Shape encoding consistency across colors in primate V4

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THE VENTRAL VISUAL PATHWAY is the main locus of form and color encoding in the primate brain (Felleman and Van Essen 1991; Ungerleider and Mishkin 1982). Lesion studies at various stages along this pathway have demonstrated impairment on form and color discrimination tasks (Aggleton and Mishkin 1990; Cowey and Gross 1970; De Weerd et al. 1996; Dean 1976; Gross et al. 1971; Heywood and Cowey 1987; Heywood et al. 1995; Huxlin et al. 2000; Iwai and Mishkin 1969; Merigan 1996; Merigan et al. 1993; Walsh et al. 1992a, 1992b), and single-cell neurophysiological studies have demonstrated selectivity for various attributes of stimulus form and color (Baizer et al. 1977; Brincat and Connor 2004; De Valois et al. 1979; Desimone and Schein 1987; Desimone et al. 1984; Gallant et al. 1993; Gouras and Kruger 1979; Gross et al. 1972; Hegde and Van Essen 2000; Hubel and Livingstone 1990; Hubel and Weisel 1968; Ito and Komatsu 2004; Kobatake and Tanaka 1994; Komatsu et al. 1992; Movshon et al. 1978a, 1978b; Pasupathy and Connor 1999, 2001; Perrett et al. 1982; Peterhans and von der Heydt 1991; Schein and Desimone 1990; Tanaka et al. 1991; Thorell et al. 1984; Zeki 1973, 1977). However, we do not know how neuronal selectivity for form and color interact. This is because most studies that investigate form encoding present all visual stimuli in a single color (for example, see Desimone and Schein 1987; Gallant et al. 1993; Pasupathy and Connor 1999, 2001), and studies that investigate color encoding do so with a single shape (for example, see Schein and Desimone 1990; Komatsu et al. 1992). This experimental strategy of characterizing stimulus dimensions one at a time is dictated largely by practical constraints of recording stability and experimental duration, but an implicit assumption of this approach is that tuning for shape (color) is consistent across colors (shapes), i.e., shape and color tuning are separable. Such tuning separability is attractive from a decoding standpoint, because if tuning for color and shape are separable, a simple basis function decoding approach can be used to decode both the shape and color of the stimuli from a population of neurons with sufficient overlap and coverage in the shape × color space. If, however, tuning were not separable, experimentalists would need to arrive at an efficient way to jointly study shape and color tuning, and the brain would need to implement appropriate algorithms to decode color and shape information from such populations of neurons.

To assess tuning separability, one would ideally want to study the responses to many shapes presented in many different colors. This, however, is highly impractical in experiments involving awake fixating primes; for example, recording the neuronal response to 10 repeats of 100 shapes presented in 10 different colors takes ~5 h, not including the initial receptive field characterization. Therefore, rather than take on this difficult endeavor, as a first step to examining the separability of shape and color tuning of neurons, we compared responses to 56–136 shapes presented in 2 different colors. We targeted neurons in extrastriate cortical area V4, an intermediate stage along the ventral visual pathway. We found that many V4 neurons showed strong consistency in shape preferences across colors, in keeping with previous results from inferior temporal (IT) cortex (Komatsu and Ideura 1993). Our results suggest that neurons that are likely to contribute to shape discrimination (those with less eccentric receptive fields and those that exhibited greater dispersion of responses across shapes) showed greater consistency of shape responses across color. From a practical standpoint, our results empirically suggest that greater than 10 stimulus repeats are essential to obtain a good estimate of the true consistency in shape responses across colors for the experimental and analytical methods used here.

