2019; Kar et al., 2019). This CNN has been recently argued to be the current best model of the primate ventral visual processing regions (Kar et al., 2019). All the CNNs used were trained with ImageNet images (Deng et al., 2009).

To understand how the specific training images would impact CNN representations, besides CNNs trained with ImageNet images, we also examined Resnet-50 trained with stylized ImageNet images (Geirhos et al., 2019). We examined the representations formed in Resnet-50 pretrained with three different procedures (Geirhos et al., 2019): trained only with the stylized ImageNet Images (RN50-SIN), trained with both the original and the stylized ImageNet Images (RN50-SININ), and trained with both sets of images and then fine-tuned with the stylized ImageNet images (RN50-SININ-IN).

Following O'Connor et al. (2018), we sampled between 6 and 11 mostly pooling and FC layers of each CNN (see Supplemental Table 1 for the specific CNN layers sampled). Pooling layers were selected because they typically mark the end of processing for a block of layers before information is pooled and passed on to the next block of layers. When there were no obvious pooling layers present, the last layer of a block was chosen. For a given CNN layer, we extracted the CNN layer output for each object image in a given condition, averaged the output from all images in a given category for that condition, and then z-normalized the responses to generate the CNN layer response for that object category in that condition (similar to how fMRI category responses were extracted). Cornet-S and the different versions of Resnet-50 were implemented

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

in Python. All other CNNs were implemented in Matlab. Output from all CNNs were analyzed and compared with brain responses using Matlab.

Comparing the representational structures between two states of a transformation in the brain and CNNs

Due to differences in measurement noise across the different brain regions, even if the representational structures were identical for the two states of a given transformation, the correlation between the two could vary across brain regions. To account for this potential variability across brain regions, we used a split-half approach by splitting the data into odd and even halves and averaging the data within each half. To determine the extent to which object category representations were similar between the two states of each transformation in a brain region, within each half of the data, we first obtained the category dissimilarity vector for each of the two states of a given transformation. This was done by computing all pairwise Euclidean distances for the object categories sharing the same state of a transformation and then taking the off-diagonal values of this representation dissimilarity matrix (RDM) as the category dissimilarity vector. We then correlated the category dissimilarity vectors across the two states of a given transformation across the two halves of the data using Spearman rank correlation and took the average as the raw RDM correlation (e.g., correlating odd run upper position with even run lower position and vice versa, and then taking the average of these two correlations). We calculated the reliability of RDM correlation by correlating the category dissimilarity vectors within the same state of a given transformation across the two halves of the data using Spearman rank correlation and took the average as the reliability measure (e.g., correlating odd run upper position with even run upper position and correlating odd run lower position with even run lower position, and then taking the average of these two correlations). The final corrected RDM correlation was computed as the raw RDM correlation divided by the corresponding reliability measure. This was done separately for each ROI of each participant. Occasionally the absolute value of the reliability measure was lower than that of

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

the raw RDM correlation, yielding the corrected RDM correlation to be outside the range of [-1, 1]. Since correlation should not exceed the range of [-1, 1], any values exceeding the range were replaced by the closest boundary value (1 or -1). Without such a correction we obtained very similar line plots as those shown in Figure 2, but with a few large error bars due to a few excessively large values obtained during the RDM normalization process.

To determine the extent to which object category representations were similar between the two states of each transformation in a CNN layer, from the CNN layer output, we first generated the object category dissimilarity vector for each state of a given transformation. We then correlated these vectors between the two states of the transformation using Spearman rank correlation. This was done for each sampled layer of each CNN.

To assess the similarity between the brain and CNN in their overall cross-transformation RDM correlation profile across regions/layers, we directly correlated the two using Spearman rank correlation. Before doing so, we first obtained the reliability of the RDM correlation profile across the group of human participants by calculating the lower and upper bounds of the noise ceiling following the procedure described by Nili et al. (2014). Specifically, the upper bound of the noise ceiling was established by taking the average of the Spearman correlation coefficients between each participant's RDM correlation profile and the group average RDM correlation profile including all participants, whereas the lower bound of the noise ceiling was established by taking the average of the Spearman correlation coefficients between each participant's RDM correlation profile and the group average RDM correlation profile excluding that participant. To evaluate the similarity in RDM correlation profile between the brain and a given CNN, we obtained the Spearman correlation coefficient between the CNN and each human participant and tested these values against the lower bound of the noise ceiling obtained earlier using a one-tailed *t* test. When the number of layers sampled in a CNN did not match the number of brain regions tested, bilinear inteprelation was used to down sample the CNN profile to

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

match with that of the brain. This allowed us to preserve the overall response profile of the CNN while still being able to carry out our correlation analysis. One-tailed *t* tests were used here as only testing values below the lower bound of the noise ceiling was meaningful here. If a CNN was able to fully capture the RDM correlation profile of the human brain, then its RDM correlation profile with the brain should be no different or exceed the lower bound of the noise ceiling.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

References

Baker N, Lu H, Erlikhman G, Kellman PJ (2018) Deep convolutional networks do not classify based on global object shape. PLOS Comput Biol 14:e1006613.

Ballester, P, de Araújo RM (2016) On the Performance of GoogLeNet and AlexNet Applied to Sketches. In AAAI (pp. 1124-1128).

Bao P, She L, McGill M, Tsao DY (2020) A map of object space in primate inferotemporal cortex. Nature https://doi.org/10.1038/s41586-020-2350-5.

Bashivan P, Kar K, DiCarlo JJ (2019) Neural population control via deep image synthesis. Science 364:eaav9436.

Benjamini Y, Hochberg Y (1995) Controlling the False Discovery Rate - a Practical and Powerful Approach to Multiple Testing. J Roy Stat Soc B Met 57:289-300.

Bettencourt KC, Xu Y (2016) Understanding location- and feature-based processing along the human intraparietal sulcus. J Neurophysiol 116:1488–97.

Brincat SL, Connor CE (2004) Underlying principles of visual shape selectivity in posterior inferotemporal cortex. Nat Neurosci 7:880-886.

Cadieu CF, Hong H, Yamins DLK, Pinto N, Ardila D, et al. (2014) Deep neural networks rival the representation of primate IT cortex for core visual object recognition. PLOS Comput Biol 10:e1003963.

Carlson T, Hogendoorn H, Fonteijn H, Verstaten FAJ (2011) Spatial coding and invariance in object-selective cortex. Cortex 47:14-22.

Cichy RM, Chen Y, Haynes JD (2011) Encoding the identity and location of objects in human LOC. Neuroimage 54:2297-2307.

