Learning a Model of Shape Selectivity in V4 Cells Reveals Shape Encoding Mechanisms in the Brain

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The mechanisms involved in transforming early visual signals to curvature representations in V4 are unknown. We propose a hierarchical model that reveals V1/V2 encodings that are essential components for this transformation to the reported curvature representations in V4. Then, by relaxing the often-imposed prior of a single Gaussian, V4 shape selectivity is learned in the last layer of the hierarchy from Macaque V4 responses. We found that V4 cells integrate multiple shape parts from the full spatial extent of their receptive fields with similar excitatory and inhibitory contributions. Our results uncover new details in existing data about shape selectivity in V4 neurons that with additional experiments can enhance our understanding of processing in this area. Accordingly, we propose designs for a stimulus set that allow removing shape parts without disturbing the curvature signal to isolate part contributions to V4 responses.

Key words: learning shape; shape selectivity; sparse coding; V4

Significance Statement

Selectivity to convex and concave shape parts in V4 neurons has been repeatedly reported. Nonetheless, the mechanisms that yield such selectivities in the ventral stream remain unknown. We propose a hierarchical computational model that incorporates findings of the various visual areas involved in shape processing and suggest mechanisms that transform the shape signal from low-level features to convex/concave part representations. Learning shape selectivity from Macaque V4 responses in the final processing stage in our model, we found that V4 neurons integrate shape parts from the full spatial extent of their receptive field with both facilitatory and inhibitory contributions. These results reveal hidden information in existing V4 data that with additional experiments can enhance our understanding of processing in V4.

Introduction

Transformation of the shape signal in the ventral stream from low-level visual representations of V1 (oriented edges) (Hubel and Wiesel, 1959; Hubel, 1963) and V2 (corners and junctions) (Hegdé and Van Essen, 2000; Ito and Komatsu, 2004) to more abstract representations in IT (objects, faces, etc.) (Tanaka, 1996; Kobatake et al., 1998) is still unknown. V4, as an intermediate processing stage in this pathway and as the major source of input to IT, is believed to play a role in this transformation (Roe et al., 2012; Pasupathy et al., 2020). Yet, selectivities to shape features in V4 neurons add to this mystery. Specifically, with many V4 neurons selective to convex and concave shape parts at a specific position relative to the object center (Pasupathy and Connor, 1999, 2001, 2002), it remains unclear how such part-based and object-centered curvature representations are achieved in the ventral stream. Here, we tackle this problem in two steps: (1) transformation of the shape signal into an object-center curvature encoding in the ventral stream; and (2) part-based selectivity in V4.

Step 1: signed curvature encoding

Findings of shape processing in V4 provide evidence for selectivity to two curvature components: curvature magnitude (deviation from a straight line) and curvature sign (convexity-concavity, determined according to a set origin), together defining the scalar called signed curvature. Figure 1a depicts how two curve segments can share the same curvature sign with different curvature magnitudes or have the same curvature magnitude but different curvature signs. A V4 neuron selective to acute convexities at the top right side of its receptive field (RF) exhibits strong responses to stimuli in Figure 1a-2 and not to those on either side (for such a tuning in a Macaque V4 cell, see Pasupathy and Connor, 2001, their Fig. 5).
The angular position and curvature (APC) model introduced in Pasupathy and Connor (2001) revealed signed curvature selectivity in V4 neurons. Despite the observed selectivities to both curvature magnitude and sign, existing models of V4 encode curvature magnitude but none models curvature sign (for details, see Table 1). Lack of a curvature sign encoding in these models results in responses that are in contrast to the reported observations in V4. Figure 1 gives a simple example to demonstrate this disparity. Therefore, when the goal is to understand the development of a signed curvature representation in the ventral stream, these models leave a gap in our understanding of shape signal transformation from orientation encodings to selectivity to a signed curvature representation. This gap is especially evident in the APC model with direct mapping of stimulus shape to the position and signed curvature domain.

**Step 2: part-based selectivity**

Pasupathy and Connor (2001) fit boundary conformation tunings in V4 cells with a Gaussian function in the APC space. However, with the strong prior of fitting a single Gaussian to V4 responses, complex and long-range interactions between shape parts within the RF cannot be captured. Fitting two Gaussians with positive and negative weights, Pasupathy and Connor (2001) reported improvement in predicted responses and suggested a “more complex analysis would provide a much better description of shape tunings.” Nevertheless, the single-Gaussian approach has been used in recent V4 studies (El-Shamayleh and Pasupathy, 2016; Popovkina et al., 2019), providing a limited picture of part-based selectivity in V4. With complex response patterns in IT (Brincat and Connor, 2004), we asked whether similar patterns can be observed in V4 cells as a source of input to IT.

In this work, we introduced a hierarchical network modeling neurons in V1, V2 and V4, dubbed SparseShape, that explicitly models both curvature magnitude and sign. Hence, a signed curvature encoding is achieved that could explain the shape signal transformation in the ventral stream. Then, given model signed curvature encodings, we learned shape part combination...
patterns with no hard constraints on the number of parts, position, or contribution, and investigated the potential impact of including inhibitory shape parts in V4 responses. Specifically, given local curvature cell responses, for each Macaque V4 neuron from the study by Pasupathy and Connor (2001), we used a supervised sparse model to learn a set of contour segments that determine the neuron responses. To the best of our knowledge, SparseShape is the first hierarchical model that provides an explicit signed curvature formulation in the primate ventral pathway.

Materials and Methods

In what follows, we will make a distinction between our model and brain areas by referring to those as layers and areas, respectively. That is, a set of model neurons implementing cells in a brain area will be referred to as a model layer. For example, model layer V2 implements cells in brain area V2. Moreover, whenever a brain area name is preceded with “m,” it is referring to the corresponding model layer, for example, “mV2” for model layer V2.

SparseShape, whose architecture is depicted in Figure 2a, combines and extends two previous models: RBO (Mehrani and Tsotsos, 2021) and 2DSIL (Rodríguez-Sánchez and Tsotsos, 2012). In Figure 2a, each model neuron type in the hierarchy is represented with a single box. The color of each box indicates whether the model neuron is borrowed from the RBO, 2DSIL, remodeled from 2DSIL, or new in SparseShape. In SparseShape, simple and complex cells extract oriented edges. These model neurons represented by magenta boxes in Figure 2a were implemented in both 2DSIL and RBO with the same formulation and parameter settings that we also used in SparseShape. Complex cell responses modulated by early recurrence from the dorsal stream result in border ownership (BO). Model dorsal neurons and BO cells shown in blue boxes in Figure 2a are borrowed from the RBO network. Combining simple and complex cell responses result in two types of endstopped neurons: curvature degree (mEsDeg) and curvature direction (mEsDir). These two types of curvature cells shown in green boxes in Figure 2a are adopted following the endstopping implementation in 2DSIL. Figure 3a depicts the configuration of simple and complex cells that result in curvature degree endstopped cells that at four scales represent curvature magnitude. Figure 3b depicts simple and complex neuron configurations that yield curvature direction representations. Although Rodríguez-Sánchez and Tsotsos (2012) indicated selectivity to curvature sign for neurons in Figure 3b, the example in Figure 3c with one such neuron superimposed on two shapes with convex-concave parts shows that these cells only signal curvature direction. Hence, we will call them curvature direction cells in what follows.