MATERIALS AND METHODS

Animal preparation for the experiments described in this study, including implants, surgeries, and behavioral training, conformed to National Institutes of Health guidelines and was approved by the Institutional Animal Care and Use Committee at the University of Washington. All methods were previously described in detail by Bushnell et al. (2011a), but briefly, two rhesus monkeys (Macaca

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also subsets of shapes in Fig. 1) were dictated by the parameters of that
data from the remaining 42 cells were collected as part of the
features known to be effective at driving responses of a large fraction of
the experiment described below. We studied the responses of each such
cell that all parts of all stimuli were entirely within the estimated RF area (estimated RF diameter = \(1.0^o + 0.625 \times \) RF eccentricity, based on data from Gattass et al. 1988) of the cell under study. In every case, the stimulus size so-chosen fit within the RF boundary measured by our fine grid-mapping procedure (see above).
The two colors of the shape stimuli were customized for each cell
such that both evoked moderate to strong responses and were visually
distinct from each other. Color choices were based on either detailed color characterization (35 cells; see above) or preliminary characterization by the experimenter (25 cells). The distance in CIE space between the chosen colors (color distance) essentially reflected the
width of color tuning, because we chose two colors that were farthest
apart in CIE space and still evoked responses from the cell. Thus the
chosen colors were closer together for cells with narrow color tuning and
farther apart for cells with broader tuning. Of the 60 cells, 52 were
tested with 2 colors that differed in their chromaticity but were at the
same luminaire contrast relative to the background. Of the remaining
8 cells, 7 were tested with 2 colors that differed in both their
chromaticity and luminaire contrast, and one with achromatic stimuli at
different luminance contrasts.
For each stimulus presentation, we counted spikes in a 300-ms window shifted by 50 ms to account for average latency of V4 neurons (Bushnell et al. 2011a). We then averaged these counts across stimulus repeats and divided by the counting window duration (300 ms) to obtain the spike rate. Across neurons, the number of stimulus repeats ranged from 4 to 20 (median 10).

RESULTS
To assess whether shape preferences of V4 neurons are consistent across colors, we studied the responses of 60 single neurons in 2 monkeys to a variety of complex shapes (see Fig. 1) presented in 2 different colors (see MATERIALS AND METHODS). Results for an example neuron are shown in Fig. 2. In preliminary (qualitative) color characterization, this neuron did not show strong color tuning, and we chose green and magenta, both of which evoked strong responses, as the stimulus colors. We studied responses of this neuron to 14 different complex shapes (rows in Fig. 2, A and B) presented at 8 different orientations (columns) in green (Fig. 2A) and magenta (Fig. 2B). Many shapes evoked strong responses from this cell, and the shape preferences across the two colors were quite consistent as demonstrated by the scatter plot in Fig. 2C. We quantified the consistency in shape responses by calculating the linear correlation coefficient, \(r_c\), between responses to shapes in the two colors. The value of \(r_c\) ranges from –1, for perfectly inconsistent responses, to 1, for perfect consistency. For this example neuron, \(r_c\) was 0.87. In addition to the strong correlation, it is also clear from the scatter plot (Fig. 2C) that the neuron responded more strongly to color 1 (points lie mainly below the diagonal); a two-way ANOVA revealed main effects for both color and shape and an interaction between the two factors (\(P < 0.01\)). A strong correlation in responses across colors and a significant interaction between color and shape (as exhibited by this cell) are not at odds with each other; a simple scaling of shape responses by color, for example, could produce the observed result.

Two additional examples are shown in Fig. 3. Figure 3, A–C, shows an example neuron that exhibited a moderate color preference during preliminary color characterization, responding preferentially to blue and more weakly to red. A two-way ANOVA revealed main effects for both color and shape and an interaction between the two factors (\(P < 0.01\)). Only a few shapes evoked strong responses from this cell, but the preferred
Fig. 2. Responses of an example V4 neuron with highly consistent shape responses across colors. A and B: responses to 14 shapes (rows) presented at 8 orientations (columns) in green (A) and magenta (B). The background gray level of each icon represents the average response, per scale bar, across N = 20 repeats to the superimposed shape. Qualitatively, this neuron did not show strong color preferences, but 2-way ANOVA revealed significant (P < 0.01) main effects for color, shape, and their interaction on the responses of the cell, which were marginally stronger to shapes in green (A). Shape preferences were consistent across colors: in both colors, responses were strong to several shapes with a concavity to the right or lower right of the shape. The RF of this neuron was centered at 8.2° from the fixation point. C: scatter plot of responses shown in A (X-axis) and B (Y-axis). Points lie below the line of slope = 1 (dashed line). The correlation coefficient between responses in the 2 colors (rC) was 0.87.