Cichy RM, Sterzer P, Heinzle J, Elliott LT, Ramirez F, Haynes JD (2013) Probing principles of large-scale object representation: Category Preference and location encoding. Hum Brain Mapp 34:1636-1651.

Cichy RM, Khosla A, Pantazis D, Torralba A, Oliva A (2016) Comparison of deep neural networks to spatiotemporal cortical dynamics of human visual object recognition reveals hierarchical correspondence. Sci Rep 6:27755.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Cichy RM, Kaiser D (2019) Deep neural networks as scientific models. Trends Cogn Sci 23:305-317.

Dale AM, Fischl B, Sereno MI (1999) Cortical surface-based analysis. I. Segmentation and surface reconstruction. Neuroimage 9:179-194.

Deng J, Dong W, Socher R, Li LJ, Li K, Fei-Fei L (2009) ImageNet: A largescale hierarchical image database. In IEEE conference on computer vision and pattern recognition. CVPR (pp. 248–255).

DiCarlo JJ, Cox DD (2007) Untangling invariant object recognition. Trends Cogn Sci 11: 333–341.

DiCarlo JJ, Zoccolan D, Rust RC (2012) How does the brain solve visual object recognition? Neuron 73:415-434.

DiCarlo JJ, Manusell JHR (2003) Anterior inferotemporal neurons of monkeys engaged in object recognition can be highly sensitive to object retinal position. J Neurophysiol 89:3264-3278.

Eickenberg M, Gramfort A, Varoquaux G, Thirion B (2017) Seeing it all: Convolutional network layers map the function of the human visual system. NeuroImage 152:184–94.

Farah MJ (2004) Visual agnosia. Cambridge, Mass.: MIT Press.

Gatys LA, Ecker AS, Bethge M (2017) Texture and art with deep neural networks. Curr Opin Neurobiol 46:178–86.

Geirhos R, Rubisch P, Michaelis C, Bethge M, Wichmann FA, Bren-del W (2019) ImageNet-trained CNNs are biased towards texture; increasing shape bias improves accuracy and robustness. In International Conference on Learning Representations.

Goodale MA, Milner AD, Jakobson LS, Carey DP (1991) A neurological dissociation between perceiving objects and grasping them. Nature 349:154–156.

Grill-Spector K, Kushnir T, Hendler T, Malach R (2000) The dynamics of object-selective activation correlate with recognition performance in humans. Nat Neurosci 3:837-843.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Grill-Spector K, Kushnir T, Edelman S, Itzchak Y, Malach R (1998) Cue-invariant activation in object-related areas of the human occipital lobe. Neuron 21:191-202.

Grill-Spector K, Kushnir T, Edelman S, Avidan G, Itzchak Y, Malach R (1999) Differential processing of objects under various viewing conditions in the human lateral occipital complex. Neuron 24:187-203.

Güçlü U, van Gerven MAJ (2017) Increasingly complex representations of natural movies across the dorsal stream are shared between subjects. NeuroImage 145:329–36.

Hong H, Yamins DLK, Majaj NJ, DiCarlo JJ (2016) Explicit information for category-orthogonal object properties increases along the ventral stream. Nat Neurosci 19: 613–622.

Hung CP, Kreiman G, Poggio T, DiCarlo JJ (2005) Fast readout of object identity from macaque inferior temporal cortex. Science 310:863-866.

Ito M, Tamura H, Fujita I, Tanaka K (1995) Size and position invariance of neuronal responses in monkey inferotemporal cortex. J Neurophysiol 73: 218–226.

Kar K, Kubilius J, Schmidt K, Issa EB, DiCarlo JJ (2019) Evidence that recurrent circuits are critical to the ventral stream's execution of core object recognition behavior. Nat Neurosci 22:974-983.

Khaligh-Razavi S-M, Kriegeskorte N (2014) Deep supervised, but not unsupervised, models may explain IT cortical representation. PLOS Comput Biol 10:e1003915.

Kheradpisheh SR, Ghodrati M, Ganjtabesh M, Masquelier T (2016) Deep networks can resemble human feed-forward vision in invariant object recognition. Sci Rep 6:32672.

Kourtzi Z, Kanwisher N (2000) Cortical regions involved in perceiving object shape. J Neurosci 20:3310–3318.

Kriegeskorte N (2015) Deep neural networks: a new framework for modeling biological vision and brain information processing. Annu Rev Vis Sci 1:417–46.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Kriegeskorte N, Kievit RA (2013) Representational geometry: integrating cognition, computation, and the brain. Trends Cogn Sci 17:401-412.

Kubilius J, Bracci S, Op de Beeck HP (2016) Deep neural networks as a computational model for human shape sensitivity. PLOS Comput Biol 12:e1004896.

Kubilius J, Schrimpf M, Hong H, et al. (2019) Brain-like object recognition with high-performing shallow recurrent ANNs. In: Neural Information Processing Systems. Vancouver, British Columbia, Canada.

LeCun Y (1989) Generalization and network design strategies. In Connectionism in Perspective, Pfeifer R, Schreter Z, Fogelman F, Steels L, Eds. Zurich, Switzerland: Elsevier.

LeCun Y, Bengio Y, Hinton G (2015) Deep learning. Nature 521:436-444.

Li N, Cox DD, Zoccolan D, DiCarlo JJ (2009) What response properties do individual neurons need to underlie position and clutter “invariant” object recognition? J Neuorphysiol 102:360-376.

Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RB (1995) Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc Nati Acad Sci USA 92:8135-8139.

Murty NAR, Arun SP (2017) A balanced comparison of object invariances in monkey IT neurons. eNeuro 4:e0333-16.2017.

Nili H, Wingfield C, Walther A, Su L, Marslen-Wilson W, Kriegeskorte, N (2014) A toolbox for representational similarity analysis. PLOS Comput Bio 10:e1003553.

O’Connell TP, Chun MM (2018) Predicting eye movement patterns from fMRI responses to natural scenes. Nat. Commun 9, 5159.

Orban GA, Van Essen D, Vanduffel W (2004) Comparative mapping of higher visual areas in monkeys and humans. Trends Cogn Sci 8:315-324.

Rajalingham R, Issa EB, Bashivan P, Kar K, Schmidt K, DiCarlo JJ (2018) Large-scale, high-resolution comparison of the core visual object recognition

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

behavior of humans, monkeys, and state-of-the-art deep artificial neural networks. J Neurosci 38:7255–69.

Rust NC, DiCarlo JJ (2010) Selectivity and tolerance ("invariance") both increase as visual information propagates from cortical area V4 to IT. J Neurosci 30: 12978–12995.

Sary G, Vogels, R, Orban GA (1993) Cue-invariant shape selectivity of macque inferior temporal neurons. Science 260:995-997.