In SparseShape, we modeled the curvature sign representation according to the observation that it can be uniquely determined for any point on the bounding contour of a simple planar closed shape by combining two signals: inside-outside and curvature direction (i.e., the direction toward which the contour curves; Fig. 1b). Neural correlates for both signals in the ventral stream, namely, BO (Zhou et al., 2000) and endstopping (Dobbins et al., 1987; Ito and Komatsu, 2004), support the plausibility of the proposed model. Therefore, curvature sign (mEsSign) encoding is achieved by combining mBO responses with that of curvature direction (mEsDir) neurons. In addition to support from available biological findings, the mBO and mEsDir neurons that give rise to a curvature sign encoding have geometric interpretations that are explained in detail below. Curvature sign (mEsSign) is new in SparseShape compared with 2DSIL, as indicated by the red box in Figure 2a. Combining curvature sign and curvature degree signals yield the signed curvature representation manifested in model local curvature (mLocalCurv) neurons, enclosed in an orange box in Figure 2a, that are remodeled from the original 2DSIL network. In 2DSIL, model local curvature cells combined curvature direction and curvature degree responses and therefore did not encode signed curvature. In SparseShape, however, a proper signed curvature encoding is achieved in these remodeled cells. Finally, model local curvature cells feed their signal to model shape-selective cells in the output layer of SparseShape representing V4 selectivities. The set of weights in this final stage is learned by using a supervised sparse coding algorithm, replacing the heuristic approach used in 2DSIL.

The SparseShape network meets known biological properties with its parameters set according to neurophysiological findings. Our model implements edge- and border-selective neurons at 12 orientations in (0, π) and combines responses of mBO neurons with edge and border selectivity at the same orientation to a single inside-outside signal that is fed to mEsSign cells. Following 2DSIL and RBO, SparseShape implements neurons at 4 scales that result in 8 mLocalCurv maps (4 scales representing curvature magnitude × 2 signs).

Additionally, neurons up to and including mBO, mEsDeg, and mEsDir are the same as those in RBO and 2DSIL, the computational details of which can be found elsewhere (Rodríguez-Sánchez and Tsotsos, 2012; Mehrani and Tsotsos, 2021). Below are outlines of the computations of new and remodeled neurons in SparseShape and the supervised learning step.
Model endstopped: curvature sign. Intuitively, a contour segment of a simple closed curve is convex when the contour segment curves toward inside the shape. Figure 1b gives examples for which curvature direction and inside-outside information determine curvature sign for contour segments as parts of two shapes. Both curvature direction and inside-outside information have geometric interpretations (for details, see Pressley, 2010): for each point on a contour segment, curvature direction denotes the direction of the tangent vector derivative, whereas inside-outside information represents the direction of the unit normal to the curve. When the tangent derivative and unit normal have similar directions, the signed curvature is positive and the curve is convex; otherwise, the contour segment is concave (assuming exclusion of inflection points). In our proposed hierarchy, curvature direction and inside-outside signal are modeled in mEsDir and mBO cells, together making the curvature sign modeling possible in this network.

In SparseShape, at each visual field location, a pair of mBO neurons with identical local feature selectivity but opposite side-of-figure preferences are modeled. Similarly, a pair of mEsDir with opposite direction selectivities but identical orientation are modeled. Between each pair, the neuron with stronger response is called the winning cell, for example, the winning mBO neuron. When the direction of the winning mEsDir and mBO neurons is in agreement, the contour segment is convex and concave otherwise, resulting in the following implementation of mEsSign cells:

Figure 2. The proposed model. a, The SparseShape hierarchy combines and extends two previously introduced hierarchical models: RBO (Mehrani and Tsotsos, 2021) and 2DSIL (Rodríguez-Sánchez and Tsotsos, 2012). The color of each box represents the origin of the neuron from 2DSIL, RBO, or SparseShape. 2DSIL models curvature magnitude and direction through endstopped neurons. To achieve a signed curvature encoding, inside-outside information is represented by incorporating the RBO network modeling BO. In SparseShape, new neurons modeling curvature sign are added to the network that enable signed curvature selectivity in the mV4 layer. Accordingly, the model local curvature cells are remodeled with feedforward signals from curvature degree and sign cells. Similarly, mV4 cells are remodeled with the sparse coding step. b, The various components of the supervised sparse coding algorithm are shown in the cyan box in this figure corresponding to the cyan arrow in a. Given mLocalCurv maps and Macaque V4 responses to stimuli in the training set, the algorithm looks for a combination of shape conformations that could best explain mV4 responses. To account for the various positions of shape parts, a set of 9 Gaussian kernels spanning a $3 \times 3$ grid over the RF filter mLocalCurv responses at each cell. The filtered responses form the part-based vector. The sparse code vector denotes the weight of each part contributing to the responses. The parameters of the Gaussian kernels are fixed while the sparse code vector is learned in this step.
Convex and concave curves, similar to the example HMAX cell in these neurons only encode curvature direction and will exhibit similar responses to both convex and concave shape parts in these two shapes. Interestingly, the configuration of orientation-selective neurons in 2DSIL feeding to mV4 neurons consists of 8 curvature maps, 4 scales respectively. Positive and negative signs indicate facilitatory/inhibitory contributions. Responses of these neurons encode deviation from a straight line.

\[
R_{\text{mESDeg}}(x, y, \theta) = \begin{cases} R_{\text{mESDeg}}(x, y, \theta + \pi/2) & \text{if } \text{mESDeg} \text{ is concave} \\ R_{\text{mESDeg}}(x, y, \theta - \pi/2) & \text{if } \text{mESDeg} \text{ is convex} \end{cases}
\]

\[
R_{\text{mESSign}}(x, y, \theta) = \begin{cases} R_{\text{mESSign}}(x, y, \theta + \pi/2) & \text{if } \text{mESSign} \text{ is concave} \\ R_{\text{mESSign}}(x, y, \theta - \pi/2) & \text{if } \text{mESSign} \text{ is convex} \end{cases}
\]

where \( R_{\text{mESDeg}} \) and \( R_{\text{mESSign}} \) denote the direction of winning mESDeg and mESSign neurons and the multiplication tests their direction alignment. \( \phi \) represents the response of neuron type \( x \) with \( x \in \{\text{mESDeg}, \text{mESSign}\} \) and \( \theta \) denotes the orientation selectivity of the corresponding mESDir or mBO cell. The function \( \phi \) rectifies negative responses to zero.

