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Wide dynamic range of contrast-encoding in neural responses in macaque V1

Abbreviated title: Contrast-encoding in V1

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Abstract

The dynamic range of contrast-encoding in the early visual system has been investigated at both single-neuron and population levels in animals using oriented stimuli such as gratings and Gabor patches. However, contrast-encoding of unoriented stimuli such as Gaussians has been less explored, even though such stimuli can evoke a large population response. In studies that employ Gaussians, contrast response functions (CRFs) of neurons and neural populations in primary visual cortex are typically characterized across a limited range of Weber contrasts up to 100%, which may not adequately reflect the statistics of contrast in natural scenes. Indeed, our preliminary analysis shows that locations with center-surround contrasts far exceeding the level comparable to a Gaussian stimulus of 100% Weber contrast are ubiquitous in natural scenes. Thus, our current understanding of contrast encoding remains incomplete in the context of natural environments. Here, we measured spiking activities of individual neurons using electrophysiology and population responses using widefield calcium imaging in V1 of fixating male macaques (*Macaca mulatta*) while Gaussian stimuli were presented over a wide range of Weber contrasts, up to 900%. Both the average spiking response and the average population response continued to increase robustly above 100% Weber contrast. Only a small minority of neurons saturated below 100% Weber contrast. These results demonstrate that the dynamic range of contrast-encoding in V1 is broader than previously assumed and aligns more closely with the statistics of contrast in natural scenes.

Significance Statement

The dynamic range of contrast-encoding in V1 has typically been characterized using only a limited range of contrasts, often excluding the high contrasts commonly found in natural scenes. We measured contrast response functions of individual neurons and neural populations in V1 across a much wider range of contrasts. We found that the responses of the majority of neurons, as well as the overall population, increased robustly up to extremely high contrasts. These findings suggest that the dynamic range of contrast encoding in V1 extends well beyond the commonly tested range.

Introduction

A fundamental goal of visual neuroscience is to understand how key properties of natural scenes are encoded by the visual system. One such property is contrast. Since the spatial pattern of contrast remains relatively invariant to variations in uniform illumination, it is used by the brain to encode and recognize specific patterns of surface reflectance and shadow across different lighting conditions. For instance, responses of retinal ganglion cells (RGCs) to contrasts are largely invariant to background luminance (Sakmann and Creutzfeldt, 1969). Transforming photoreceptor responses into contrast responses early in the visual system reduces the range of values that need to be encoded in subsequent processing. Contrast signals contain most of the useful information in natural scenes but generally have a much smaller range than luminance across a scene and time of day.

The dynamic range of contrast-encoding by neurons is typically assessed by measuring a contrast response function (CRF). Because most V1 neurons are orientation-selective, the CRFs of V1 neurons have been studied primarily using Gabor and grating stimuli (Albrecht and Geisler, 1991; Albrecht and Hamilton, 1982; Albrecht et al., 2002; Geisler and Albrecht, 1997; Palmer et al., 2017; Seidemann et al., 2016; Sit et al., 2009). However, V1 neurons also respond to unoriented stimuli, such as Gaussians. While Gabors strongly activate a select subpopulation at a given retinotopic location, Gaussians moderately activate almost all of the neurons at that location. Indeed, imaging results in macaque V1 suggest that Gabors and Gaussians of equivalent size and maximal luminance produce similar magnitudes of V1 population response, and are equally detectable by macaques (Chen et al., 2012) and humans (Watson and Ahumada, 2005).

Furthermore, natural stimuli are composed of mixtures of narrow- and broad-band stimuli such as Gabors and Gaussians, respectively. Therefore, it is important to characterize the CRFs of V1 neurons to Gaussians in addition to Gabors.

Most behavioral and physiological vision experiments add visual stimuli to a uniform grey background having half the maximum display luminance. This limits Weber contrast defined as:

$$C_w (\%) = \frac{L_{max} - L_{bg}}{L_{bg}} \cdot 100$$

to 100%. CRFs of V1 neurons or neural populations measured in this way often begin to saturate at Weber contrasts lower than 100% (Chen et al., 2022; Kumar et al., 2019). However, the statistics of local contrasts in natural scenes have not been studied systematically, leaving open the possibility that bright patches with luminance that is more than twice that of their local background are common in natural scenes. If that were the case, then V1 neurons and neural populations might encode Weber contrasts well beyond the previously explored range.

We quantified local contrasts in five natural scene images and found that patches with center-surround contrasts (see Methods) exceeding the level comparable to a Gaussian stimulus of 100% Weber contrast are indeed common. This observation raises the plausible hypothesis that V1 neural populations continue to increase their response to stimuli with Weber contrast above 100%, which is beyond the previously explored range. Consistent with this hypothesis, our recent study showed that low-power optogenetic stimulation in V1 can evoke a significantly higher population response than a Gaussian

of 100% Weber contrast (Chen et al., 2022). Together, these findings highlight the importance of measuring V1 responses to a wider range of contrasts.