Sawamura H, Georgieva S, Vogels R, Vanduffel W, Orban GA (2005) Using functional magnetic resonance imaging to assess adaptation and size invariance of shape processing by humans and monkeys. J Neurosci 25: 4294–4306.

Schwartz EL, Desimone R, Albright TD, Gross C (1983) Shape recognition and inferior temporal neurons. Proc Nati Acad Sci USA 80:5776-5778.

Schwarzlose RF, Swisher JD, Dang S, Kanwisher N (2008) The distribution of category and location information across object-selective regions in human visual cortex. Proc Nati Acad Sci USA 105: 4447–4452.

Sereno MI, Dale AM, Reppas JB, Kwong KK, Belliveau JW, Brady TJ, Rosen BR, Tootell RB (1995) Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. Science 268:889–893.

Serre T (2019) Deep learning: The good, the bad, and the ugly. Annu. Rev. Vis. Sci. 5:21.1–21.28.

Swisher JD, Halko MA, Merabet LB, McMains SA, Somers DC (2007) Visual Topography of Human Intraparietal Sulcus. J Neurosci 27:5326-5337.

Tacchetti A, Isik L, Poggio TA (2018) Invariant recognition shapes neuroal representations of visual input. Annu Rev Vis Sci 4:403–22.

Tahan L, Konkle T (2019) Reliability-based voxel selection. Neuroimage in press.

Tovee MJ, Rolls ET, Azzopardi P (1994) Translation invariance in the responses to faces of single neurons in the temporal visual cortical areas of the alert macaque. J Neurophysiol 72:1049-1060.

Ullman S, Assif L, Fetaya E, Harari D (2016) Atoms of recognition in human and computer vision. Proc Nati Acad Sci USA 113:2744–49.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Vaziri-Pashkam M, Xu Y (2019) An information-driven two-pathway characterization of occipito-temporal and posterior parietal visual object representations. Cereb Cortex 29:2034–2050.

Vaziri-Pashkam M, Taylor J, Xu Y (2019) Spatial frequency tolerant visual object representations in the human ventral and dorsal visual processing pathways. J Cogn Neurosci 31:49–63.

Vuilleumier P, Henson RN, Driver J, Dolan RJ (2002) Multiple levels of visual object constancy revealed by event-related fMRI of repetition priming. Nat Neurosci 5:491-499.

Willenbockel V, Sadr J, Fiset D, Horne GO, Gosselin F, Tanaka JW (2010) Controlling low-level image properties: The SHINE toolbox. Behavior Research Methods 42:671-684.

Williams MA, Dang S, Kanwisher NG (2007) Only some spatial patterns of fMRI response are read out in task performance. Nat Neurosci 10:685–686.

Xu Y, Vaziri-Pashkam M (2020) Limited correspondence in visual representation between the human brain and convolutional neural networks. *bioRxiv.*

Yamins DLK, DiCarlo JJ (2016) Using goal-driven deep learning models to understand sensory cortex. Nat Neurosci 19:356–65.

Yamins DLK, Hong H, Cadieu CF, Solomon EA, Seibert D, DiCarlo JJ (2014) Performance-optimized hierarchical models predict neural responses in higher visual cortex. Proc Nati Acad Sci USA 111:8619–24.

Zhang C, Bengio S, Hardt M, Recht B, Vinyals O (2016) Understanding deep learning requires rethinking generalization. Paper presented at the 4th International Conference on Learning Representations, Toulon, France, April 24–26.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Supplemental Table 1. The CNNs and the layers examined in this study.

CNN name	Depth/Blocks	Layers	N of Layers Sampled	Sampled Layer Names and Locations (indicated in the parenthesis)
Alexnet	8	25	6	'pool1' (5), 'pool2' (9), 'pool5' (16), 'fc6' (17), 'fc7' (20), 'fc8' (23)
Cornet-S	4	42	6	'V1_outpt' (8), 'V2_output' (18), 'V4_output' (28), 'IT_output' (38), 'decoder_avgpool' (39), 'decoder_output' (42)
Densenet-201	201	709	6	'pool1' (6), 'pool2_pool' (52), 'pool3_pool' (140), 'pool4_pool' (480), 'avg_pool' (706), 'fc1000' (707)
Googlenet	22	144	6	'pool1-3x3_s2' (4), 'pool2-3x3_s2' (11), 'pool3-3x3_s2' (40), 'pool4-3x3_s2' (111), 'pool5-7x7_s1' (140), 'loss3-classifier' (142)
Inception_v3	48	316	11	'average_pooling2d_1' (29), 'average_pooling2d_2' (52), 'average_pooling2d_3' (75), 'average_pooling2d_4' (121), 'average_pooling2d_5' (153), 'average_pooling2d_6' (185), 'average_pooling2d_7' (217), 'average_pooling2d_8' (264), 'average_pooling2d_9' (295), 'avg_pool' (313), 'predictions' (314)
Inception-resnet_v2	164	825	7	'max_pooling2d_1' (12), 'max_pooling2d_2' (19), 'average_pooling2d_1' (29), 'max_pooling2d_3' (285), 'max_pooling2d_4' (648), 'avg_pool' (822), 'predictions' (823)
Mobilenet_v2	54	155	10	'block_2_project_BN' (26), 'block_4_project_BN' (43), 'block_6_project_BN' (61), 'block_8_project_BN' (78), 'block_10_project_BN' (96), 'block_12_project_BN' (113), 'block_14_project_BN' (130), 'block_16_project_BN' (148), 'global_average_pooling2d_1' (152), 'Logits' (153)
Resnet-18	18	72	6	'pool1' (6), 'res2b_relu' (20), 'res3b_relu' (36), 'res4b_relu' (52), 'pool5' (69), 'fc1000' (70)
Resnet-50	50	177	6	'max_pooling2d_1' (5), 'activation_10_relu' (37), 'activation_22_relu' (79), 'activation_40_relu' (141), 'avg_pool' (174), 'fc1000' (175)
Resnet-101	101	347	6	'pool1' (5), 'res2c_relu' (37), 'res3b3_relu' (79), 'res4b22_relu' (311), 'pool5' (344), 'fc1000' (345)
Squeezenet	18	68	5	'pool1' (4), 'pool3' (19), 'pool5' (34), 'conv10' (64), 'pool10' (66)
Vgg-16	16	41	8	'pool1' (6), 'pool2' (11), 'pool3' (18), 'pool4' (25), 'pool5' (32), 'fc6' (33),'fc7' (36), 'fc8' (39)
Vgg-19	19	47	8	'pool1' (6), 'pool2' (11), 'pool3' (20), 'pool4' (29), 'pool5' (38), 'fc6' (39),'fc7' (42), 'fc8' (45)
Xception	71	171	8	'block2_pool' (18), 'block4_pool' (42), 'block6_sepconv3_bn' (68), 'block8_sepconv3_bn' (94), 'block10_sepconv3_bn' (120), 'block12_sepconv3_bn' (146), 'avg_pool' (168), 'predictions' (169)