A neuron that shows strong shape selectivity will be associated with large shape dispersion because it will exhibit a large dynamic range in its responses across shapes and, thus, a large variance-to-mean ratio across shapes; a neuron with weak shape selectivity will exhibit similar responses across shapes and a small variance-to-mean ratio. Therefore, V4 neurons that exhibit poor consistency due to color dependence of shape selectivity will be associated with large shape-response dispersion, whereas those that are unselective to shape will be associated with low dispersion values.

Figure 4A shows a histogram of shape consistency values for the 60 cells in our data set. Consistency values ranged from −0.03 to 0.93 (mean 0.49; median 0.54). Thus many V4 neurons showed shape preferences that were strongly consistent across the two colors tested, but many others showed weak or no consistency. The lack of consistency in shape responses could result if a neuron’s shape tuning is color dependent, i.e., a neuron prefers one shape in color 1 but a different one in color 2. However, poor shape consistency could also result if the neuron in question is simply not shape selective. Such a neuron will respond similarly to a variety of shapes, and consistency across colors will be close to zero because the range of responses across shapes will simply reflect the inherent noise in the neuron’s response. To identify poorly shape-selective neurons in our data set, we quantified the strength of shape selectivity by calculating shape-response dispersion. This metric, which provides a measure of the shape information capacity of a neuron, was quantified as the ratio of the variance to the mean response across shapes in a given color. If ni represents number of stimuli and ri is the mean response to the ith stimulus, then shape dispersion is equal to Var/µ, where

\[ \mu = \frac{1}{n_i} \sum_{i=1}^{n_i} r_i \]

\[ \text{Var} = \frac{1}{n_i} \sum_{i=1}^{n_i} (r_i - \mu)^2 \]

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Figure 4B summarizes the relationship between shape dispersion (X-axis) and shape consistency (Y-axis) across our data set. Data from each cell are denoted by a pair of dots connected by a line segment; each dot denotes shape dispersion based on stimuli in one color (see Fig. 4 legend for further details). Across our sample of V4 neurons there was a wide range in dispersion values, but one trend is evident: shape-selective neurons, i.e., neurons with high shape dispersion, were associated with high shape consistency values. To illustrate this point more clearly, we divided the population of neurons into two groups: those with shape dispersion values >1.5...
(strongly selective = 22) and those with dispersion values ≤ 1.5 (weakly selective = 38). Mean shape consistency for the strongly selective and weakly selective groups was 0.71 and 0.36, respectively, and the Fisher-transformed mean value for the strongly selective group was significantly larger than that for the weakly selective group (t-test, P < 0.01). In fact, among strongly selective neurons, shape consistency was 0.5 for 19/22 neurons. Note that in Fig. 4B, whereas neurons with high dispersion values were associated with high consistency, the converse is not true, i.e., neurons that exhibit highly consistent responses across colors (for example, r_C > 0.5) are not always associated with high shape dispersion values. Those neurons with high consistency and low shape dispersion values (top left corner of plot, Fig. 4B) were cells that typically exhibited a small dynamic range in their response across shapes even though such responses were highly consistent. Because shape dispersion does not take the noise variance of the neurons into account, we also quantified shape selectivity using the one-way ANOVA F-test statistic (Fig. 4C), which measures the ratio of across-shape variability to within-shape variability. Results were very similar to those in Fig. 4B: there was a strong positive correlation between Fisher-transformed shape consistency and the F value (r = 0.74 and 0.63 for preferred and nonpreferred colors, respectively). Figure 4D shows the histogram of shape consistency values for cells divided into two groups on the basis of whether they exhibited...
significant shape selectivity for both colors as based on the one-way ANOVA ($P < 0.05$). Among the shape-selective group (44/60), shape consistency ranged from 0.16 to 0.93 (mean 0.61; median 0.63). These results suggest that cells with low dispersion and a lack of shape selectivity may have low consistency values because the variance across shape is largely due to noise. Interestingly, we also found that the RF eccentricity of individual neurons showed a weak but significant negative correlation with shape dispersion ($r = -0.32; P < 0.02$) and shape consistency ($r = -0.42; P < 0.01$). These results are consistent with the idea that cells more likely to contribute to shape coding, i.e., those with less eccentric RFs and high shape-response dispersion, have more consistent shape tuning across colors.

