Biased orientation representations can be explained by experience with non-uniform training set statistics

Short title: Orientation biases in convolutional neural networks

Margaret Henderson[1], John Serences[1,2,3]

[1]Neurosciences Graduate Program, University of California, San Diego, La Jolla, California 92093-1090 USA
[2]Department of Psychology, University of California, San Diego, La Jolla, California 92093-0109 USA
[3]Kavli Foundation for the Brain and Mind, University of California, San Diego, La Jolla, California 92093 USA

Author Contributions:
All authors conceived the experiments and edited the manuscript. MH implemented the experiments and analysis and wrote the manuscript. JTS supervised the project.

Correspondence:
Margaret Henderson
Neurosciences Graduate Program
University of California, San Diego
9500 Gilman Drive, La Jolla, CA, 92093
mmhender@ucsd.edu

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Abstract

Visual acuity is better for vertical and horizontal compared to other orientations. This cross-species phenomenon is often explained by "efficient coding", whereby more neurons show sharper tuning for the orientations most common in natural vision. However, it is unclear if experience alone can account for such biases. Here, we measured orientation representations in a convolutional neural network, VGG-16, trained on modified versions of ImageNet (rotated by 0°, 22.5°, or 45° counter-clockwise of upright). Discriminability for each model was highest near the orientations that were most common in the network's training set. Furthermore, there was an over-representation of narrowly tuned units selective for the most common orientations. These effects emerged in middle layers and increased with depth in the network. Our results suggest that biased orientation representations can emerge through experience with a non-uniform distribution of orientations, supporting the efficient coding hypothesis.

Author Summary

Observers tend to have more precise vision for items that are oriented vertically or horizontally compared to items oriented diagonally. This perceptual bias may be an adaptation to the statistics of the visual environment, where items such as trees, buildings, and the horizon naturally create horizontal and vertical edges. Here, we tested this hypothesis by taking a popular computational model of the visual system (a convolutional neural network, or CNN), and training it to perform object recognition on images that were either upright or rotated.

Measuring orientation representations in the trained model revealed that orientation discriminability was highest near whichever orientations were most common in the training image set, and more neural network units showed a preference for those orientations. These results support the hypothesis that orientation biases reflect an adaptation to environmental statistics.

Introduction

Contrary to common intuition, visual perception is not perfectly uniform across orientation space. One example of this principle is the “oblique effect”, which has been demonstrated in humans and a wide range of animal species, including cats, octopi and goldfish, among others. This effect describes the finding that observers’ ability to discriminate small changes in orientation, as well as other forms of acuity, tend to be worst for stimuli that have edges oriented diagonally (oblique orientations) and better for stimuli with edges oriented vertically or horizontally (cardinal orientations) (1,2). In visual cortex, this finding has been linked to a larger number of orientation tuned neurons with a preference for cardinal orientations, as has been shown in cats (3), and macaques (4,5), among other species. Some evidence also suggests that cardinally-tuned neurons may have narrower tuning than other orientations, which may also contribute to higher acuity (3,6).

One compelling explanation for the origin of the oblique effect is the efficient coding hypothesis, which suggests that because the brain operates with limited resources, coding

resources should be preferentially allocated to stimuli that are highly probable during natural vision (7,8). On this view, biased orientation perception may reflect an adaptation to the statistics of natural images, in which vertical and horizontal orientations are most common (8,9). Support for an experience-driven account of the oblique effect includes evidence that in primates, the over-representation of cardinal orientations in visual cortex increases with age (4). Additionally, exposing developing kittens or mice to an environment with contours of only one orientation can induce changes in the distribution of cortical orientation tuning, suggesting some degree of plasticity (6,10–12).

In addition, innate factors may also contribute to the efficient coding of cardinal orientation. For instance, while it is possible to significantly modify the distribution of orientation tuning preferences in visual cortex through experience, exposing an animal to only diagonal lines during development does not entirely obliterate tuning for cardinal orientations (6,12). Similarly, rearing animals in complete darkness can result in a more extreme over-representation of cardinal-tuned units (13). In both mice and ferrets, it has been suggested that innate factors result in a strong oblique effect early in development, while visual experience tends to make orientation tuning more uniform over time (14,15). These observations are consistent with the efficient coding account if we assume that the visual system can adapt to environmental regularities over the course of evolution, resulting in feature biases that are encoded in the genome.

However, factors that are independent of visual input statistics may also separately contribute to the presence of cardinal orientation biases in animals. For example, some anatomical properties of the visual system naturally give a privileged status to the cardinal axes, such as the horizontal raphe of the retina, the role of the horizontal axis in vestibular and oculomotor system organization, and the distinction between processing of vertical and horizontal disparity (16). Such properties need not be related to the orientation content of natural images, but may instead reflect general physical and/or developmental constraints. It is plausible that the presence of these architectural factors leads to cardinal biases, independent from the statistics of natural images. Thus, whether the efficient coding mechanism alone can account for the emergence of the oblique effect has not been clearly established.

Here, we addressed this question by examining whether a convolutional neural network (CNN) exhibits biased orientation representations. We focus on the popular VGG-16 model, a standard feedforward network that achieves high performance at classifying objects in natural images (17). We first test whether a pre-trained VGG-16 model exhibits the classical oblique effect, assessed using the Fisher information measured at entire layers of the network, and the distribution of single-unit tuning properties. In addition to a test of the efficient coding hypothesis, measuring orientation bias in this pre-trained model will provide an assessment of whether existing CNNs, often used as models of the primate visual system (18,19), exhibit this defining characteristic of biological vision.

We next trained VGG-16 models on modified versions of the ImageNet database (20) that had been rotated by 0°, 22.5° or 45° relative to upright. This allowed us to determine whether a bias centered around other axes can be induced equally as well as a cardinal bias, and whether the biases observed in the pre-trained network were simply artifacts of some intrinsic property of the CNN (e.g. a square pixel grid that results in a cardinal reference frame). We demonstrate that, contrary to this alternative, networks trained on rotated images exhibited rotated biases that were consistent with the networks' training set statistics. These results suggest that general visual experience with a non-uniform orientation distribution is sufficient to promote the formation of biased orientation representations. Further, our findings highlight how biased training data can fundamentally impact visual information processing in neural network models.

Results

We measured the activation responses of several trained VGG-16 networks (Figure 1A) (17) presented with oriented images (Figure 1B) to evaluate whether each network showed non-uniformities in its orientation representations across feature space. First, we tested whether a pre-trained VGG-16 model (21) exhibits the classical oblique effect. Next, we evaluated whether this bias changed in a predictable way when networks with the same architecture were trained on modified versions of the ImageNet database (Figure 4A).