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Supplementary Results

Besides examining the two Euclidian transformation involving position and size, we also tested two non-Euclidian transformations involving a change in image statistics (original vs controlled images) and the spatial frequency (SF) content of an image (high vs low SF). Although object representation has been shown to be invariant to the cues defining the shape (e.g., luminance, motion, or texture contrast) in macaque IT and human LOT and VOT (Sary et al., 1993; Grill-Spector et al., 1998), and the fact that we could recognize a line-drawing of a car just as easily as we do with a photograph of a car (which is similar to a SF transformation), tolerance for these two non-Euclidean image transformations has never been directly tested.

Details of the human fMRI image stats and SF experiments have been described in two previously published studies (Vaziri-Pashkam & Xu, 2019 and Vaziri-Pashkam et al., 2019). They are summarized here for the readers' convenience. Six and ten participants took part in the image stats and SF experiments, respectively. In the image stats experiment, we tested image stats tolerance and presented images at fixation either in the original unaltered format or in the controlled format (subtended 4.6º x 4.6º) (Supplementary Figure 4a left). Half of the 16 blocks contained original images and the other half, controlled images. Other details of the experiment were identical to that of position experiment. In the SF experiment, only six of the original eight object categories were included and they were faces, bodies, houses, elephants, cars, and chairs. Images were shown in 3 conditions: Full-SF, High-SF, and Low-SF (Supplementary Figure 4a right). In the Full-SF condition, the full spectrum images were shown without modification of the SF content. In the High-SF condition, images were high-pass filtered using an FIR filter with a cutoff frequency of 4.40 cycles per degree. In the Low-SF condition, the images were low-pass filtered using an FIR filter with a cutoff frequency of 0.62 cycles per degree. The DC component was restored after filtering so that the image backgrounds were equal in luminance. Each run contained 18 blocks, one for

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

each of the category and SF condition combination. Each participant completed a single scan session containing 18 experimental runs, each lasting 5 minutes. Other details of the experiment design were identical to that the position experiment. Only the results from the High-SF, and Low-SF conditions were included in the present analysis.

Results from the human fMRI image stats and SF experiments were analyzed following the same procedure as described in Methods. We obtained similar results for these two types transformations as we did for the position and size transformations in the human brain. Specifically, RDM correlation across the two states of each transformation linearly increased from lower to higher visual regions (the averaged linear correlation coefficients were .43 and .28, respectively for image stats and SF, and both were greater than 0, $t(5) = 2.58$, $p = 0.025$ for image stats, and $t(9) = 1.93$, $p = 0.043$ for SF). RDM correlation between the two states of each transformation was also significantly higher for the average of LOT and VOT than the average of V1 to V3 ($t(5) = 3.17$, $p = 0.012$ for image stats; and $t(9) = 2.37$, $p = 0.021$, for SF; the difference between LOT and VOT and those among V1 to V3 were not significant, all $Fs < 2.11$, $ps > .20$; see Supplementary Figure 4b). These results remain the same whether z-normalized Euclidean distance measure or correlation measure was used, and remained qualitatively similar even when Pearson correlation, rather than Spearman rank correlation, was applied (see Supplementary Figure 5). Thus across both the two types Euclidian transformations examined (i.e., position and size) and the two types of non-Euclidian transformations examined here (i.e., image stats and SF), object representational structure across transformations becomes increasingly invariant from lower to higher ventral visual regions.

As in the main study, we next examined whether CNNs exhibit a similar pattern in RDM correlation across the two states of image stats and SF transformation from lower to higher layers. Despite differences in the exact architecture, depth, and presence/absence of recurrent processing, all 14 CNNs exhibited overall similar trajectories for a given transformation. Specifically, RDM

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

correlations fluctuated across the different CNN layers, more drastically for SF than image stats, and showed an inverted U-shape between lower and higher layers in a large number of CNNs (Supplementary Figure 4b), rather than an increase in RDM correlation from lower to higher layers. This response pattern again differed from the monotonic increase in RDM correlation from lower to higher brain regions.