Poor consistency in some cells could be due to an underestimation of the correlation metric $r_C$ as computed on the basis of finite stimulus repeats. If we denote the true responses to shapes in the two colors by vectors $X$ and $Y$, respectively, then the true shape consistency $= \text{Corr}(X, Y)$. However, when we study shape responses with a finite number of repeats $N$, assuming additive noise, mean estimates will be $X + Z_X$ and $Y + Z_Y$, where $Z_X$ and $Z_Y$ denote noise in the estimates of $X$ and $Y$, respectively. The measured shape consistency, $r_C$, is therefore $\text{Corr}(X + Z_X, Y + Z_Y)$. If $Z_X$ and $Z_Y$ are independent of the true means and of each other, then it is easy to see that $\text{Corr}(X + Z_X, Y + Z_Y) = \text{Cov}(X, Y)/\text{Var}(X + Z_X)\text{Var}(Y + Z_Y) = \text{Corr}(X, Y)$. As $N$ increases and approaches infinity, the standard errors in the estimates of the mean responses decrease, i.e., $Z_X$ and $Z_Y$ decrease, and $\text{Corr}(X + Z_X, Y + Z_Y)$ will increase and approach the true correlation. In our experiments, due to practical constraints, $N$ ranged from 4 to 20 across cells.

To empirically assess the size of the underestimate caused by the finite repeats, Fig. 5 plots the minimum number of repeats across stimuli vs. shape tuning consistency. Because we used a pseudorandom stimulus protocol (see Materials and Methods), a minimum number of repeats equal to $N$ implies that data collection was terminated during the $(N + 1)$th run and the mean responses for the different stimuli were based on $N$ or $N + 1$ repeats. Across our data set, there was a significant positive correlation between $N$ and Fisher-transformed shape consistency ($r = 0.58; P < 0.0001$). Thus, as expected, shape responses were more consistent when we obtained more stimulus repeats, and shape consistency values based on four repeats ($r_{C4}$) were less than those based on all available repeats for any given cell (Fig. 5B). To compute shape consistency based on four repeats, for each cell we randomly chose four repeats for each color and shape, computed shape dispersion based on the chosen trials, and repeated this bootstrap procedure 100 times. The average across the 100 repetitions is reported as $r_{C4}$ in Fig. 5. The difference between $r_C$ and $r_{C4}$ ($Y$-axis, Fig. 5C), which quantifies the change in shape consistency as number of repeats increases from four to $N$, provides a measure of the underestimate in shape consistency as a function of $N$ ($X$-axis, Fig. 5C). As $N$ increases, $r_C - r_{C4}$ also increases and plateaus somewhat at $r_C - r_{C4} \approx 0.3$ for $N > 10$. This can also be visualized as a plateau in mean shape consistency (red crosses in Fig. 5A) at $-0.7$ for $N > 10$. Thus $r_C$ for $N < 10$ repeats appears to be severely underestimated. On the basis of this empirical evidence, we propose that for the inherent noise and dynamic range of V4 neurons, and for the present experimental and analytical conditions, $N > 10$ is essential to avoid biases in correlation metrics based on mean.