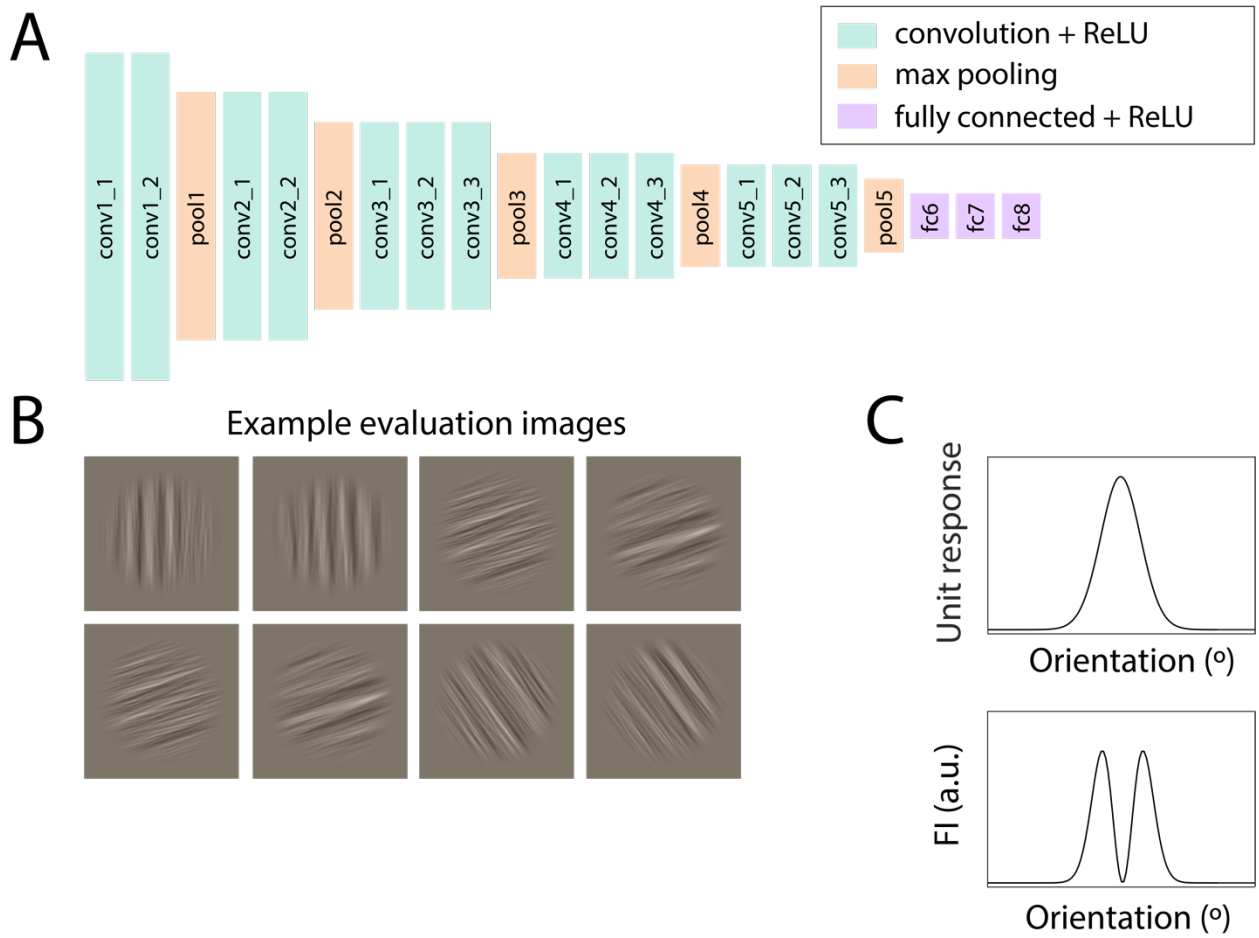

Figure 1. Evaluating orientation discriminability in a trained neural network model. **(A)** Schematic of the VGG-16 network architecture, with layers arranged from shallowest (left) to deepest. **(B)** Examples of oriented images used to measure orientation representations in the pre-trained network. Images were generated by filtering ImageNet images within a narrow orientation range, preserving their broadband spatial frequency content. Orientations varied between 0-179°, in steps of 1° (see *Methods, Evaluation stimuli)*. **(C)** Cartoon depiction of the approximate relationship between an example single unit tuning function and the Fisher information (FI) measured from that unit as a function of orientation.

Measuring cardinal biases in a pre-trained VGG-16 model

We first evaluated non-uniformity at the level of each pre-trained network layer by computing the layer-wise Fisher information (FI), which reflects how well each layer's activations can distinguish small changes in orientation (see *Methods, Computing Fisher information*). Briefly, the contribution of each network unit to the layer-wise FI is the squared slope of a unit's tuning function at each orientation normalized by the variance of the response at that orientation. Thus, the steep part of a unit's tuning function will carry more information because two similar orientations will evoke different responses (Figure 1C). However, the flat parts of a unit's tuning curve (i.e. at the peak or in the tails) will not carry very much information because the unit will respond about the same to two similar orientations.

For a pre-trained VGG-16 model, plotting FI as a function of orientation reveals noticeable deviations from uniformity, particularly at deep layers of the network (navy blue curves in Figure 2A). While the first layer of the model (conv1_1), gives a relatively flat profile of FI with respect to orientation, by layer 7 (conv3_1), peaks in FI are apparent around the cardinal orientations, 0°/180° and 90°. At later layers of the model, the peaks in FI are more pronounced and begin to take on a characteristic double-peaked shape, where FI is maximal just a few degrees to the left and right of the cardinal orientations, with a dip at the exact position of the cardinal orientations (this shape is discussed in more detail in the next section after we report statistics about the preferred orientation and width of single unit tuning functions). In contrast, when the same analysis is done on a randomly initialized VGG-16 model

(no training performed), FI is flat with respect to orientation at all layers, suggesting that a randomly initialized model does not exhibit this same cardinal bias (gray curves in Figure 2A).