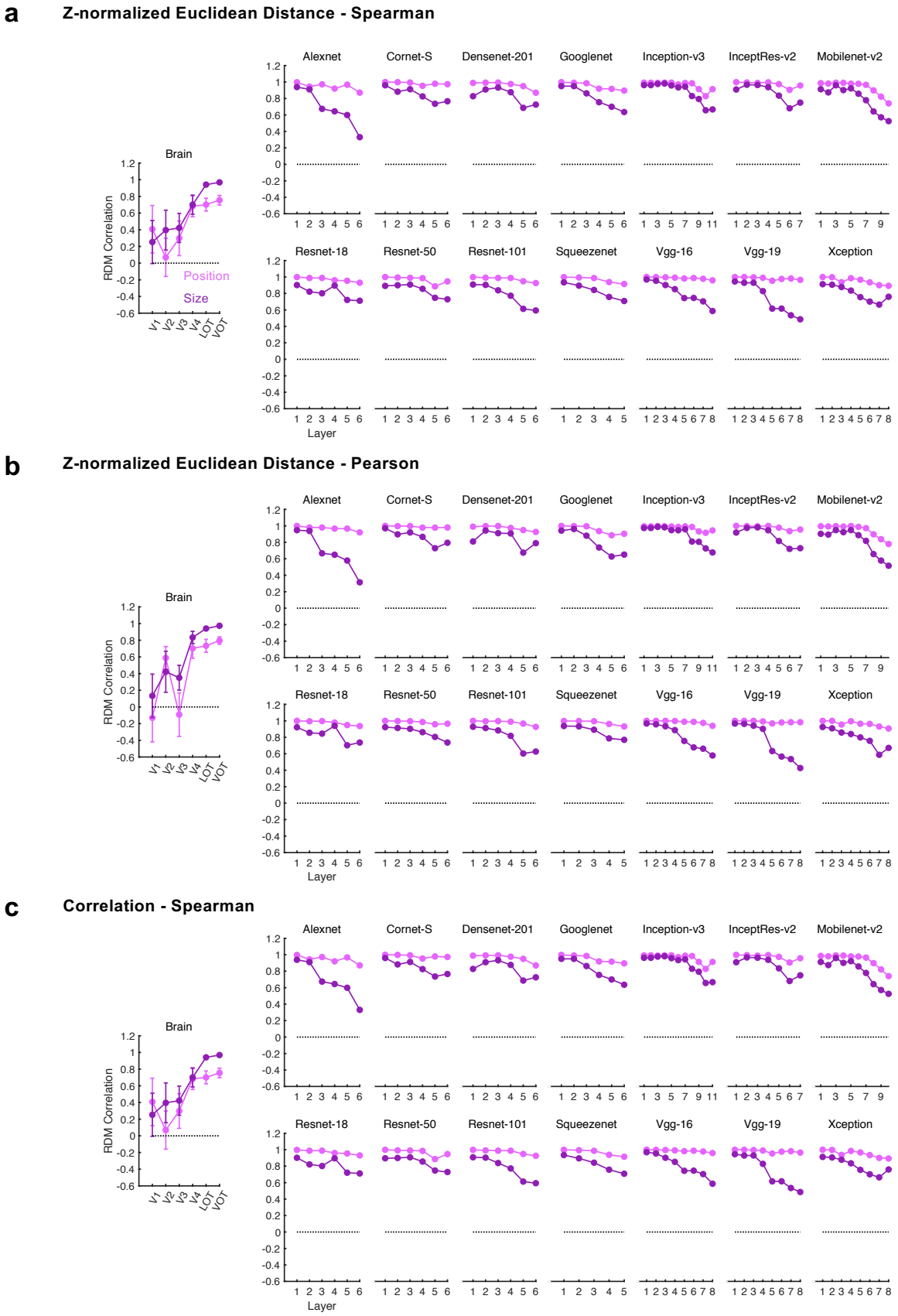
For the image stats transformation, direct correlation of the response profiles (using Spearman rank correlation) revealed in 10 out of the 14 CNNs a negative correlations between the brain and CNNs that were significantly below the lower bound of the noise ceiling of the brain response across human participants (*ts* > 2.34, *ps* < .033; Supplementary Figure 4c). Three of the four CNNs that did not show a significant effect showed a marginally significant effect (Alexnet, $t(5) = 1.64$, $p = 0.081$; VGG-16, $t(5) = 1.82$, $p = .064$; and VGG-19, $t(5) = 1.62$, $p = .084$). The effect was not significant for Squeezenet ($t(5) = .47$, $p = .33$). For SF transformation, direct correlation of the response profiles between the brain and CNN revealed few significant or marginally significant correlations that were below the lower bound of the noise ceiling of the brain responses across human participants (Alexnet, $t(9) = 2.26$, $p = .025$; Inception-v3, $t(9) = 1.42$, $p = .094$; Mobilenet-v2, $t(9) = 1.63$, $p = .069$; Xception, $t(9) = 1.42$, $p = .094$; all other CNNs, *ts* < .94, *ps* >.19; Supplementary Figure 4c). Note that the overall response profiles were flatter for image stats and SF transformations in the brain than for the position and size transformations. Additionally, reliability for SF was low (close to 0 for the lower bound of the noise ceiling) even though more participants were included in this experiment. Both of these two factors likely contributed to the overall weaker differentiation between the brain and CNN response profiles for these two types of transformation than for position and size. Although strong conclusions may not be drawn from the direct response profile correlations for the image stats and SF transformation, given that tolerance in object representational structure steadily increased for these two transformation from lower to higher human visual regions but not from lower to higher CNN

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

layers, there still appeared to be some divergence between the brain and CNNs in how they represent these two types of transformations.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

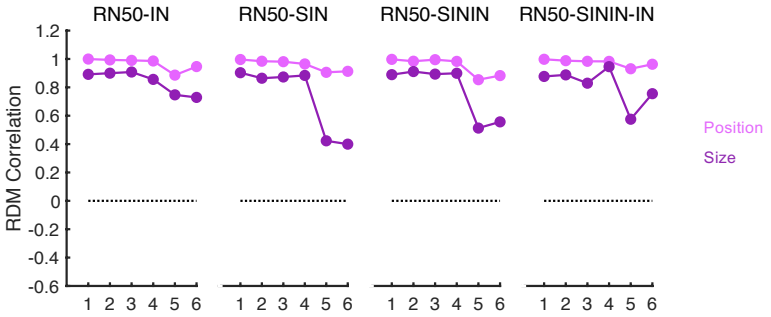
Supplemental Figure 1



Supplementary Figure 1. Correlating the object representational structures across the two states of position and size transformations within each human ventral brain regions and each sampled layer of the 14 different CNNs. **a.** The results from Z-normalized Euclidean distance measure and Spearman rank correlation. These are the same results as those reported on Figure 2 and are included here for comparison purposes. **b.** The results from Z-normalized Euclidean distance measure and Pearson correlation. **c.** The results from correlation measure and Spearman rank correlation. Very similar results were obtained from these different types of measures.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