Fig. 5: Effect of stimulus repeats on shape consistency and shape dispersion. A: scatter plot of minimum number of stimulus repetitions vs. shape consistency. For a cell, if minimum number of repeats (X-axis) is N, then mean shape responses would be based on N or N + 1 repeats, because data collection was terminated during the (N + 1)th repeat. Red crosses represent the mean shape consistency at the corresponding number of repeats. Overall, there was a trend of increasing shape consistency with increasing number of stimulus repeats, and shape consistency appears to plateau somewhat for N > 10. Fisher-transformed shape consistency and minimum number of repeats were positively correlated (r = 0.56, P < 0.0001). B: scatter plot of shape consistency values based on all stimulus repeats (rC; X-axis) vs. 4 stimulus repeats (rC4; Y-axis). We randomly chose 4 repeats without replacement and computed the mean responses and shape consistency based on those repeats. The whole procedure was repeated 100 times; the average consistency across these 100 repetitions is reported as rC4. In all except 1 case, shape consistency based on 4 repeats was less than that based on more stimulus repeats. Cells for which data collection was terminated on the 5th run, i.e., minimum number of repeats = 4, are shown as open symbols. These values do not lie on the diagonal, because although the Y-axis was based on mean responses derived from 4 repeats, the X-axis measure was based on mean shape responses derived from 4 or 5 repeats. C: bar graph of the mean difference in shape consistency values based on all stimulus repeats (rC) and 4 repeats (rC4) as a function of minimum number of repeats. X-axis is the same as in A. Y-axis is the difference between X- and Y-axes in B with cells grouped on the basis of the number of repeats. The difference rC − rC4 increases with increasing stimulus repeats, implying that there was a systematic underestimate in shape consistency for small number of stimulus repeats. D: shape-response dispersion (X-axis) vs. shape consistency (Y-axis) for cells studied with >10 repeats (n = 22 cells). This plot is similar to Fig. 4B, except that it includes only those cells studied with >10 repeats. As before, there was a strong relationship between shape dispersion and shape consistency. E: shape-response dispersion (X-axis) vs. shape consistency based on 4 stimulus repeats. Y-axis is the same as in B. As with rC4 computation described in B, shape dispersion for each cell was the average across 100 repetitions of a bootstrap procedure, each producing a shape dispersion value based on 4 randomly chosen trial repeats. This confirms that the relationship between shape dispersion and shape consistency is not due to the dependence of both measures on the number of stimulus repeats.