Model local curvature. Similar to mESDir and mESSign cells, signed curvature is encoded by a pair of mLocalCurv neurons at each visual field location to represent positive and negative signs for a given curvature magnitude. Specifically, at each scale in the hierarchy, a single map of mESDeg and a pair of mESSign (mESSign_convex and mESSign_concave) are combined to yield pairs of mLocalCurv cells as follows:

\[
R_{\text{mLocalCurv,convex}}(x, y) = \max_{\theta_1} \left( R_{\text{mESDeg}}(x, y, \theta_1) \right) \land \left( R_{\text{mESSign,convex}}(x, y, \theta_1) > R_{\text{mESSign,concave}}(x, y, \theta_1) \right)
\]

\[
R_{\text{mLocalCurv,concave}}(x, y) = \max_{\theta_1} \left( R_{\text{mESDeg}}(x, y, \theta_1) \right) \land \left( R_{\text{mESSign,concave}}(x, y, \theta_1) < R_{\text{mESSign,convex}}(x, y, \theta_1) \right)
\]

where "max" retains responses to curvature at this level of the hierarchy and marginalizes orientation. Consequently, the final layer feeding to mV4 neurons consists of 8 curvature maps, 4 scales × 2 signs, representing four levels of acuteness for convexities and concavities.

Model V4: learning RFs. Our goal was to learn V4 RFs such that complex and long-range interactions between shape parts, if they exist, can be captured. Recovering existence or equivalently lack of such interactions in V4 imparts significant insight into shape processing mechanisms in this visual area.

We trained the weights in the last layer of SparseShape, mLocalCurv to mV4, and recovered the RFs from the recordings provided to us by Dr. Anitha Pasupathy. Briefly, for each Macaque V4 cell, we assigned its responses to an mV4 cell in SparseShape and learned the weights from mLocalCurv cells to each mV4 neuron. That is, the procedure for learning the RF was repeated for each individual mV4 cell.

A naively-added, fully-connected layer from mLocalCurv to mV4 cells has more than 14K weights to learn from <366 data points. To compensate for the imbalance between the number of parameters and data, we propose imposing sparsity priors that are compatible with discoveries of V4 curvature (Carlson et al., 2011) and other brain areas involved in shape representation (Tsunoda et al., 2001). We leverage sparsity in a higher dimensional space and with a more relaxed model compared with APC. With the learned RFs, obtaining mV4 responses to any arbitrary stimulus set, such as shapes in the invariance experiment explained in Experimental design, is a simple feedforward pass (with dorsal recurrence) in SparseShape.

Our proposed sparse coding method formulates RF recovery as a supervised learning problem. Specifically, given the responses of mLocalCurv cells and Macaque V4 responses to a stimulus set, we seek a sparse combination of curvature components across the RF that can explain observed responses by minimizing the following objective function:

\[
\min_{\gamma} \sum_{t=1}^{n} \frac{1}{2} || R_t - D_t^T \gamma ||_1 + \alpha \rho || \gamma ||_1 + \frac{\alpha (1 - \rho)}{2} || \gamma ||_2^2.
\]
the error term is enforced through \( \alpha, \rho \) determines the balance between L1 and L2 norms. Both \( \alpha \) and \( \rho \) are set with cross-validation.

The part-based vector \( D_t \) is obtained by a set of Gaussian kernels that filter mLocalCurv maps. In particular, to account for a variety of shape part positions, a \( 3 \times 3 \) grid over the RF filters each mLocalCurv map. Each cell of this grid encompasses a Gaussian kernel. The parameters of each Gaussian characterize the position and extent of a particular curvature component within a cell. Putting these together, \( d_t(i) \), the \( i \)-th element of \( D_t \), is computed as follows:

\[
d_t(i) = \sum_{x,y} C(x,y,t,k) \cdot G(x,y,j;\mu_j,\Sigma_j),
\]

with \( C(x,y,t,k) \) corresponding to the responses in the \( k \)-th mLocalCurv map to stimulus \( t \) at visual location \((x, y)\) with \( k \in \{1, 2, ..., 8\} \). In this equation, \( G(x,y,j;\mu_j,\Sigma_j) \) represents the Gaussian in the \( j \)-th grid cell with parameters \( \mu_j, \Sigma_j \) and \( j \in \{1, 2, ..., 9\} \). We explored learning the parameters of the Gaussian kernels for each neuron. However, we did not find any benefits in learning these kernels compared with fixing those to predetermined kernels. As such, we fixed the parameters of the Gaussians in this work. With \( 8 \) mLocalCurv maps and \( 9 \) cell positions, \( D_t \) and \( y \) in our implementation are \( 72 \)-dimensional vectors.

Having found the desired curvature components and their weights, responses of the mV4 neurons corresponding to a given Macaque V4 cell to an arbitrary stimulus \( s \) can be obtained by:

\[
R_{mV4} = D_t^T y.
\]

The diagram in Figure 2b shows the different components of our sparse coding formulation. The cyan box in this figure corresponds to the cyan arrow in Figure 2a.

**Experimental design.** We conducted experiments with two sets of stimuli: 366 parametric shapes combining convex-concave parts into closed shapes borrowed from Pasupathy and Connor (2001) and parametric shapes with a single varying part along its contour designed according to the set from El-Shamayleh and Pasupathy (2016). The latter set was used to test invariance in mV4 responses. The former shape set, which we call the standard set, was used in all other experiments as well as training the model. The standard set shapes were scaled such that stimulus edges were offset from the RF center by 0.75 × RF size. The shapes in the invariance experiments were scaled following El-Shamayleh and Pasupathy (2016). The SparseShape network input was set to 400 × 400 pixels, and we measured 1° visual angle at 50 cm to be 32 × 32 pixels. We set mV4 RFs at 4° following Fellman and Van Essen (1991) equivalent to 128 × 128 pixels.

Supervised learning in the last layer of SparseShape was performed with electrophysiological responses of 109 Macaque V4 neurons reported by Pasupathy and Connor (2001). That is, for each Macaque V4 cell, we assigned its responses to an mV4 neuron and learned the model weights from mLocalCurv cells to the mV4 neuron. A stratified division of the standard shape set into 60%-40% train and test splits was performed for each individual neuron to ensure an assortment of responses were present in each set. A stratified split has the advantage of reducing sensitivity to the amount of training data. The hyperparameters for learning the last layer weights were determined using cross-validation over the training set followed by learning the weights with all the training shapes. All other model parameters were set according to experimental findings (Rodríguez-Sánchez and Tsotsos, 2012; Mehrani and Tsotsos, 2021).