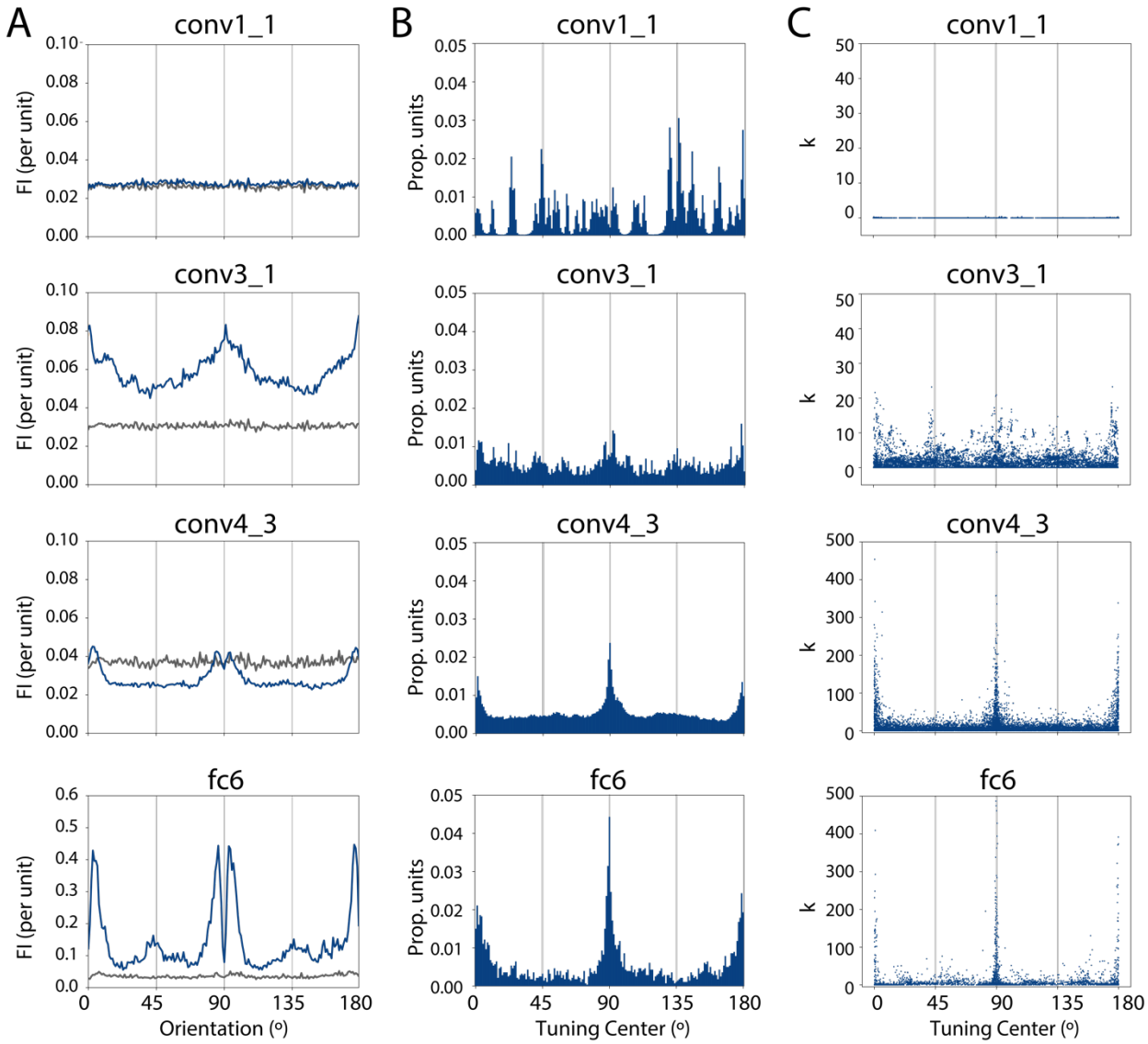

Figure 2. Pre-trained VGG-16 shows maximum orientation information just off of cardinal orientations, and non-uniformity in the distribution of single unit tuning properties. **(A)** FI is plotted as a function of orientation for several example layers of the pre-trained model (navy blue) and a randomly initialized model (gray). See *Methods, Computing Fisher information* for details. **(B)** Distribution of the tuning centers of pre-trained network units that were well-fit by a Von Mises function. See Figure S1 for the proportion of well-fit units per layer, and the distribution of centers for the randomly initialized model. **(C)** Concentration parameter (k)

versus center for individual units in the pre-trained model (data in the top three panels of C have been down-sampled to a maximum of 10,000 points for visualization purposes).

To quantify this effect at each layer, we computed a metric which we term the Fisher Information Bias (FIB), which captures the relative height of the peaks in FI compared to a baseline (see *Methods, Fisher information bias*). We defined three versions of this metric, the FIB-0, FIB-22, and FIB-45, which denote the height of peaks in FI around the cardinal orientations, around orientations 22.5° counter-clockwise of cardinals, and around orientations 45° counter-clockwise of cardinals, respectively. For example, to get the FIB-0, we take the mean FI in 20° bins around 0° and 90°, subtract the mean FI in in a baseline orientation range, and divide by the sum of these two means. Because the pre-trained model showed peaks in FI around cardinals only, we focus on the FIB-0 in this section; the FIB-22 and FIB-45 are discussed in the following section (*Training networks on rotated images*). We found that for the pre-trained model, the FIB-0 increased with depth in the network, showing values close to zero for the first four layers, then showing positive values that increase continuously at each layer (navy blue line in Figure 3). In contrast, we found less evidence for a cardinal bias in the randomly initialized model, shown by smaller values of the FIB-0 at all layers (gray line in Figure 3). The difference in FIB-0 between the pre-trained and randomly initialized models was significant starting at the fifth layer (conv2_2), and at all layers deeper than conv2_2 (one-tailed t-test, FDR corrected q=0.01). However, there was a small increase in the FIB-0 at the later layers of the randomly initialized model, reflecting a weak cardinal bias (at the deepest layer, the FIB-0

was still more than 5x as large for the pre-trained model as for the random model). We return to this issue for more consideration in the *Discussion*.

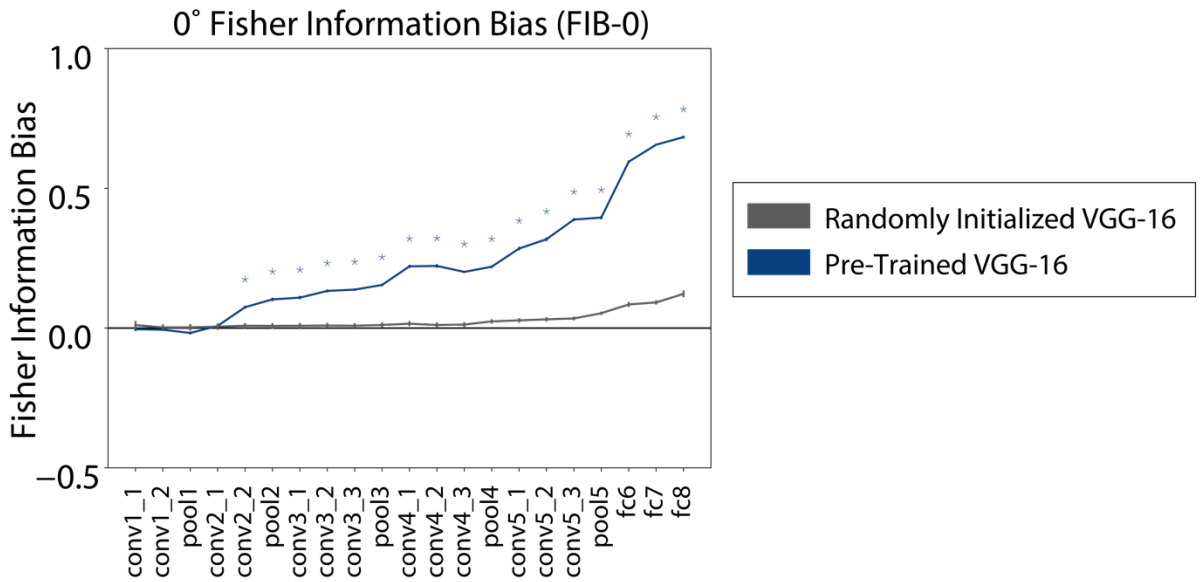

Figure 3. Cardinal bias in a pre-trained VGG-16 model increases with depth. FIB-0, a measure of cardinal information bias (see *Methods, Fisher information bias)*, plotted for a pre-trained model (navy blue) and a randomly initialized control model (gray), with asterisks indicating layers for which the pre-trained model had significantly higher FIB-0 than the random model (one-tailed t-test, FDR corrected q=0.01). Error bars reflect standard deviation across four evaluation image sets.

Having demonstrated that a pre-trained CNN exhibits an advantage for discriminating cardinal versus other orientations, we were next interested in whether this bias was linked to the distribution of tuning properties across single units at each layer, as has been observed in the brains of animals such as cats and macaques (3,4,22). To investigate this, we computed the average orientation tuning profiles for individual units in response to stimuli of all orientations and fit these profiles with Von Mises functions to estimate their center and concentration

parameter (or width, denoted *k*). Units that were not well-fit by a Von Mises were not considered further (approximately 30% of all units, see *Methods, Single-unit tuning analysis* and Figure S1. Figure 2B shows the distribution of fit centers for all units in four example layers of the pre-trained model that were well-fit by a Von Mises function. These distributions show peaks at random locations for the first layer of the network, but exhibit narrow peaks around the cardinal orientations for the deeper conv4_3 and fc6 layers. In contrast, the randomly initialized model did not show an over-representation of cardinal-tuned units (Figure S1). In addition, plotting the concentration parameter for each unit versus the center (Figure 2C) shows that for the deepest three layers shown, the most narrowly-tuned units (high k) generally have centers close to the cardinal orientations. Together, these findings indicate that middle and deep layers of the pre-trained network have a large proportion of units tuned to cardinal orientations, and that many of these units are narrowly tuned.