responses. Figure 5D shows shape dispersion vs. shape consistency (same as Fig. 4B) for only those cells studied with >10 repeats (n = 22 cells). All except three cells exhibited strong consistency (rC > 0.5) in their shape responses; the three cells with values close to 0.3 were associated with low shape dispersion and exhibited weak tuning for shape. This matched what we found by eye: we could not find any examples of color-dependent shape tuning. Cells that exhibited strong shape selectivity showed consistent selectivity in both colors; other cells showed a mush of responses with no discernible shape tuning.

As with shape consistency, the number of stimulus repeats also influences shape dispersion for the same reason discussed above. Therefore, for all cells, we recalculated shape consistency and shape-response dispersion using N = 4 and the bootstrap procedure described above. The average shape consistency and shape dispersion values across 100 iterations for each cell are shown in Fig. 5E. These results are very similar to those reported in Fig. 4, confirming that the relationship between shape tuning and shape consistency was not trivially due to differences in N across cells.

We next investigated how the chosen stimulus colors and the color-selective properties of neurons influenced the observed shape consistency values. Specifically, it is possible that the spread of shape consistency values was simply a function of the colors that were chosen for any given cell: neurons studied with similar colors (closer in the CIE space, and thus evoking similar responses) may have been associated with higher consistency values than those studied with more disparate colors. Figure 6A, which plots the distance between the tested colors in CIE space vs. shape consistency for each cell, demonstrates that this was not the case. Across the 60 cells, color distances ranged from 0 (for 1 cell that was studied with achromatic stimuli at 2 different luminance contrasts, see MATERIALS AND
Methods to 0.57 (median 0.19, mean 0.21). Both low and high color distance values were associated with high shape consistency values, and the correlation between the Fisher-transformed shape consistency values and color distance was not significantly different from zero. This suggests that cells studied with colors closer together in the CIE space were not especially associated with higher consistency values, confirming that the high consistency observed is not an artifactual result of studying some cells with similar chromaticities. It is also possible that the spread of consistency values was a function of the color-selective properties of neurons: cells that do not receive chromatic inputs, which are therefore not color selective, may exhibit more consistency than cells that are color selective. We used two methods to address this question. For all 60 neurons, we conducted a two-way ANOVA with color and shape as factors, to investigate whether the two colors differentially modulated the responses of the neurons. Fifty-one of the 60 cells showed a main effect of color and/or an interaction between color and shape (44/60 cells exhibited a significant interaction term, \( P < 0.05 \)); many of these color-selective neurons exhibited highly consistent responses (filled bars, Fig. 6B). In fact, cells that were not color selective tended to exhibit weaker consistency in shape responses. Second, for the 35 cells that underwent detailed color characterization, we assessed the strength of color selectivity by computing color-response dispersion. Color-response dispersion was computed on the basis of detailed color characterization conducted with a single preferred shape of the cell (see Materials and Methods) and thus was fully independent of the data used to compute shape consistency and shape-response dispersion. Analogous to shape-response dispersion, color-response dispersion was quantified as the ratio of the variance to the mean of the responses across all 25 chromaticities at the same luminance contrast as the colors in which the stimuli were presented (see Materials and Methods). In the few cases where the stimulus colors were at different luminance contrasts, we computed color-response dispersion at both luminance contrasts (see Fig. 6 legend). Cells that show weak or no color selectivity will respond similarly to all colors and have small color-response dispersion values (far left of X-axis, Fig. 6C), whereas strongly color-selective neurons will exhibit a large dispersion of color responses. Across our data set, color-response dispersion ranged from 0.22 to 3.8 (X-axis, Fig. 6C). However, unlike shape-response dispersion, there was no clear trend in the relationship between color-response dispersion and shape consistency. In other words, weak color selectivity (low color-response dispersion) did not imply high shape-response consistency. Altogether, Fig. 6, B and C, indicates that highly consistent shape responses across colors observed in our data set cannot be simply attributed to the lack of color selectivity, and thus chromatic inputs, in those cells. Even in the presence of chromatic inputs, it is possible that shape selectivity is informed only by luminance inputs to cells and that chromatic inputs simply provide a shape-independent modulation of the overall response. Under this hypothesis, cells studied with two colors at the same luminance contrast but different chromatic contrasts (52/60 cells in our database) will exhibit high consistency, but cells studied with chromaticities equiluminant with the background, i.e., 0% luminance contrast, will not exhibit any shape selectivity or consistency. Three cells in our present data set were studied with colors that were equiluminant with the background; all three exhibited significant shape selectivity (ANOVA, \( P < 0.01 \)) and moderate levels of shape consistency (\( r_c = 0.25, 0.40, 0.69 \)), arguing against the above hypothesis. These results are also consistent with our recent finding that many V4 neurons exhibit selectivity for shapes defined solely by chromatic contrasts (Bushnell et al. 2011b).