**Visualizing learned RFs.** Visualizing the learned RFs provides a powerful pictorial tool in revealing shape tuning. Here, we provide a brief explanation of how learned RFs can be visualized as depicted in Figure 7b. Given the mV4 response formulation in Equations 4 and 5, shape tuning in mV4 cells is determined according to three main components: model local curvature neurons signaling presence/absence of contour segments of a particular signed curvature, the Gaussian kernels specifying position/extent of contour segments within the RF, and the learned sparse code vector. In SparseShape, mLocalCurv neurons are analytically defined; therefore, their selectivity is independent of mV4 responses. Accordingly, for each mLocalCurv map in the model, we first determined the contour segment in the standard stimuli dataset that invokes the strongest responses for neurons in the map. Then, for each mLocalCurv map, we create an auxiliary map by replicating this isolated contour segment in each cell of a \( 3 \times 3 \) grid identical to the one we used in computing the part-based vector (Eq. 4). Each auxiliary map is then convolved by the set of Gaussian kernels as specified in Equation 4 and multiplied by its corresponding learned weights in the sparse code vector \( y \). Finally, a summation of all of these maps yields the learned RF.

**Model comparison.** Our goal was to understand signed curvature encodings and part-based selectivities in V4 neurons. This goal can be best achieved by training and evaluating the model with available neural data. Therefore, we conducted this study with responses of Macaque V4 neurons reported in Pasupathy and Connor (2001), provided to us by Pasupathy. Specifically, we trained and evaluated our model according to responses of Macaque V4 neurons. To measure model performance, we evaluate individual mV4 cell predictions following Pasupathy and Connor (2001). That is, we report Pearson’s \( r \) correlation coefficients between predicted and observed Macaque V4 responses, separately for train and test sets. Although correcting for trial-to-trial noise could afford an unbiased estimate in reported correlations (Pospisil and Bair, 2021), the Macaque V4 responses we used in our study consisted of a single response per neuron per shape in the standard dataset with no noise analysis incorporated. In other words, with the available data, there was no flexibility to evaluate performance on a trial-to-trial basis and with noise. Therefore, following Pasupathy and Connor (2001) and Cadieu et al. (2007), we report correlation coefficients. Additionally, we report mean absolute error (MAE) of responses following Rodríguez-Sánchez and Tsotsos (2012).

We compare our model performance against two previous hierarchical models for V4, namely, 2DSIL (Rodríguez-Sánchez and Tsotsos, 2012) and HMAX (Cadieu et al., 2007). Among previous hierarchical models (Table 1), these two models are closely related to our proposed model with direct comparison with Macaque V4 data from the study by Pasupathy and Connor (2001) that we also used for training/testing our mV4 cells. Additionally, both models used the same stimulus set as SparseShape, the standard set, for their experiments and evaluation. Both 2DSIL and HMAX modeled curvature magnitude and direction across a contour segment using a 2D Gaussian. Both models used heuristic approaches to determine weights representative of V4 selectivities in their hierarchies. HMAX used a greedy algorithm to recover V4 RFs (see Cadieu et al., 2007, their Fig. 9), while shape templates in 2DSIL were computed based on common shape parts among each neuron’s preferred stimuli. In HMAX, the recovered RFs do not necessarily result in curvature-like configurations; whereas in 2DSIL, having a shape template is not guaranteed (they reported results for 75 of 109 Macaque V4 cells).

Alongside HMAX and 2DSIL, we compare our model performance with that of the APC model (Pasupathy and Connor, 2001). APC represents signed curvature and thus is most similar to SparseShape, but it was proposed to recover tunings rather than to explain mechanisms. As such, it is important to keep in mind that, whereas our goal was to understand the transformation of the signal in a step-by-step manner to a signed curvature encoding, the APC model avoids the need to bypass crucial steps in this transformation and perform a direct mapping of stimulus shape to the position and signed curvature domain to recover tunings.

In addition to fitting the tunings in the two-dimensional APC space (we term this the APC-2D model), Pasupathy and Connor (2001) evaluated a four-dimensional APC model (three curvatures and one angular-position) by considering the two neighboring curvature components on either side of a shape part. We call this model APC-4D. It is worth mentioning that Pasupathy and Connor (2001) also modeled V4 responses with two Gaussian peaks in the 2D space of curvature and angular position to recover complex tuning functions. In this model, they allowed both positive and negative amplitudes for the Gaussians to capture facilitatory and inhibitory contributions. Hence, we call this variant APC-2D–inh. Despite incorporating inhibitory shape contributions, Pasupathy and Connor (2001) reported “the average increase in \( r \) was
moderate (0.07)" in APC–2D–inh compared with APC–2D. For this reason, we keep APC–2D as the representative tuning for comparison purposes. Finally, we compare SparseShape with the correlations of neurons in Alexnet (Krizhevsky et al., 2017).

An ideal comparison of our model results to the published results of the HMAX and APC models would require their original code, and neither model code is available. As a result, we extracted correlation coefficients of these models from their correlation histograms in Cadieu et al. (2007, their Fig. 5) and Pasupathy and Connor (2001, their Fig. 9), respectively. These authors did not publish the parameterizations for their model fit to each individual V4 neuron; and even if we had access to their code, there is no guarantee that we could find the parameter initialization that led to their published results. Comparison to their published results via extracted correlations remains the only option. Had we had access to their fit models, direct comparison between the models would be possible. For example, we could report MAE for HMAX and APC along with 2DSIL and SparseShape. Similarly, training on the same validation/train/test sets as those used to train/test HMAX neurons could provide a like-for-like comparison between SparseShape and HMAX. We had model shape neuron responses of 2DSIL that we used for comparison and computation of correlation coefficients for this model. Correlation coefficients of Alexnet were computed as follows: for each biological V4 neuron, we isolated a model cell across all convolutional layers of Alexnet with the largest correlation coefficient in response to the shape stimulus set. This procedure resulted in 109 model cells in Alexnet most similar in responses of the 109 Macaque V4 cells.

Code accessibility. Our code is available on the Open Science Framework website: https://osf.io/u3zka/?view_only=297fc30c24142d682912166bab33dc.

Results

Shape part selectivity

Figure 4a depicts responses of a Macaque V4 neuron to the standard shape set and response differences between Macaque V4 and its corresponding mV4 cell. Small response differences suggest similar selectivities in Macaque V4 and mV4 cells that are also confirmed with the strong correlations demonstrated in Figure 4b. To measure this similarity in the population, we computed the MAE separately for train and test shapes for all 109 Macaque V4 cells, illustrated in Figure 5a. This figure demonstrates a decrease of MAE in SparseShape versus 2DSIL in 75 Macaque V4 neurons. Additionally, the remaining 34 cells follow a similar trend in train and test MAE. The average MAE over all mV4 cells is 0.09 in SparseShape versus 0.18 in 2DSIL. MAEs for the rest of the models were not available; therefore, these models are missing in Figure 5a.