These findings may provide an explanation for the double-peaked shape of the FI curves for the pre-trained model at deep layers (Figure 2A). Since FI is related to the slope of a unit's tuning function, it is expected to take its maximum value on the flanks of a tuning curve, where slope is highest, and take a value of zero at the tuning curve peak (Figure 1C). Thus, having a large number of narrowly-tuned units with their peaks precisely at 0° and 90° could result in layer-wise FI having local maxima at the orientations just off of the cardinals.

Training networks on rotated images

Having demonstrated that a pre-trained VGG-16 network exhibits a much stronger cardinal orientation bias compared to a randomly initialized network, we next tested whether training a model on rotated images would result in rotated biases. This test is needed to demonstrate that the frequently-observed cardinal bias is not the only possible orientation bias that can be induced in a visual system through exposure to a set of images with non-uniform statistics. We trained networks on three modified versions of the ImageNet dataset (20), consisting of images that were rotated by either 0°, 22.5°, or 45° in a clockwise direction relative to the upright position (Figure 4A). Separately, we also verified that the image statistics of each of the modified sets exhibited the expected distribution, such that vertical and horizontal orientations were most common in the upright training set, orientations 22.5° counter-clockwise of cardinals were most common in the -22.5° rotated set, and orientations 45° counter-clockwise of cardinals were most common in the -45° rotated set (Figure 4B).

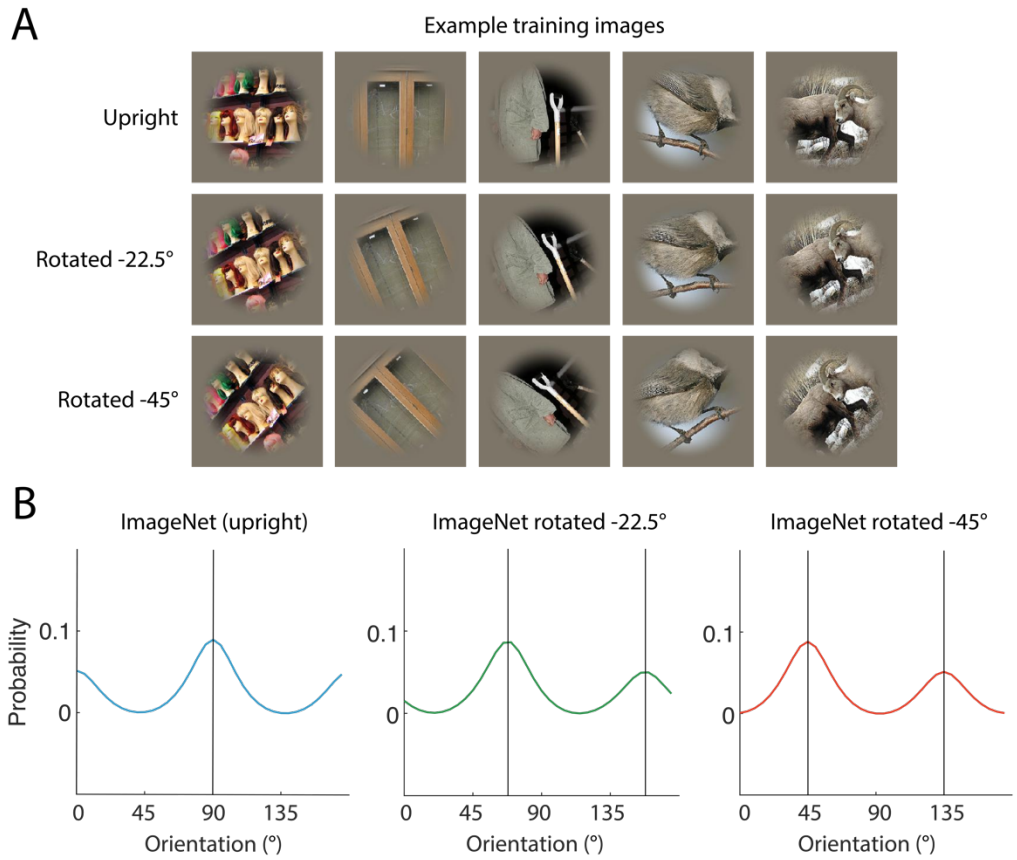

Figure 4. Rotated images used to train VGG-16 networks. **(A)** Separate networks were trained on either upright or rotated versions of the ImageNet image set, with a smoothed circular mask applied to remove vertical and horizontal image edges. **(B)** Orientation content from images in each of the training sets in (A) was measured using a Gabor filter bank (see *Methods, Measuring image set statistics*).

Our results indicate that training on rotated images shifted the orientation bias by a predictable amount. FI for the models that were trained on upright images shows a relatively similar shape to the pre-trained model, with peaks appearing at a few degrees to the left and right of the cardinal orientations (Figure 5A). This demonstrates that though our training procedure and image set were not identical to those used for the pre-trained model, they resulted in the

formation of similar orientation biases. In contrast, the models trained on rotated images each showed a FI curve that was similar in shape but shifted relative to the curve from the model trained on upright images, such that the peaks in FI were always near the orientations that were most common in the training set images (Figure 5D,5G).

The distribution of single-unit tuning properties also shifted with training set statistics. In the upright-trained model, the highest proportion of units had their tuning near the cardinals, while the networks trained on 22.5° and 45° rotated images had more units with tuning at either 22.5° or 45° counter-clockwise relative to the cardinal orientations, respectively (Figure 5B,5E,5H). Additionally, for all models, the most narrowly-tuned units tended to be those that were tuned to the orientations most common in the training set (Figure 5C,5F,5I). As described above, the high number of narrowly-tuned units with their centers close to these most common orientations may underly the double-peaked shape seen in FI.