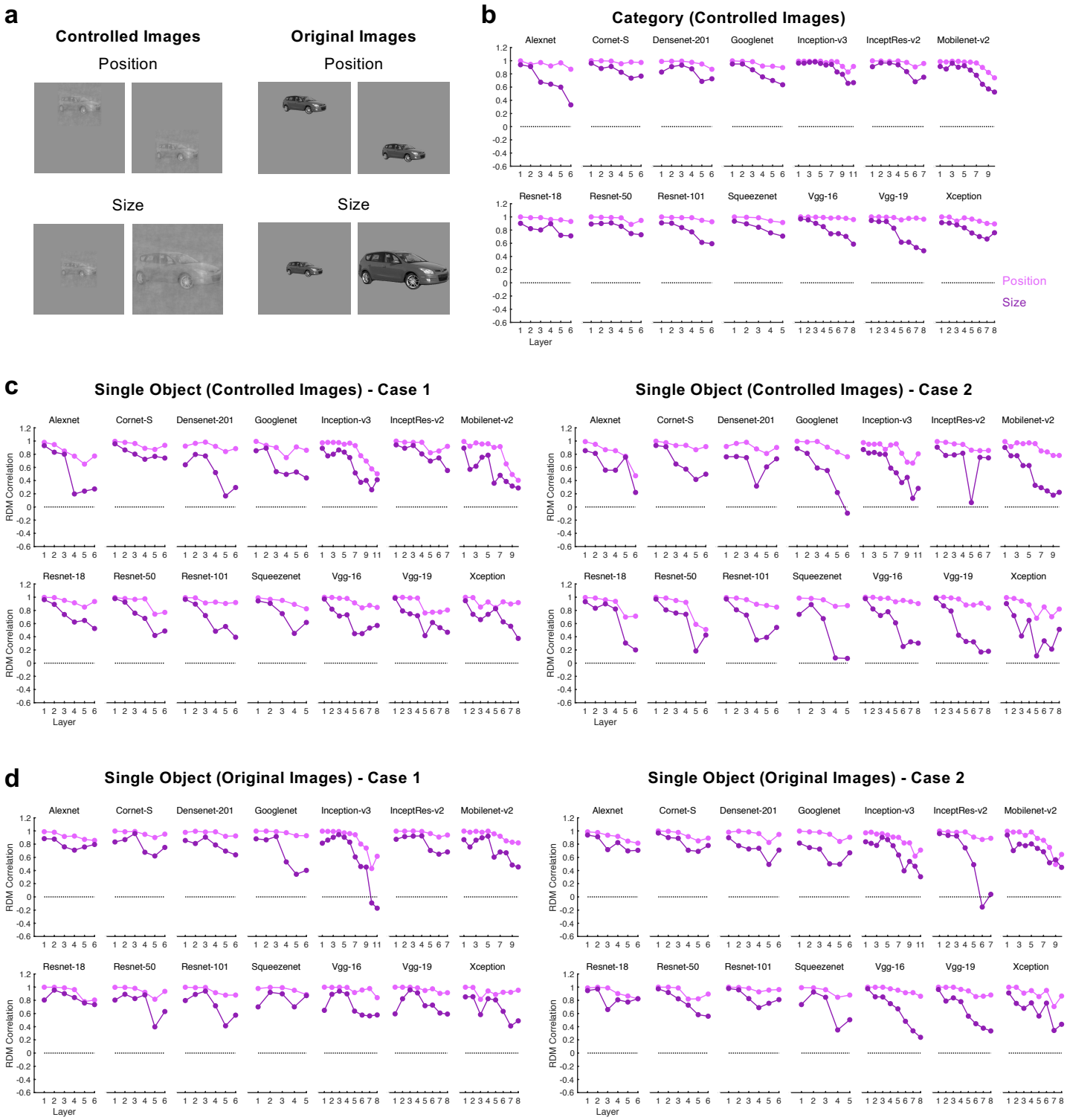
Supplemental Figure 2



Supplementary Figure 2. Correlating the object representational structures across the two states of position and size transformations within each sampled layer of Resnet-50 pretrained either with the original ImageNet images (RN50-IN), the stylized ImageNet Images (RN50-SIN), both the original and the stylized ImageNet Images (RN50-SININ), or both sets of images and then fine-tuned with the stylized ImageNet images (RN50-SININ-IN). The results do not appear to differ substantially across these different training regimes.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

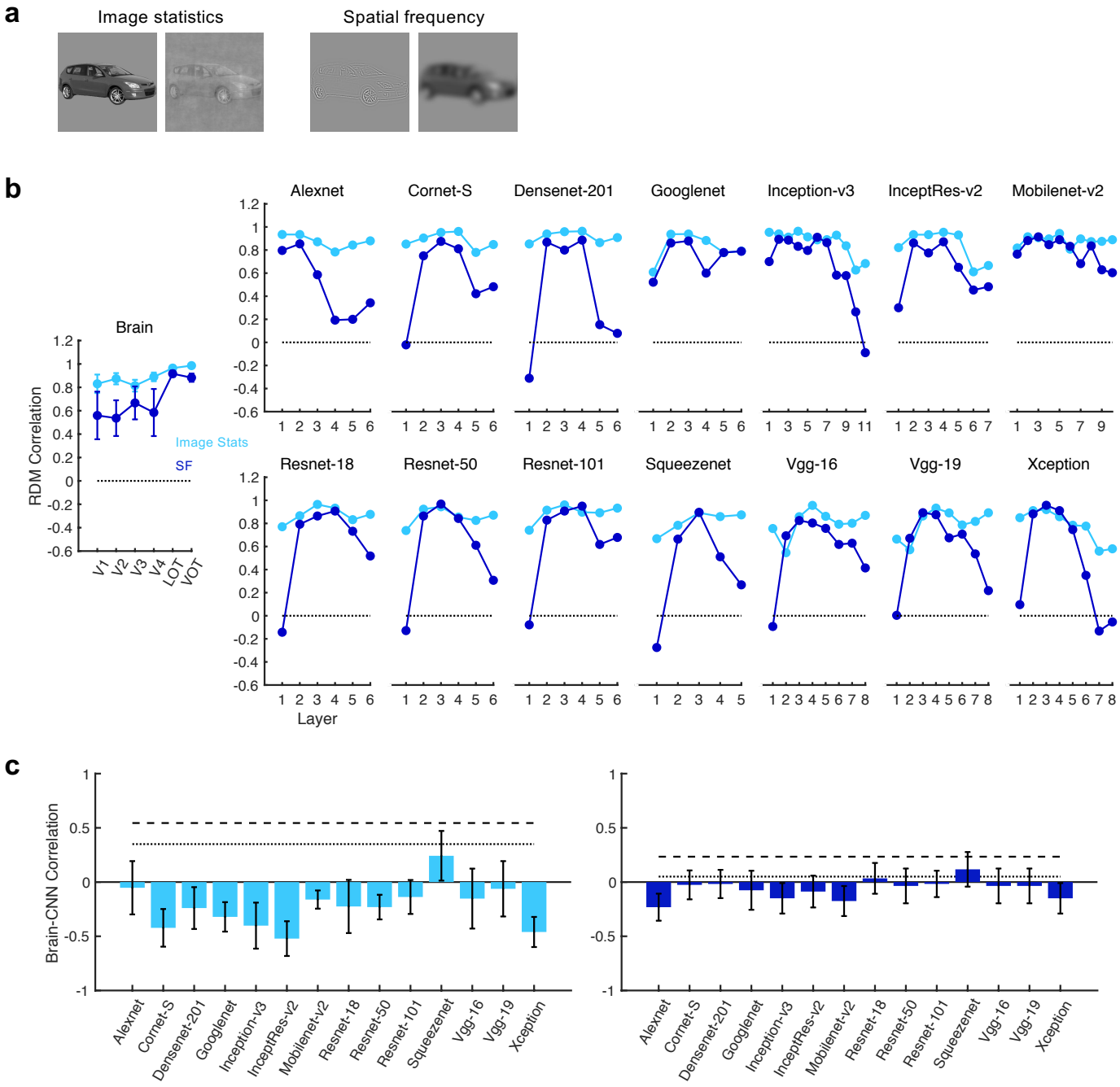
Supplemental Figure 3



Supplementary Figure 3. Comparing the representational structure correlation for object categories and single objects for position and size transformations in 14 different CNNs. **a.** The stimuli used. Both the controlled and the original images were used in this analysis. **b.** The representational structure correlation for object categories, using the controlled images. These are the same results as those reported on Figure 2 and are included here for comparison purposes. **c.** The representational structure correlation for single objects, using the controlled images. A single exemplar was chosen from each of the eight object categories for this analysis. This analysis was carried out twice, each involving a different exemplar from a given category. **d.** The representational structure correlation for single objects, using the original images. Other details are identical to **c**. Similar results were obtained for object categories and single objects such that object representational structures became more variable across the two states of each transformation over the course of CNN processing. If anything, the decrease in invariance was more drastic for the single objects than for the object categories.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Supplemental Figure 4