We computed the correlation coefficients, r, as a goodness-of-fit measure between Macaque and model cell responses following Pasupathy and Connor (2001) and Cadieu et al. (2007). While the APC model was fit based on responses to all 366 stimuli, HMAX used a six-fold cross-validation and reported the average correlation coefficient. In other words, HMAX fits six models to each V4 cell and reports the average performance of the six models. Cross-validation correlations are not appropriate indicators of the generalization abilities of the model; and with six models learned for each neuron, it is unclear which must be considered as the true model of the cell. However, in absence of generalization data from HMAX, we compare SparseShape with their reported cross-validation correlations. SparseShape evaluation is based on separate train/test splits that were explained earlier. Figure 5b illustrates the correlation coefficient distributions for APC–2D, APC–4D (extracted from correlation histograms in Pasupathy and Connor, 2001, their Fig. 9), HMAX (extracted from correlation histograms in Cadieu et al., 2007, their Fig. 5), Alexnet (extracted from Pospisil et al., 2018, their Fig. 14), 2DSIL, and SparseShape. A ridgeline plot separates these distributions. For easier comparison, SparseShape–train/test distributions are plotted as solid and dotted curves, respectively, in rows of other models.

Despite the slight shift in the correlations distribution for HMAX–train compared with SparseShape–train depicted in Figure 5b, both models have comparable medians at 0.72 and 0.71, indicating a great overlap between the simulated populations. In contrast, SparseShape–test distribution is slightly shifted with a larger median at 0.6 compared with 0.57 for HMAX–test, demonstrating better generalization ability over the standard set for SparseShape. The impressive correlations and recovery of V4 selectivities that HMAX displays are based on the assumption that there are no intermediate computational stages between orientation (complex) neurons and 2D shape cells. This is in line with the way computer vision has viewed the problem of 2D shape over the past; it is not consistent with the available neurobiology, however, that shows a much richer connectivity (see Ungerleider et al., 2008) that would suggest this assumption is oversimplifying the network. This has a number of consequences. HMAX neurons are insensitive to the position of the shape within their RF as we demonstrated in Figure 1c, whereas V4 cells do exhibit sensitivity to shape position (Pasupathy and Connor 1999). An intermediate step of curvature sign between orientation selectivity in V1 and shape selectivity in V4 would have provided what is required to make these cells position aware, as our model shows. Second, the assumption leads to HMAX being a single-task network: it may provide a good fit to a particular set of V4 data, but when situated in a full network (e.g., detailed by Ungerleider et al., 2008, and many others), HMAX alone may not play the full role for which those neurons are responsible. Other perceptual functions, such as BO, figure-ground segmentation, localizing concave or convex shape elements, recognizing sharpness of shape, and more, would fall outside the range of HMAX.

Interestingly, Alexnet with a deep convolutional neural network architecture is outperformed by all other models, except for 2DSIL and APC–2D, demonstrating a poor fit of its units to V4 data.

The APC distributions are most interesting. Despite the fit to the whole standard set, both APC–4D and APC–2D distributions are shifted to smaller correlations compared with the SparseShape. Larger correlation coefficients in APC–4D versus APC–2D, as pointed out by Pasupathy and Connor (2001), suggest complex configuration encodings in V4 cells. Likewise, comparing APC–4D and SparseShape distributions suggests a complicated pattern of interactions between shape parts within V4 RFs, beyond a combination of three adjacent parts.

Pasupathy and Connor (2001) reported moderate improvement in correlation coefficients in their APC–2D–inh model by fitting two Gaussians with arbitrary contributions (facilitatory and inhibitory) in the APC space. To quote Pasupathy and Connor (2001), they suggested that “the two-Gaussian analysis is just one fairly simple approach, and it may be that another, more complex analysis would provide a much better description of shape tuning.” Despite this suggestion, the APC–2D model has been used in recent V4 studies (El-Shamyyleh and Pasupathy, 2016; Popovkina et al., 2019), thus not capturing some of the details that APC–2D–inh might include. In contrast, the correlation coefficients of SparseShape versus those of both APC–2D and APC–2D–inh suggest that our model captures details that a simple two-Gaussian model cannot. For example, the supervised sparse coding step in SparseShape with no hard constraints imposed on the number of contributing shape parts provides a
fairly simple approach to reveal a richer description of shape tuning in these neurons as explored next.

**Sparsity**
To measure the number of parts contributing to mV4 responses in SparseShape, we examined the sparsity of the learned sparse code vector as the percentage of its nonzero elements separately for convex and concave parts for each mV4 cell. Figure 6a demonstrates the sparsity distribution for the population with each neuron displayed as a dot. This distribution suggests contributions from more than a single or even three shape parts to mV4 responses. Additionally, convex sparsity median at 0.53 compared with 0.5 for concave sparsity implies a bias toward convexities in agreement with the observations reported previously (Pasupathy and Connor, 1999; Carlson et al., 2011).

With more convex parts contributing to mV4 responses, one possibility is smaller convex weights compared with fewer but larger concave weights to compensate for this imbalance. To evaluate this possibility, for each neuron, we normalized the sparse code vector with maximum set at 1. Then, we took the largest weight from each signed curvature type (each mLocalCurv map), resulting in an eight-element vector for each neuron. Considering the population distribution over each element of this vector, a shift to larger weights is expected from signed curvature components with substantial contributions to mV4 responses. Interestingly, as illustrated in Figure 6b, all distributions are relatively overlapping, except for that of

![Figure 4](https://example.com/figure4.png)

**Figure 4.** Responses of a learned mV4 cell. **a**, Two rows Macaque V4 responses and response differences with mV4 to the stimulus set introduced by Pasupathy and Connor (2001). White icon in a square represents each shape. The intensity of the ground in each square indicates the response strength. Small response differences in the second row demonstrate a similar pattern of responses in the mV4 cell and the Macaque V4 cell. **b**, Macaque V4 responses plotted against mV4 activations illustrate a strong correlation between these responses ($r = 0.86$ and $r = 0.83$ for train and test shapes, respectively).
Figure 5. Model performance evaluation. 

a, MAE in responses of model V4 cells for 2DSIL and SparseShape. Neuron errors are plotted in two rows for better visualization. SparseShape improves the performance measured as the mean difference of responses with biological V4 cells compared with 2DSIL.