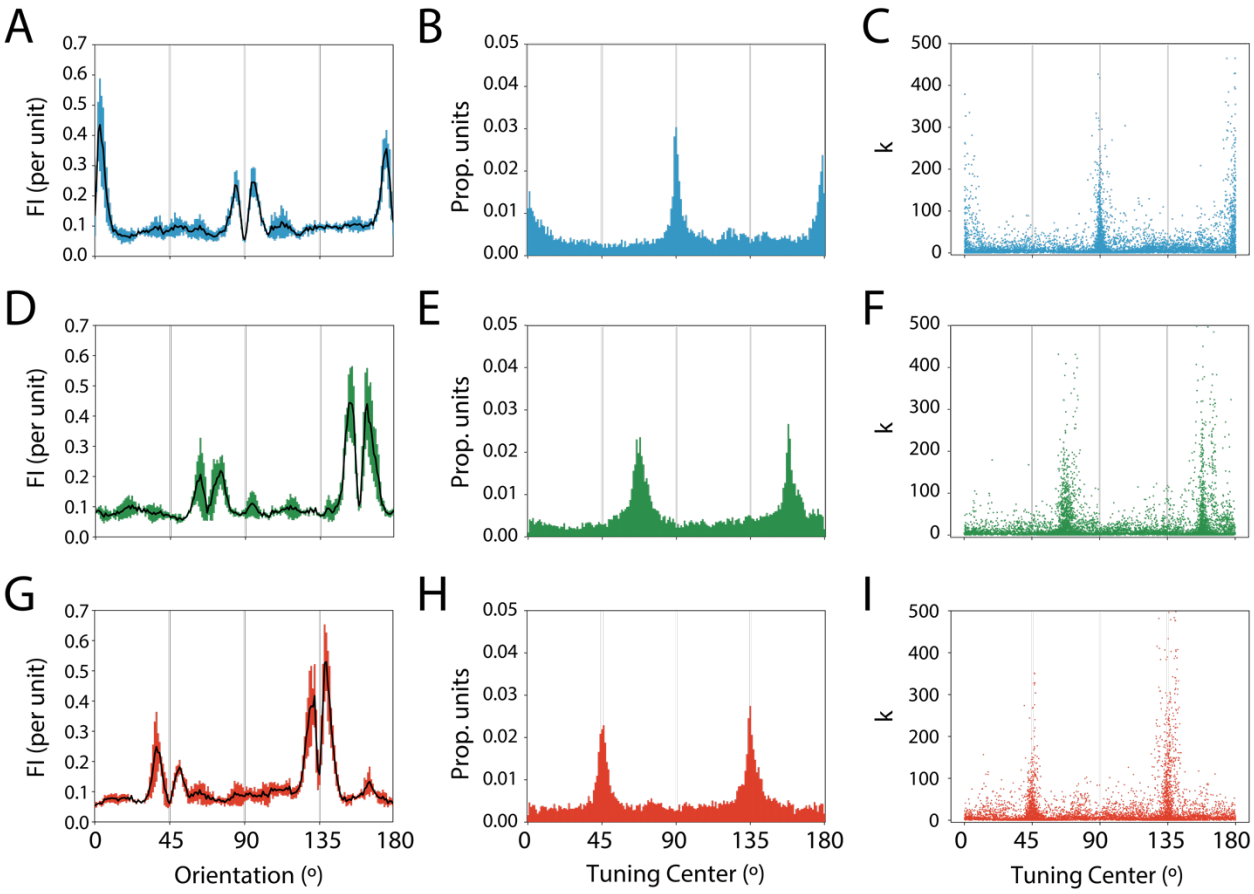

Figure 5. When networks are trained on rotated images, both population-level information and single unit tuning distributions reflect modified training set statistics. **(A-C)** show data from one example layer (fc6) of four separately initialized networks trained on upright images, **(D-F)** show data for fc6 of networks trained on images rotated 22.5° counter-clockwise of upright, **(G-I)** show data for fc6 of networks trained on images rotated 45° counter-clockwise of upright. For each group of networks, panels **(A,D,G)** show FI plotted as a function of orientation, with error bars reflecting standard deviation across four networks with the same training image set **(B,E,H)** show distribution of fc6 unit tuning centers, combining data across networks **(C,F,I)** show concentration parameter (k) versus center for individual units.

Calculating the FIB for each of these models further demonstrated how these effects emerged across the processing hierarchy. Like the pre-trained model, the models trained on upright images showed high values of the FIB-0 at middle and deep layers: models showed significantly higher FIB-0 than the randomly initialized models for pool1, conv3_1, and all layers deeper than conv3_1 (one-tailed t-test, FDR corrected q=0.01) (Figure 6A). In contrast, the models trained on images rotated by 22.5° and 45° showed higher values for the FIB-22 and FIB-45, respectively (Figure 6B,6C). In models trained on images rotated by 22.5°, the FIB-22 significantly exceeded that of the random models at pool2 and all layers deeper than pool2, with the exception of conv3_3 (one-tailed t-test, FDR corrected q=0.01). For the models trained on 45° rotated images, the FIB-45 significantly exceeded that of the random models for conv3_1 and all layers deeper than conv3_1 (one-tailed t-test, FDR corrected q=0.01).

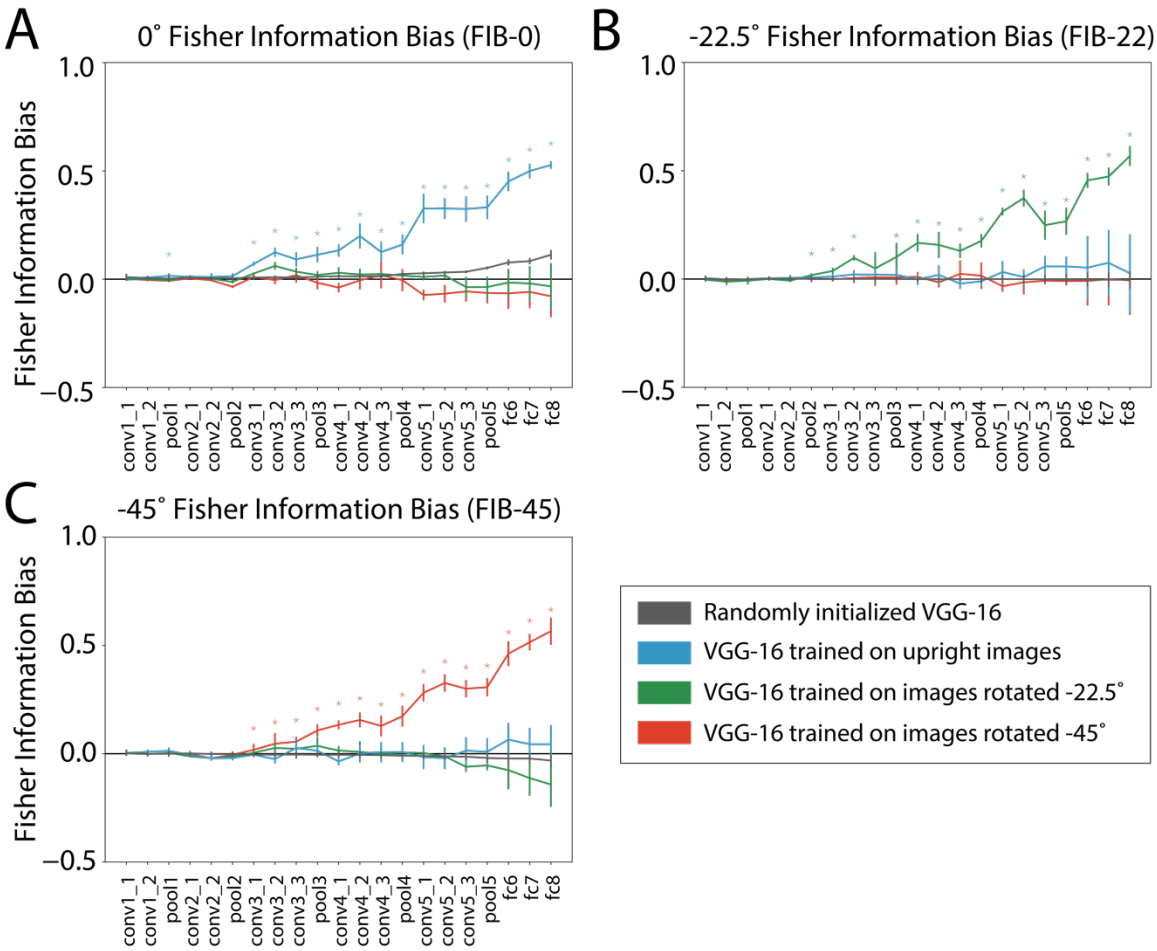

Figure 6. Networks shows biases in orientation discriminability that are consistent with training set statistics. FIB-0, FIB-22, and FIB-45 represent the relative value of FI at cardinal orientations, 22.5° counter-clockwise of cardinals, and 45° counter-clockwise of cardinals, respectively, relative to a baseline (see *Methods, Fisher information bias)*. Panels show **(A)** FIB-0, **(B)** FIB-22, and **(C)** FIB-45 for models trained on each rotated version of ImageNet (colored), and randomly initialized models (gray). Colored asterisks indicate layers for which the models corresponding to that color had significantly higher FIB than the random models (one-tailed t-test, FDR corrected q=0.01). Error bars represent the standard deviation of the FIB over four initializations of each model and four evaluation image sets.