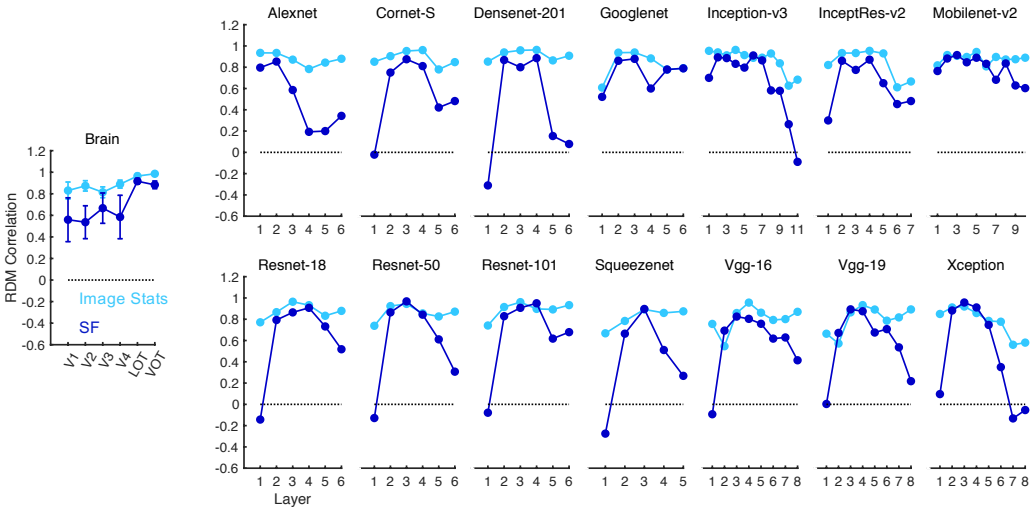


Supplementary Figure 4. Evaluating object representational structure tolerance during the course of visual processing in the human brain and 14 different CNNs for image stats and SF transformations. **a.** The two types of transformations examined: image stats (original vs controlled) and SF (high SF vs low SF). **b.** Correlating the object representational structures across the two states of image stats and SF transformations within each human ventral brain regions and each sampled layer of the 14 different CNNs using Spearman rank correlation. Results from the brain regions were corrected by the reliability of each region (see Methods). **c** Response profile correlation between the brain and each CNN plotted against the upper and lower bound of the noise ceiling of the brain response reliability across human participants. While object representational structure becomes increasingly invariant from lower to higher levels of visual processing in the human brain, CNNs do not exhibit this response profile (see Supplementary Results for more details).

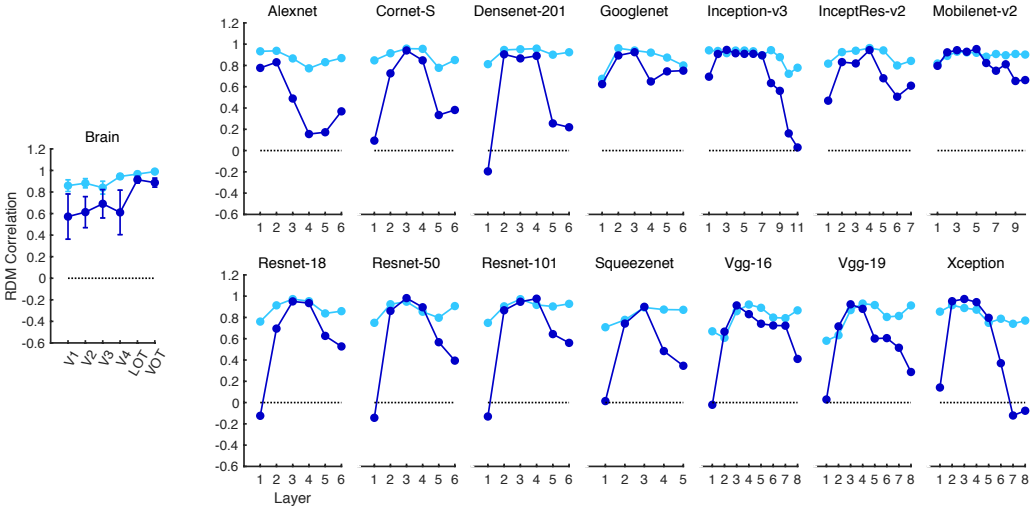
bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Supplemental Figure 5

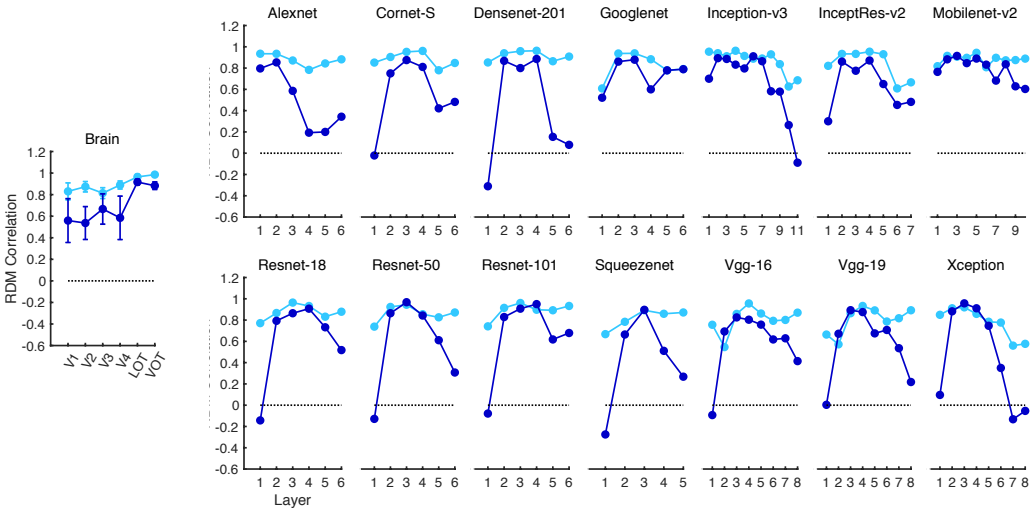
a **Z-normalized Euclidean Distance - Spearman**