b, Population distribution of correlation coefficients, $r$, for various V4 models plotted as a ridge-line plot in separate rows. Each model is indicated next to its distribution. The models are sorted according to their medians from bottom to top, with the exception of SparseShape–train. For easier comparison, SparseShape–train distribution is plotted as a solid line for HMAX–train and SparseShape–ablation–train rows and SparseShape–test distribution as a dotted curve in rows for all other models. The median for each distribution is denoted by a diamond shape, the value of which is written in white, and the median of SparseShape–train/test distributions is identified with a black circle in each row. This plot demonstrates that SparseShape has comparable distributions to HMAX with better generalization capacity over the standard shape set and improves the correlation coefficients compared with other models. This plot also includes correlation distributions of an ablation study where we limited the contribution type in SparseShape to facilitatory ones to examine the effects of inhibitory shape parts to V4 responses. Comparing SparseShape and SparseShape–ablation distributions suggest inhibitory shape parts integration in V4. Among all the models, Alexnet and 2DSIL with smaller correlations compared with the rest of the models demonstrate a poor fit of their neurons to V4 data.
Contribution types
If V4 neurons indeed integrate V2 responses in both excitatory and inhibitory manners, models limited to facilitatory weights neglect accounting for important contributions to V4 responses. In SparseShape, both types of contributions are explored during learning and accounted for in the model. To assess the effect of contribution type to mV4 responses, we considered the population distribution of the sum of facilitatory and inhibitory weights in the normalized sparse code vector (max at 1).

Interestingly, as depicted in Figure 6c, the distributions plotted separately for convex and concave parts demonstrate larger inhibitory effects from both convex and concave parts, suggesting that excluding inhibitory contributions result in an incomplete understanding of V4 shape processing. To further investigate the effect of inhibitory contributions, we performed an ablation study in which we restricted part contributions to excitatory ones in SparseShape. With this imposed constraint, as demonstrated in Figure 5b, SparseShape–ablation–train and test correlation distribution medians are decreased to 0.62 and 0.52, respectively. These results, compared with train/test medians at 0.71 and 0.6 in SparseShape.
with inhibitory part contributions, highlight the importance of inhibition in V4 responses.

**RF visualization**

Visualizing the recovered RFs reveals shape selectivities in each mV4 cell. In SparseShape, modeling a hierarchy of representations that include intermediate- and higher-level feature of signed curvature makes explaining the recovered RFs effortless. For instance, Figure 7 shows an example neuron response along with a visualization of its recovered RF. Figure 7b demonstrates selectivity to mild and broad convexities in the top/bottom/right part of the RF. Responses of this cell are inhibited with appearance of mild convexities on bottom right and bottom left parts of the RF, respectively. The recovered RF can be qualitatively verified with the Macaque V4 responses in Figure 7a. For example, the shapes within the green box in Figure 7a have three convex parts on facilitatory positions causing relatively strong activations of the cell. The same shapes rotated with two convex parts within the inhibitory parts of the RF (encompassed with a magenta rectangle) invoke weaker activations in the neuron.

Figure 7b presents an interesting observation: the contributions to this neuron’s responses are from the full spatial extent of the cell with interacting shape parts separated at almost 0.75 × RF size. To quantify the extent of shape part interactions within the RF for each neuron, we computed the distance of all pairs of contributing parts in the RF and took the maximum distance among all parts. Figure 7c shows the mV4 population distance histogram indicating that the majority of neurons integrate shape parts from at least as far as three-fourths of

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**Figure 7.** Recovered mV4 RFs. **a.** Responses of an mV4 cell are shown. The shapes inside the green box evoke strong activations in the biological neuron. Same shapes but rotated at ~45 degrees inside the magenta box evoke much weaker activations in this cell. **b.** The recovered RF of the same neuron whose responses are shown in a. Red and blue represent facilitatory and inhibitory contributions, respectively. Shapes with medium/broad convexities at the top, bottom, and right part of the RF evoke strong activations in the cell. In contrast, medium/broad convexities in the bottom right and left parts of the RF inhibit neuronal responses. The recovered RF displays that shape parts from the spatial extent of the neuron’s RF, as far as 0.75 × RF size, are combined to account for its selectivity. Such long-range interactions between shape parts were not captured in the APC model because of fitting a single Gaussian to neuron responses. **c.** Population histogram of shape part distances within mV4 RFs. The majority of mV4 cells integrate shape parts that are apart at least as far as three-fourths of the RF diameter, suggesting that V4 neurons incorporate V2 responses from the full span of their RF. The 0.95 × RF diameter is for shape parts on the diagonal of the simulated square-shaped RFs.
their RF diameter. This observation suggests that a single-Gaussian prior is far too limiting to capture all the factors contributing to V4 responses.

Visualizing the pattern of learned weights provides a better picture of selectivities in V4 cells. It can also be used as a tool for forming testable hypotheses for shape selectivity in these neurons. For example, if further mining of the learned weights in these neurons reveals RF areas dedicated to facilitatory/inhibitory shape parts, the analysis could assist in introducing models similar to the difference of Gaussians or Gabor models explaining orientation selectivity in simple cells in V1. Such an attempt, if made, will be a step toward better understanding of 2D shape processing in V4. We left further analysis of the learned weights for a future work.

Invariance
El-Shamayleh and Pasupathy (2016) reported a normalized curvature encoding in V4 cells. We probed our mV4 cells to determine whether the learned selectivities encode normalized or absolute curvature (for definitions and details of their experimental setting, see El-Shamayleh and Pasupathy, 2016). For this purpose, we prepared shapes of varying scales similar to those used by El-Shamayleh and Pasupathy (2016) and evaluated systematic shifts in tuning centroids in mV4 responses. Briefly, if these neurons exhibit scale invariance, their tuning peak would not shift with changes in scale. Therefore, measuring the shift in tuning centroids as a function of scale would result in slopes close to zero. To examine whether the observed invariance in responses could be attributed to the shift in the position of boundary configuration, we tested our mV4 responses to changes in stimuli position within RF, similar to El-Shamayleh and Pasupathy (2016). Figure 8a demonstrates a few examples of mV4 neuron responses with scale-invariant selectivities as indicated by the small slopes. Population histograms of tuning centroid slopes, depicted in Figure 8b, c, suggest that the learned mV4 neurons exhibit invariance properties similar to Macaque V4 cells (compare with histograms in El-Shamayleh and Pasupathy, 2016, their Figs. 5, 9).

Results from this experiment are interesting in that our mV4 neurons were trained with a single scale stimulus set. However, the learned weights in SparseShape generalized to account for these variations in responses of Macaque V4 cells.