Discussion

We investigated whether CNNs trained to perform object classification exhibit biased orientation representations that reflect non-uniformities in the statistics of the training set images. We found that middle and deep layers of a pre-trained VGG-16 network (17,21) represented orientation with higher discriminability near the cardinal (vertical and horizontal) orientations, with relatively lower discriminability around oblique (diagonal) orientations. Bias was also seen in the tuning properties of single units in the network: there was an over-representation of units that preferred the cardinal orientations, and units tuned to the cardinal orientations had narrower tuning profiles. Furthermore, when we trained models with the same architecture on rotated versions of ImageNet, each of these effects shifted by a predictable amount, such that discriminability was highest near whichever orientations were most common in the network's training set. These results demonstrate that general visual experience with non-uniform image statistics is sufficient to produce the biases that are observed for low-level feature representations in a wide array of biological visual systems.

In general, the strength of the biases we measured tended to increase with depth in each network, showing little or no bias in the first 4-6 layers (Figure 3, Figure 6). In primates, neural correlates of the oblique effect, reflected by an over-representation of cardinal-tuned neurons, have been shown in V1 (5,23,24), V2 (4), and IT cortex (22). To relate these physiology findings to our results, we can consider a recent finding that for a similar network, VGG-19, the ability of network activations to explain data from primate V1 was best at an intermediate layer,

conv3_1, suggesting that earlier layers of the model might be more analogous to processing in the retina and/or lateral geniculate nucleus (25). Therefore, our observation that bias did not emerge until the middle layers of the VGG-16 model is roughly consistent with a cortical origin for the oblique effect. The finding that the bias continues to increase with depth in the network is also consistent with some behavioral and physiological results suggesting that the primate oblique effect may be dependent on higher-order processing beyond V1 (4,16).

Another property of the biases we observed was that the FI measured in deep layers of each network tended to peak just a few degrees off of the orientations that were most common in the training set, with a dip at the precise locations of the most common orientations. As discussed above, this double-peaked shape follows from the fact that FI is highest on the flanks of tuning curves, and many narrowly-tuned units in deep layers tended to have their centers around the most common orientations. However, this finding is not generally reflected in human psychophysics, in which the ability to make small orientation discriminations tends to show a single maximum around each of the cardinal orientations (1,8). One potential reason for this apparent discrepancy is that in this experiment, we were able to present a relatively large number of images (8640 per image set) to the CNN, with images finely spaced by 1° steps in orientation, whereas psychophysics experiments typically present fewer images at more coarsely spaced orientations (8,16,26). Additionally, we were measuring directly from every unit without any additional sources of downstream noise or interference, which may have made the double-peaked shape of Fisher information more apparent than it would be when estimating orientation thresholds from behavior (27). It is also possible that this qualitative difference between the FI curves we measured and the shape of human discriminability

342 functions represents an actual difference between visual processing in CNNs and primates.
343 More extensive behavioral experiments may be needed to resolve this.
344
345 Finally, we also observed weak evidence for a cardinal bias in FI measured from the deep layers
346 of a random network with no training (Figure 3, Figure 6A). This may indicate that some aspect
347 of the model's architecture, such as its use of a square image grid, square convolutional kernels,
348 and pooling operations over square image regions, introduced an intrinsic cardinal reference
349 frame. However, the possible presence of such a reference frame cannot account for the
350 effects we observed for several reasons. First, the magnitude of the FIB-0 was 5x lower for the
351 deepest layer of the random models as compared to the trained-upright models, and the
352 random models did not show an over-representation of cardinal-tuned units, while the upright-
353 trained models did (Figure 2B, Figure 5B, Figure S1). This suggests that the network response
354 properties underlying any intrinsic cardinal FI bias were different than those underlying the
355 experience-driven biases we observed. Second, the magnitude of the shifted biases we
356 measured in models trained on rotated images were of similar magnitude to the cardinal biases
357 we measured in models trained on upright images (Figure 6), which demonstrates that having
358 an intrinsic reference frame that matches the orientation distribution of training images is not
359 required for a substantial bias to emerge. These results suggest that training may be able to
360 override some intrinsic response properties of CNNs. However, they also highlight the general
361 importance of examining the biases inherent in CNNs before making analogies to the visual
362 system.
363

These findings also have general relevance for the use of CNNs in vision research. First, our results show that a popular CNN model exhibits a form of the classical oblique effect, suggesting that this key aspect of low-level primate vision is reproduced by the model. This adds to a growing body of work demonstrating similarities between deep neural networks and the brains and behavior of primates (28–32). Second, we have demonstrated that non-uniformities in the statistics of training set images can dramatically influence the feature representations that are learned by a CNN. Specifically, image features that are over-represented during training are likely to be more discriminable by the trained network, which may lead to a performance advantage for processing certain stimuli over others. Accounting for such influences is critical for avoiding unwanted algorithmic biases, particularly in modeling high-level visual functions such as face recognition (33,34).

Overall, our results suggest that the classical oblique effect is reproduced in a CNN trained to perform object recognition on an image set containing an over-representation of cardinal orientations. Furthermore, a rotated version of this bias can be induced by training a CNN on rotated versions of these same images. These results indicate that general visual experience, without the presence of an innate bias that matches the viewed orientation distribution, is sufficient to induce the formation of orientation biases, providing support for an experience-driven account of the oblique effect.

Materials and Methods

Training stimuli

During training, each model was presented with a modified version of the ILSVRC-2012-CLS training image set, a set of ~1.3 million colored images with substantial variability in layout and background, each including an object in one of 1,000 categories (20,35). Three modified versions of this image set were generated, corresponding to rotations of 0°, 22.5°, and 45° counter-clockwise relative to vertical (Figure 4A). The purpose of generating a 0° (no rotation) version of the image set was to provide a control to isolate the effect of image rotation from any other properties of our modified image set.

To generate each version of the image set, we loaded each image from the original ILSVRC image set, rotated it by the specified amount, and cropped the image centrally by a specified amount that was the same for all rotations. Images were then scaled to a size of [224 x 224] pixels, and multiplied by a smoothed circular mask. The smoothed mask set to background all pixels at a radius of more than 100 pixels from the center, retained all pixels at a radius of less than 50 pixels from the center, and applied a cosine function to fade out the intermediate pixels. Finally, the background pixels were adjusted to a grey color that closely matches the mean RGB value of the training ImageNet images (17). All image processing for training set images was done in Python 3.6 (Python Software Foundation, Wilmington DE) using the Python Imaging Library. For each training set, a corresponding validation set was generated using the

same procedure, and this validation set was used to evaluate performance during training. When preprocessing the images for training and validation, we modified the procedure from Simonyan and Zisserman's paper by skipping the random rescaling and random left-right flipping steps. The purpose of this was to preserve the original spatial frequency and orientation content of the images as closely as possible.

Evaluation stimuli

Networks were evaluated using sets of images that had known orientation content (Figure 1B). To generate these image sets, we randomly sampled images from the ILSRVC-2012-CLS image set and filtered them to have a particular orientation content. Before filtering each image, we first rotated it by a randomly chosen value in the range of 0-179 degrees, then cropped it centrally to a square and scaled to a size of [224 x 224] as described above. This was done to prevent any dependencies between orientation and other low-level image properties, such as spatial frequency content and luminance contrast, in the final filtered images. After this step, we converted to grayscale, z-scored the resulting luminance values, and masked the image with the smoothed circular mask described above. The image was then padded with zeros to a size of [1012 x 1012] pixels, and transformed into the frequency domain. We multiplied the frequency-domain representation by an orientation filter consisting of a circular Gaussian (Von Mises) function centered at the desired orientation (k=35) and a bandpass spatial frequency filter with Gaussian smoothed edges (0.02 to 0.25 cycles/pixel, SD=0.005 cycles/pixel). We then replaced the image's phase with random values uniformly sampled between -pi to +pi, and

transformed back into the spatial domain. Next, we cropped the image back to its original size of [224 x 224], multiplied again by the smoothed circular mask, and converted the image into a 3-channel RGB format. Finally, the luminance in each color channel was normalized to have a mean equal to the mean of that color channel in the training ImageNet images and a standard deviation of 12 units. All image processing for the evaluation image sets was done using Matlab R2018b (MathWorks, Natick MA).