b **Z-normalized Euclidean Distance - Pearson**



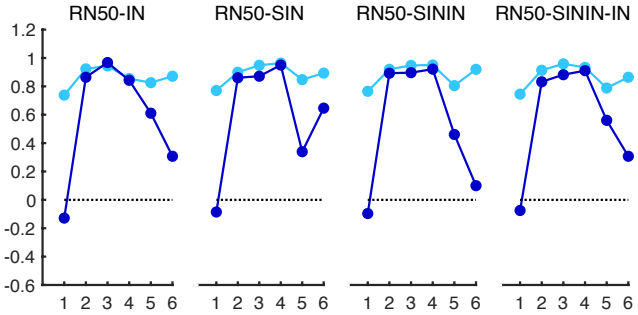
c **Correlation - Spearman**



Supplementary Figure 5. Correlating the object representational structures across the two states of image stats and SF transformations within each human ventral brain regions and each sampled layer of the 14 different CNNs. **a.** The results from Z-normalized Euclidean distance measure and Spearman rank correlation. These are the same results as those reported on Supplementary Figure 4 and are included here for comparison purposes. **b.** The results from Z-normalized Euclidean distance measure and Pearson correlation. **c.** The results from correlation measure and Spearman rank correlation. Very similar results were obtained from these different types of measures.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

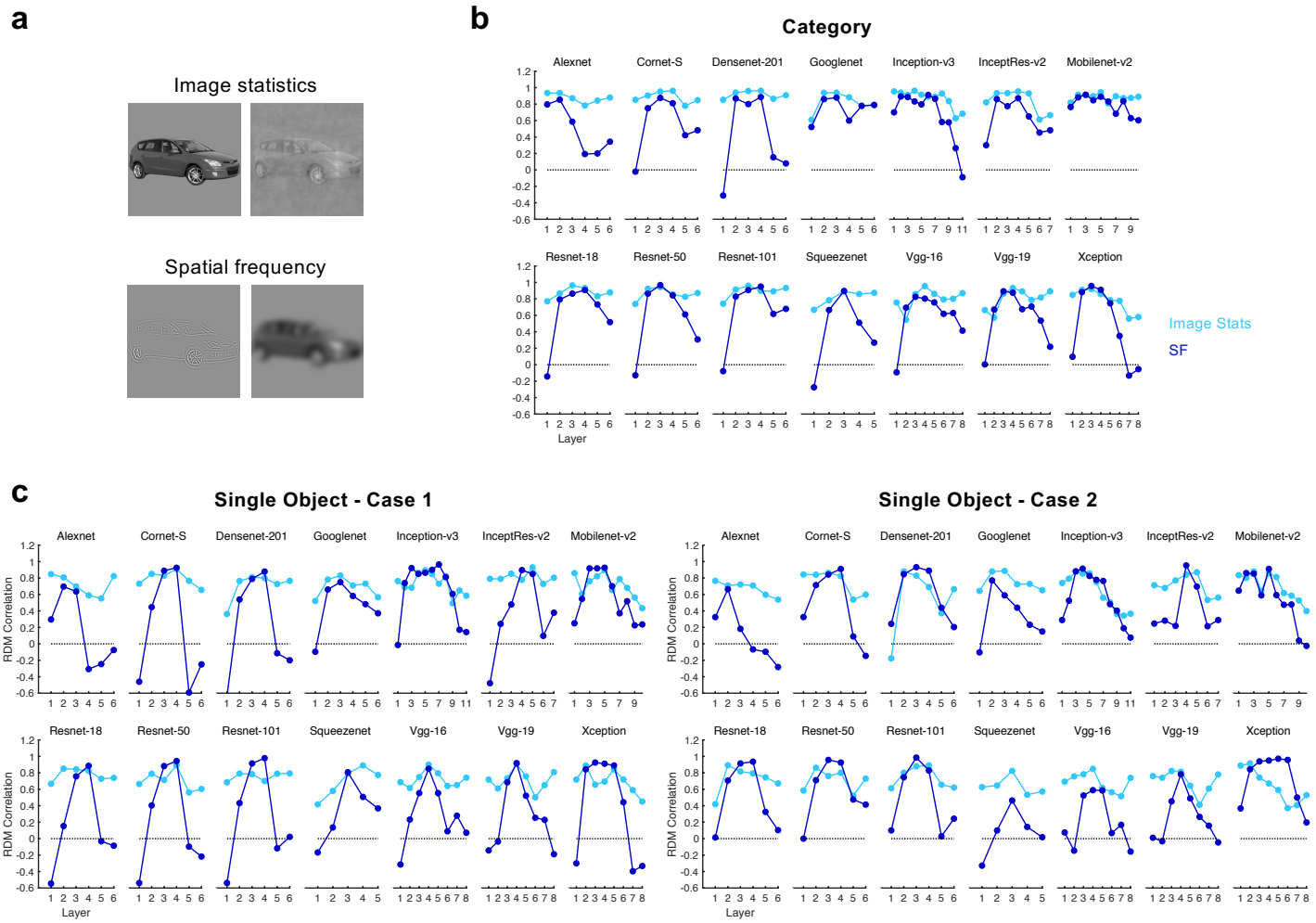
Supplemental Figure 6



Supplementary Figure 6. Correlating the object representational structures across the two states of image stats and SF transformations within each sampled layer of Resnet-50 pretrained either with the original ImageNet images (RN50-IN), the stylized ImageNet Images (RN50-SIN), both the original and the stylized ImageNet Images (RN50-SININ), or both sets of images and then fine-tuned with the stylized ImageNet images (RN50-SININ-IN). The results do not appear to differ substantially across these different training regimes.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.11.246934; this version posted August 12, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Supplemental Figure 7



Supplementary Figure 7. Comparing the representational structure correlation for object categories and single objects for image stats and SF transformations in 14 different CNNs. **a.** The stimuli used. **b.** The representational structure correlation for object categories. These are the same results as those reported on Supplementary Figure 4 and are included here for comparison purposes. **c.** The representational structure correlation for single objects. A single exemplar was chosen from each of the eight object categories for this analysis. This analysis was carried out twice, each involving a different exemplar from a given category. Similar results were obtained for object categories and single objects with object representational structure correlation fluctuated over the course of CNN processing. If anything, the fluctuation in correlation was more drastic for the single objects than for the object categories.