Finally, we asked how color modulates shape responses, whether it provides an additive modulation, multiplicative modulation, or both. The response \( R \) of a neuron that shows highly consistent shape responses across colors could be written as.
two colors, modulation, for all different colors just provided an additive modulation, above equation, neurons ranged from 0.13 to 0.91 (F responses in the two colors. Of the 60 cells, 47 had a significant to confirm these findings and more precisely characterize the is an additive modulation in addition to the gain modulation by was 2.67 spikes/s, on average. These results suggest that there modulation of shape responses. Drawing conclusions about the ratio of additive modulation is greater than the ratio of gains, s modulation ([f(c1)/f(c2)]) was zero for all (c1)/(c2), whereas a negative intercept from shapes in the two colors, they used only 2 stimuli in 2 colors. A neuron that appears linear across a narrow range (of 4 stimuli) may not appear so when a larger range of stimuli are considered. Further experiments in IT cortex with a larger stimulus set are required to determine whether this difference is due to the number of stimuli or if it is, in fact, a difference in how V4 and IT cortex combine color and shape information. Our discovery of multiplicative combination of color and shape information in V4 is consistent with a previous demonstration that tuning for shape and texture, also a surface property like color, in IT cortex can be well described by a multiplicative model (Kotesles et al. 2008). Finally, Komatsu and Ideura (1993) also demonstrated that the occurrence of color and shape selectivity in a single IT neuron were independent of each other. In other words, whether or not a cell was shape selective had no bearing on whether it was color selective. Across the 35 cells that underwent detailed shape and color characterization, we found that the dispersion in shape responses was not significantly correlated with the dispersion in color responses (Fig. 6D; r = 0.14; P = 0.46). This suggests that the strengths of color and shape selectivity in V4 might also be independent of each other, in keeping with IT studies. Implications for decoding. Primates can recognize a wide variety of shapes regardless of their position, size, viewing angle, presence of occluders, etc. This is a computationally challenging problem, and past studies have hypothesized that such invariant recognition can be achieved by a population of neurons that exhibit shape tuning that is invariant of other stimulus attributes (Ito et al. 1995; Logothetis et al. 1995; Vogels and Orban 1996). Neurons in IT cortex have been shown to exhibit shape preferences that are consistent across position in the visual field even though response magnitude itself may depend on position (DiCarlo and Maunsell 2003; Ito et al. 1995; Logothetis et al. 1995; Schwartz et al. 1983; Tovee et al. 1994; Zoccolan 2007). Preserving the rank order of shape preferences is sufficient to successfully decode stimulus iden-
tity using linear decoding methods (Li et al. 2009). If rank order is not preserved, i.e., shape tuning is not consistent across position or other stimulus attributes, stimulus identity may still be decoded, but this would require nonlinear/computationally intensive algorithms.

Our results demonstrate that many neurons in area V4, especially those cells that show higher values of dispersion in shape responses, exhibit consistent shape preferences across colors, i.e., the rank order of shape preference is preserved across colors. Thus these neurons exhibit a crucial property for supporting invariant recognition. For example, the shape and color of a stimulus can be successfully decoded by using a simple basis function decoding procedure from the activity of a group of V4 neurons that show consistent shape tuning across colors. Basis function decoding is simple (the identity of a stimulus is given by the sum of the tuning functions weighted by the response of the corresponding neuron to the stimulus in question) and could be easily implemented across neural populations (Zhang et al. 1998). The size of the population required for successful recognition depends on the width of tuning functions, which requires additional experiments to determine. In addition to decoding simplicity, the consistency of shape selectivity across colors has an enormous practical advantage because it allows experimentalists to quantify detailed shape $\times$ color tuning functions of V4 neurons without having to quantify shape tuning functions in every color. For example, one could measure detailed shape tuning in one color and then quantify the multiplicative and additive modulations provided by the different colors with a much reduced shape stimulus set ($n$ could be as small as 2). Thus one could reconstruct the entire shape $\times$ color tuning function for $n$ shapes and $m$ colors with as few as $n + 2m$ measurements; such an approach does not suffer from the combinatorial explosion ($n \times m$ stimuli) caused by a detailed shape characterizations in every color.

Finally, cortical neurons tend to be noisy, and characterization of tuning properties are based on mean responses derived from multiple stimulus repeats. Given the practical constraints of holding well-isolated single units, there is an inherent trade-off between number of different stimuli and number of repetitions of each stimulus. In studies that attempt to characterize tuning over a large space of shape or color, the number of stimulus repeats is often held low in the interest of presenting a larger variety of stimuli. Our results indicate that this strategy could have a deleterious effect: as expected, large standard errors in mean responses caused by low repeats could produce biased estimates of the properties being characterized. In our case, a low number of repeats implied a systematic negative bias in the shape consistency that was most pronounced when the number of repeats was $<10$. In conclusion, our results caution physiologists to consider the biases induced by low stimulus repeats and the trade-off between number of stimuli and the number of repeats of a given stimulus when designing their studies.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Author contributions: B.N.B. and A.P. performed experiments; A.P. conception and design of research; A.P. analyzed data; A.P. interpreted results of experiments; A.P. prepared figures; A.P. edited and revised manuscript; A.P. approved final version of manuscript.

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