Using the above procedures, we generated four evaluation image sets, each starting with a different random set of ImageNet images. Images in each evaluation set had orientations that varied between 0° and 179°, in steps of 1°, resulting in 180 discrete orientation values. Throughout this paper, we use the convention of 0° for vertical and 90° for horizontal orientations, with positive rotations referring to the clockwise direction, and negative rotations referring to the counter-clockwise direction. Each evaluation set included 48 examples of each orientation, for a total of 8640 images per set.

Measuring image set statistics

To verify that the modified versions of the ImageNet images had the anisotropic orientation statistics that we expected, we measured the orientation content of each training image using a Gabor filter bank. The filter bank included filters at orientations from 0° to 175° in 5° steps, at spatial frequencies of 0.0200, 0.0431, 0.0928, and 0.200 cycles per pixel. The filter bank was generated using the *gabor* function in Matlab R2018b (MathWorks, Natick MA). Before filtering each image, we converted each image to grayscale, and subtracted its background color so that

452 the background was equal to zero. Filtering was done in the frequency domain. After converting
453 back to the spatial domain, we averaged the magnitude of the filtered image across all pixel
454 values to obtain a single value for each filter orientation and spatial frequency. To visualize the
455 distribution of orientation content across all images, we z-scored the magnitude values across
456 the orientation dimension, averaged over spatial frequency, and divided the resulting values by
457 their sum to estimate the probability distribution over orientation. This analysis was done on
458 the training set images only, which included ~1300 images in each of 1000 categories, for a
459 total of ~1.3 million images.
460
461 *Network training and evaluation*
462
463 We trained VGG-16 networks (17) on three different modified versions of the ImageNet dataset
464 (see *Training stimuli* for details). For each of the three image sets, we initialized and trained
465 four VGG-16 networks (replicates), giving a total of 12 models. All models were trained using
466 Tensorflow 1.12.0 (36), using the TF-slim model library (21) and Python 3.6 (Python Software
467 Foundation, Wilmington DE). All models were trained using the RMSProp algorithm with
468 momentum of 0.80 and decay of 0.90. The learning rate was 0.005 with an exponential decay
469 factor of 0.94, and the weight decay parameter was 0.0005. Networks were trained until
470 performance on the validation set (categorization accuracy and top-5 recall) began to plateau,
471 which generally occurred after around 350K-400K steps. The validation images used to evaluate
472 performance were always rotated in an identical manner to the training set images. Training
473 was performed on an NVIDIA Quadro P6000 GPU (NVIDIA, Santa Clara CA). All evaluation was

performed using the first checkpoint saved after reaching 400K steps. As noted above, we did not perform data augmentation steps during image pre-processing for training. Removing these procedures may have contributed to the relatively low final classification performance that we observed (top-5 recall accuracy ~60%).

To measure activations from each trained network, we split the evaluation image sets (consisting of 8640 images each) into 96 batches of 90 each. We then passed each batch through each trained network and measured the resulting activations of each unit as the output of the activation function (a rectified linear operation). We saved the activations for each unit in each layer for all images, which were then submitted to further analysis. We performed this evaluation procedure on a total of 17 networks: the 12 models trained on modified ImageNet images, a pre-trained VGG-16 network from the TF-slim model library (21), and four randomly initialized VGG-16 models that served as a control. All subsequent analyses were performed using Python 3.6 (Python Software Foundation, Wilmington DE).

Computing Fisher information (FI)

To measure the ability of each network layer to discriminate small changes in orientation, we estimated Fisher information (FI) as a function of orientation. To estimate FI for each network layer, we first computed FI for each unit in that layer, then combined information across units. FI for each unit was computed based on the slope and variance of that unit's activation at each point in orientation space, according to the following relation:

$$FI_i(\theta) = \frac{\left(\frac{\partial f_i(\theta)}{d\theta}\right)^2}{v_i(\theta)}$$

Where $f_i(\theta)$ is the unit's measured orientation tuning curve, and $v_i(\theta)$ is the variance of the unit's responses to the specified orientation. We estimated the slope of the unit's tuning curve at θ based on the difference in its mean response (μ_i) to sets of images that were Δ=4° apart (using different values of Δ did not substantially change the results).

$$\left(\frac{\partial f_i(\theta)}{d\theta}\right) \cong \frac{\mu_i(\theta_1) - \mu_i(\theta_2)}{\Delta}$$

Where

$$\theta_1 = \theta - \frac{\Delta}{2}$$

$$\theta_2 = \theta + \frac{\Delta}{2}$$

We presented an equal number of images (48) at each orientation, so the pooled variance was calculated as:

$$v_i(\theta) = \frac{v_i(\theta_1) + v_i(\theta_2)}{2}$$

Finally, we summed this measure across units of each layer to obtain a population level estimate of FI.

$$FI_{pop}(\theta) = \sum_{i=0}^{nUnits} FI_i\,(\theta)$$

Where $nUnits$ is the number of units in the layer. We computed $FI_{pop}(\theta)$ for theta values between 0° and 179°, in steps of 1°. When plotting FI (Figure 2A, Figure 5A), to aid comparison of this measure across layers with different numbers of units, we divided FI_{pop} by the total number of units in the layer, to capture the average FI per unit.

Fisher information bias (FIB)

To quantify the amount of bias (non-uniformity) in Fisher information at each layer of the network, we computed a measure which we refer to as the Fisher information bias (FIB). For the pre-trained model and the networks trained on upright images, we expected the network to over-represent cardinal orientations, showing peaks in FI around vertical and horizontal. However, the models trained on rotated images were expected to show peaks rotated by a specified amount relative to the cardinal orientations. To account for these different types of bias, we computed three versions of the FIB: one that measures the height of peaks in FI around the cardinal orientations (FIB-0), one that measures the height of peaks in FI that are 22.5° counter-clockwise of the cardinals (FIB-22), and one that measures the height of peaks in FI that are 45° counter-clockwise of the cardinals (FIB-45), relative to a baseline. The equation for each FIB measure is as follows:

$$FIB = \frac{FI_{peaks} - FI_{baseline}}{FI_{peaks} + FI_{baseline}}$$

Where FI_{peaks} is the sum of the FI values in a range $\pm 10°$ around the orientations of interest (0° and 90° for FIB-0, 67.5° and 157.5° for FIB-22, and 45° and 135° for FIB-45), and $FI_{baseline}$ is the sum of the FI values in a range $\pm 10°$ around the orientation chosen as a baseline (22.5° and 112.5°). Since FI is necessarily positive, each of these FIB measures can take a value between +1 and -1, with positive values indicating more information near the orientations of interest relative to the baseline (peaks in FI), and negative values indicating less information near the orientations of interest relative to baseline (dips in FI).