Discussion
Our goal was to understand the shape signal transformation in the ventral stream up to V4. The present work used findings of the various visual areas involved in shape processing in this stream along with geometry and machine learning to propose a step-by-step explanation for this transformation. We refrained from using end-to-end deep neural networks because explaining what is learned in each layer of these deep architectures is still an open problem. Instead, we took an alternative approach and proposed a mechanistic model with explicit algorithmic steps that could explain the role each component plays in the shape signal transformation from orientation selectivity to abstract representations of signed curvature and part-based selectivity in V4. We stood on the shoulder of experimental findings of the brain, where possible, and designed the model and set its parameters accordingly. Only in absence of such knowledge, we gained from a machine learning algorithm to unlock new information hidden in existing V4 data: our results indicate contributions from multiple parts from the full spatial extent of RF in both facilitatory and inhibitory manners.

Throughout this manuscript, we made the effort to demonstrate the important role both curvature magnitude and sign representations play in achieving a signed curvature encoding. Recently, Pasupathy et al. (2020) referred to V4 representations as “object-centered.” We, instead, used the geometric term “signed curvature” to emphasize selectivity to both curvature magnitude and curvature sign in V4 neurons as was initially reported in Pasupathy and Connor (1999, 2001, 2002). Object-centered V4 selectivities refer to awareness to inside-outside (BO) and omit the curvature magnitude selectivity in these neurons.

Similarly, when it comes to a model of V4, those previous models that omit incorporating both curvature components cannot achieve a signed curvature encoding and, hence, are lacking with respect to our current understanding of shape processing in V4. Even with their impressive population distribution of correlation coefficients, HMAX falls under this category. Without incorporating curvature sign, it is not surprising that HMAX failed to exhibit similar levels of invariance to changes in position as V4 neurons; with an example, we showed (Fig. 1c) that the same configuration of oriented edges recovered in HMAX could be a convex or concave segment on the bounding contour of a shape depending on the shape position in the RF. Additionally, the HMAX hierarchy skips intermediate processing stages and jumps from orientation-selective neurons to shape selectivity in V4. As a result, some of the recovered RFs look like an ensemble of oriented edges that are difficult to interpret. Such an approach fails to explain how the shape signal transforms in the ventral stream. In contrast, with explicit modeling of intermediate representations, not only did we achieve a signed curvature encoding, but also provided a step-by-step explanation for the development of this representation in the ventral stream.

Compared with other models, SparseShape outperformed 2DSIL, Alexnet, and APC. Although APC was fit to all the shapes in the standard set and we trained our model with only 60% of shapes, SparseShape–train outperformed APC–4D. This mismatch in performance suggests that more than three juxtaposed shape parts contribute to V4 responses. This observation was confirmed in our sparsity experiment and was evident in the visualized RFs: V4 neurons integrate shape parts from the full spatial extent of their RF, which is more efficient than limiting selectivity to a small portion of the RF.

Not only long-range interactions of shape parts within the RF emerged from relaxing the priors compared with APC, a combination of facilitatory and inhibitory contributions also appeared in the recovered RFs. All previous models of V4 with direct comparison with recordings from the study by Pasupathy and Connor (2001) were limited to facilitatory contributions of parts. However, the relaxed priors in SparseShape revealed more complicated part-based selectivities in V4 neurons. Facilitatory and inhibitory part contributions in SparseShape reiterate the findings of Brincat and Connor (2004) in IT; therefore, it is not surprising to find that V4 neurons follow suit.

In SparseShape, the signed curvature encoding relies on both endstopping and BO. Discoveries of both types of representations in the ventral stream lend additional support to the development of a signed curvature encoding in this stream. Responses of V4 cells to shapes that are extended beyond the RF (Pasupathy and Connor, 1999) and similar responses in BO cells suggest that similar mechanisms govern activations in both neuron types. We acknowledge that findings of Bushnell et al. (2011) suggest...
against BO contributing to V4 responses. Their argument is on the basis of time course in BO and V4 neurons. SparseShape incorporates the RBO network to generate the BO signal. The RBO hierarchy is designed based on early recurrence from MT to BO neurons and provides an explanation for the early divergence of responses in BO cells (Mehrani and Tsotsos 2021). Whether this early divergence is relayed to V4 cells, earlier than reaching half-max responses in BO as used for the argument in Bushnell et al. (2011), or a direct recurrence from MT provides side-of-figure information to V4 neurons remains to be

Figure 8. The learned mV4 neurons exhibit scale and position invariance. a, Scale invariance in responses of mV4 neurons. Top row represents responses of three example mV4 cells to stimuli of various scales with their corresponding tuning centroid slope as a function of scale shown in the bottom row in this panel. These plots suggest that mV4 cells exhibit “normalized” curvature encoding similar to Macaque V4 neurons. The same legend applies to all plots on the first row. b, Tuning centroid slope distribution for the population of mV4 neurons in SparseShape for the scale test. c, Slope distribution for the position test. b, c, The learned mV4 neurons show similar scale and position invariance properties as Macaque V4 neurons (El-Shamayleh and Pasupathy, 2016) despite training on a single scale.
further investigated. The message here, however, is that both curvature magnitude and curvature sign (perhaps from similar mechanisms that give rise to BO) are essential to forming a signed curvature encoding. How and where from in the brain this information is provided to V4 is another question that is put forth to be investigated in the future.

Our proposed model revealed hidden information, more than those previously reported, in existing V4 data. These findings impart new insights into shape processing in V4 that require further testing and investigation in biological V4 neurons. For example, examining biological V4 responses by removing shape parts allows testing for facilitatory versus inhibitory contributions, multpart selectivity, and the extent of part integration within the RF. Removing a shape part inevitably disturbs the curvature sign in a geometric sense and might make the experimental design a challenge in this case. Luckily, Zhang and von der Heydt (2010) found that the side-of-figure preferences are maintained in BO neurons even when boundary fragments are removed from Cornsweet shapes. Additionally, the RBO network could explain illusory contours. Together, these findings provide a unique tool to further test the signed curvature encoding in the ventral stream and to enhance our understanding of contributions of shape parts to V4 responses. Specifically, if V4 cells receive inside-outside information that originates from BO cells, converting the standard stimulus set to Cornsweet shapes allows removal of shape parts without disturbing the overall inside-outside and consequently the signed curvature signal for the shape. Then, the findings from the present work can be examined in biological V4 cells. For example, removing a part that inhibits a cell’s responses according to the model is expected to increase the neuron’s activations when all other shape parts are intact. Such a study is different from those in which V4 responses to occlusion were examined (Bushnell et al., 2011; Fyall et al., 2017). In the occlusion studies, the shape is occluded with another form which disturbs BO and consequently signed curvature representations. In contrast, with the suggested experimental design, there is no occlusion but absence of a part, making testing the effect of each individual part a possibility without changing the overall shape representation.