To test whether FIB differed significantly between trained models and the randomly initialized (not trained) models, we performed t-tests between FIB values corresponding to each training set and the random models. Specifically, we tested the hypothesis that the primary form of bias measured in models corresponding to each training set (e.g. FIB-0 for the models trained on upright images, FIB-22 for the models trained on 22.5° rotated images, FIB-45 for the models trained on 45° rotated images) was significantly higher for the models trained on that image set than for the random (not trained) models. Since we generated four replicate models for each training image set, and evaluated each model on four evaluation image sets, there were 16 total FIB values at each layer corresponding to each training set. All tests were implemented as one-tailed t-tests using SciPy (version 1.1.0), assuming unequal variance. The p-values were FDR

corrected across model layers at q=0.01 (37). The same procedure was used to test for differences in FIB-0 between the pre-trained model and the control model (note that there was only one replicate for the pre-trained model, so this test included only 4 data points).

Single-unit tuning analysis

To measure the extent to which training set statistics impacted the orientation tuning of individual units in each network, we measured tuning functions based on each unit's responses to the evaluation image set, and we performed curve fitting to quantify tuning properties. First, we measured an orientation tuning function for each unit at each layer of the model by averaging its responses to all evaluation set images that had the same orientation (in each image set, there were 48 images at each of 180 orientations). Any units that had a constant response across all images or a zero response to all images were removed at this stage (this included mainly units whose spatial selectivity was outside the range stimulated by the circular image aperture, around 35% of units per layer at the earliest layers). We computed and saved an orientation tuning curve for each unit in response to each of the four evaluation image sets. We then averaged over these four evaluation sets before fitting.

To characterize the tuning curves, we fit each with a circular Gaussian (Von Mises) function, having the basic form:

$$v(\theta) = e^{(k*\cos(\theta-u)-1)}$$

Where u is a parameter that describes the center of the unit's tuning function, and k is a concentration parameter that is inversely related to the width of the tuning function. In this formulation, the k parameter modifies both the height and the width of the tuning function. To make it possible to modify the curve's height and width independently, we normalized the Von Mises function to have a height of 1 and a baseline of 0, and then added parameters for the amplitude and baseline, as follows:

$$f(\theta) = b + a * v_n(\theta)$$

Where $v_n(\theta)$ denotes the Von Mises function after normalization. This resulted in a curve with four total parameters: center, size, amplitude, and baseline.

We fit a curve of this form to each unit's average tuning function using linear least-squares regression, implemented with the optimization library in SciPy (version 1.1.0). To initialize the fitting procedure, we used the argmax of the tuning function as an estimate of its mean, the minimum value as an estimate of its baseline, and the range as an estimate of its amplitude. The concentration parameter k was always initialized at 1. Values for the center were constrained to lie within the range of [-0.0001, 180.0001], k was constrained to positive values $>10^{-15}$, and amplitude and baseline were allowed to vary freely. To prevent any bias in the center estimates due to the edges of the allowed parameter range, we circularly shifted each curve by a random amount before fitting.

After fitting was complete, we assessed the goodness of the fit using R^2. To assess the consistency of tuning across different versions of the evaluation image set, we used R^2 to assess the fit between the single best-fit Von Mises function (computed using the tuning function averaged over all evaluation image sets) and each individual tuning curve (there were four individual tuning curves, each from one version of the evaluation image set). We then averaged these four R^2 values to get a single value. We used a threshold of average $R^2 > 0.40$ to determine which units were sufficiently well-fit by the Von Mises function, and retained the parameters of those fits for further analysis.

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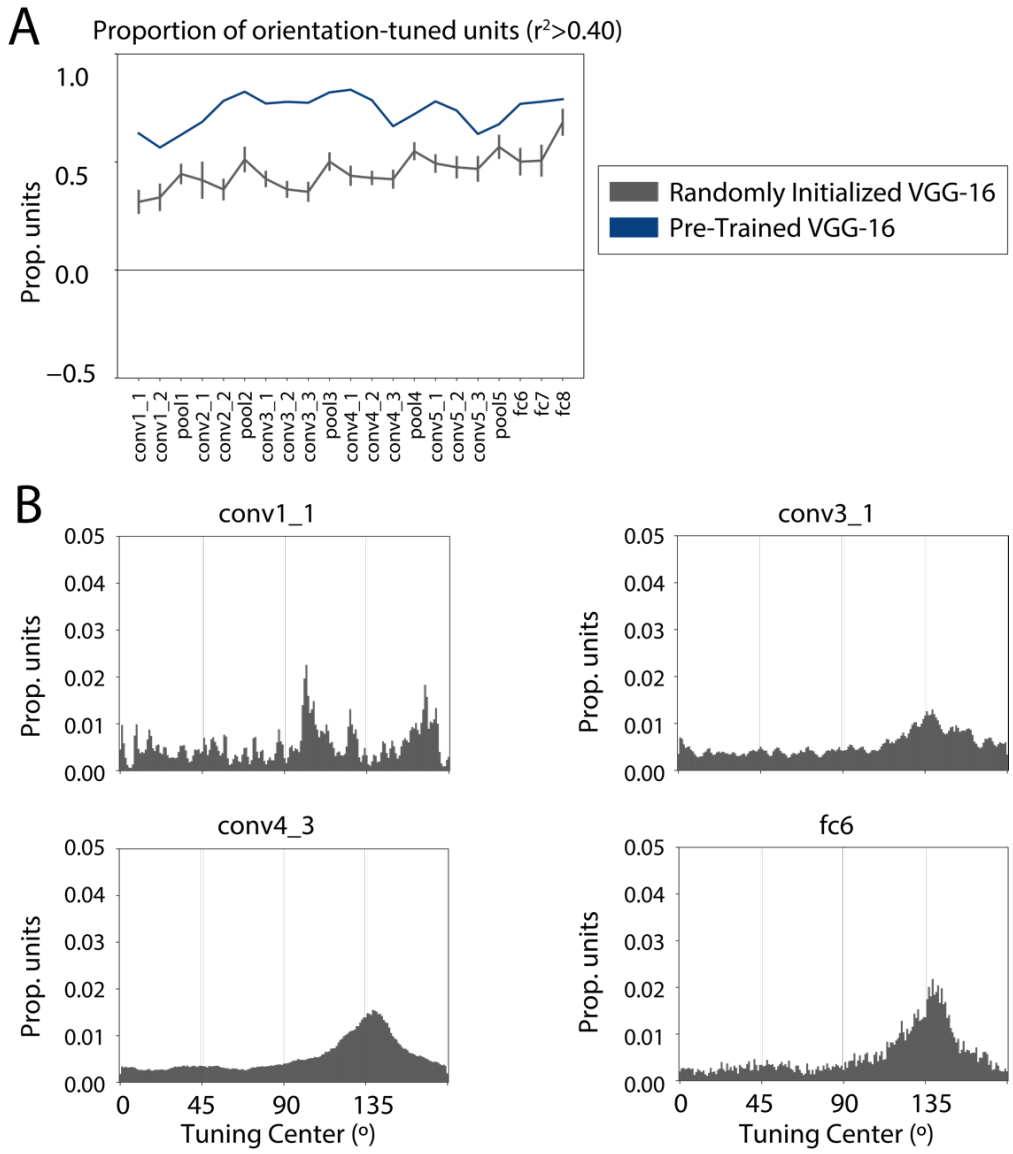
728 **Supporting Information**



729

730 **S1 Fig. (A)** Proportion of units in each layer that were well-fit by a Von Mises function (see

731 *Methods, Single-unit tuning analysis*), for a pre-trained VGG-16 model (navy blue) and randomly

732 initialized models with no training (gray). Error bars on the gray line reflect standard deviation

733 across four different random initializations of the model. **(B)** Distribution of pre-trained network

734 unit tuning centers for the randomly initialized models (distributions are combined across four

735 different random initializations of the model).