Our proposed model can be further extended. For example, in the present model, we combined responses of border- and edge-selective mBO cells. Maintaining those signals allows modeling a wider variety of mLocalCurv neurons and consequently modeling V4 responses to outline/filled shapes (Popovkina et al., 2019). Similarly, adding neurons selective to texture could lend insight into joint shape and texture processing in this area (Kim et al., 2019). Also, we did not implement mechanisms to represent inflection points (zero curvature), such as straight lines at mV4 level. Adding connections from mV1 layer to mV4 can handle such cases. Such extensions are left for future work. Finally, interesting recent findings of shape processing in V4 revealed both flat and solid shape selectivity in V4 (Srinath et al., 2021). Here, we focused on modeling neuron responses in V4 modules dedicated to 2D shape processing. However, the recent V4 findings open exciting new possibilities for future extensions of SparseShape.

References

Bushnell BN, Harding PJ, Kosai Y, Pasupathy A (2011) Partial occlusion modulates contour-based shape encoding in primate area V4. J Neurosci 31:4012–4024.

Cadieu C, Kouh M, Pasupathy A, Connor CE, Riesenhuber M, Poggio T (2007) A model of V4 shape selectivity and invariance. J Neurophysiol 98:1733–1750.

Carlsson ET, Rasquinha RJ, Zhang K, Connor CE (2011) A sparse object coding scheme in area V4. Curr Biol 21:288–293.

Dobbins A, Zucker SW, Cynader MS (1987) Endstopped neurons in the visual cortex as a substrate for calculating curvature. Nature 329:438–441.

Eguchi A, Mender BM, Evans B, Humphreys G, Stringer S (2015) Computational modelling of the neural representation of object shape in the primate ventral visual system. Front Comput Neurosci 9:100.

El-Shamyaleh Y, Pasupathy A (2016) Contour curvature as an invariant code for objects in visual area V4. J Neurosci 36:5532–5543.

Felleman DJ, Van Essen DC (1991) Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex 1:1–47.

Fyall AM, El-Shamyaleh Y, Choi H, Shea-Brown E, Pasupathy A (2017) Dynamic representation of partially occluded objects in primate prefrontal and visual cortex. Neuroscience 6:e25784. https://elifesciences.org/articles/25784.

Hatori Y, Mashita T, Sakai K (2016) Sparse coding generates curvature selectivity in V4 neurons. J Opt Soc Am A Opt Image Sci Vis 33:527–537.

Hegde J, Van Essen DC (2000) Selectivity for complex shapes in primate visual area V2. J Neurosci 20:RC61.

Hu X, Zhang J, Li J, Zhang B (2014) Sparsity-regularized hmax for visual recognition. PLoS One 9:e81813.

Hubel DH (1963) The visual cortex of the brain. Sci Am 209:54–62.

Hubel DH, Wiesel TN (1959) Receptive fields of single neurons in the cat’s striate cortex. J Physiol 148:574–591.

Ito M, Komatsu H (2004) Representation of angles embedded within contour stimuli in area V2 of macaque monkeys. J Neurosci 24:3313–3324.

Kawakami S, Ito T, Makino Y, Hashimoto M, Yano M (2020) A cell model in the ventral visual pathway for the detection of circles of curvature constituting figures. Heliyon 6:e05397.

Kim T, Bair W, Pasupathy A (2019) Neural coding for shape and texture in macaque area V4. J Neurosci 39:4760–4774.

Kobatake E, Wang G, Tanaka K (1998) Effects of shape-discrimination training on the selectivity of inferotemporal cells in adult monkeys. J Neurophysiol 80:324–330.

Kreiter A, Sutskever I, Hinton GE (2017) Imagenet classification with deep convolutional neural networks. Communications of the ACM 60:84–90.

Mehrani P, Tsotsos JK (2021) Early recurrence enables figure border ownership. Vision Res 186:23–33.

Pasupathy A, Connor CE (1999) Responses to contour features in macaque area V4. J Neurophysiol 82:2490–2502.

Pasupathy A, Connor CE (2001) Shape representation in area V4: position-specific tuning for boundary conformation. J Neurophysiol 86:2505–2519.

Pasupathy A, Connor CE (2002) Population coding of shape in area V4. Nat Neurosci 5:1332–1338.

Popovkina DV, Bair W, Pasupathy A (2019) Modeling diverse responses to filled and outline shapes in macaque area V4. J Neurophysiol 121:1059–1072.

Pasupathy A, Popovkina DV, Kim T (2020) Visual functions of primate area V4. Annu Rev Vis Sci 6:363–385.

Pressley AN (2010) Elementary differential geometry. New York: Springer.

Pospisil DA, Pasupathy A, Bair W (2018) ‘Artiphyiology’ reveals V4-like shape tuning in a deep network trained for image classification. 7:e38242.

Pospisil DA, Bair W, Pasupathy A, Bair W (2018) ‘Artiphyiology’ reveals V4-like shape tuning in a deep network trained for image classification. 7:e38242.

Pressley AN (2010) Elementary differential geometry. New York: Springer.

Rodríguez-Sánchez AJ, Tsotsos JK (2012) The roles of endstopped and curvature tuned computations in a hierarchical representation of 2D shape. PLoS One 7:1–13.

Rodríguez-Sánchez A, Oberleiter S, Xiong H, Piater J (2016) Learning V4 curvature cell populations from sparse endstopped cells. In:
Roe AW, Chelazzi L, Connor CE, Conway BR, Fujita I, Gallant JL, Lu H, Vanduffel W (2012) Toward a unified theory of visual area V4. Neuron 74:12–29.

Srinath R, Emonds A, Wang Q, Lempel AA, Dunn-Weiss E, Connor CE, Nielsen KJ (2021) Early emergence of solid shape coding in natural and deep network vision. Curr Biol 31:51–65.e5.

Tanaka K (1996) Inferotemporal cortex and object vision. Annu Rev Neurosci 19:109–139.

Tsunoda K, Yamane Y, Nishizaki M, Tanifuji M (2001) Complex objects are represented in macaque inferotemporal cortex by the combination of feature columns. Nat Neurosci 4:832–838.

Ungerleider LG, Galkin TW, Desimone R, Gattass R (2008) Cortical connections of area V4 in the macaque. Cereb Cortex 18:477–499.

Wang Y, Deng L (2016) Modeling object recognition in visual cortex using multiple firing k-means and non-negative sparse coding. Signal Processing 124:198–209.

Wei H, Dong Z (2015) V4 neural network model for shape-based feature extraction and object discrimination. Cogn Comput 7:753–762.

Zhang NR, von der Heydt R (2010) Analysis of the context integration mechanisms underlying figure–ground organization in the visual cortex. J Neurosci 30:6482–6496.

Zhou H, Friedman HS, von der Heydt R (2000) Coding of border ownership in monkey visual cortex. J Neurosci 20:6594–6611.