To measure V1 responses to a wide range of contrasts, we devised a method to generate Gaussian stimuli with Weber contrasts up to 900%. We then measured single- and multi-unit spiking activities, and widefield fluorescent calcium imaging signals (GCaMP) in fixating macaques. We show that the average unit and GCaMP responses continue to increase robustly above 100% Weber contrast, and that only a small minority of V1 neurons fully saturate below 100% contrast. Consequently, the dynamic range of V1 population responses to localized stimuli is substantially wider than previously assumed and more consistent with the statistics of contrast in natural scenes.

Materials and Methods

1. Natural scene images and center-surround contrasts

We computed the distribution of local contrast, which we refer to as ‘center-surround contrast’ (C_{cs} ; see Results), in five 16-bit linear natural scene images (50 px/deg) by converting them into grayscale intensity images and convolving them with a pair of kernels—a center kernel and a surround kernel—at each image pixel location. The two kernels were represented as two-dimensional $L \times L$ pixels square arrays that differed in the locations of their nonzero-weight pixels. For the center kernel, nonzero weights were confined to a circular region with a diameter of d_c pixels at the center. For the surround kernel, nonzero weights occupied a concentric annulus extending from the edge of the circular region of the center kernel to an outer diameter of d_s pixels. These nonzero weights were uniform within both the circular and annular regions, with each pixel assigned a weight of $1/N$, where N equals the total number of pixels in the corresponding region. All remaining pixels were assigned a weight of zero. Thus, the center and surround regions were spatially nonoverlapping. To compute C_{cs} at a given image pixel location (x, y) , the two kernels were placed on the image such that their central pixels aligned with the image pixel. Convolution of the image yielded the mean luminance of the image pixels falling within the center circle ($L_c(x, y)$) and surround annulus ($L_s(x, y)$), which were then used to calculate $C_{cs}(x, y)$. Here, we only considered image locations where all pixels of the kernels fell within the image to avoid image boundary artifacts.

The images were arbitrarily selected from our database (<https://natural-scenes.cps.utexas.edu/db.shtml>) prior to analysis.

2. Recording chamber and viral injection

We implanted two male rhesus macaques (*Macaca mulatta*; Monkey V and Monkey S) with a custom metal recording chamber over dorsal V1 in the right hemisphere to gain access to a cortical area representing the lower-left visual field. We injected 4–5 μ l of a GCaMP6f viral vector into the cortex per site at depths up to 2000 μ m (Monkey V with AAV1-CaMKIIa-GCaMP6f, and Monkey S with AAV1-CaMKIIa-GCaMP6f or AAV1-CaMKIIa-NES-GCaMP6f) based on methods from our previous study (Seidemann et al., 2016).

3. Fixation task and stimulus contrasts

We trained the monkeys to perform a fixation task in which they maintained fixation at the center of the screen while a small Gaussian stimulus (0.33° FWHM) was flashed at Weber contrast levels (0, 3, 6, 12.5, 25, 50, 100, 200, 300, 500, 900%) that varied across trials. Throughout the rest of the manuscript, we use the term “*contrast*” to refer to Weber contrast, unless noted otherwise. The task and visual stimulus were presented on a Sony CRT monitor (1024 $\times$ 768 @100 Hz) positioned 108 cm from the eyes, yielding a stimulus resolution of 50 pixels per degree. Eye position was monitored with an EyeLink 1000 Plus system. Background luminance of the monitor was lowered to 10% of its maximum (i.e., 10 cd/m²) to create a uniform dark grey background.

For Monkey S, whose retinotopy was estimated by voltage-sensitive dye imaging (Yang et al., 2007), the stimulus was placed at the corresponding retinotopic coordinates of the GCaMP expression site in the imaging area or the probe penetration site. For Monkey V, for which retinotopy was not available, we used the stimulus with high Weber contrast (900%) to estimate the receptive field center of the neurons in the recording site.

During experiments, the animals were seated in a custom chair with their head immobilized via a head-post implant. Each trial began with fixation on a white $0.1^\circ \times 0.1^\circ$ square within an approximately $2^\circ \times 2^\circ$ window at the center of the screen. After an initial fixation period of ~ 1300 ms (pre-stimulus fixation duration was varied across trials), the stimulus was presented at 2 Hz (200 ms ON and 300 ms OFF for 2 cycles). The animals were rewarded for continuing to maintain fixation for 1200 ms after the first stimulus onset. Behavioral data were collected with custom MATLAB-based software.

4. Electrophysiology

We recorded extracellular spiking activities of V1 neurons using multi-channel probes, including Plexon S-probes (N = 10) and NHP Neuropixels probes (N = 14). To prevent large drifts of the probe in the brain during the recording, we applied a small pressure on the cortex with a custom plastic insert and left the probe in the brain for 60-90 minutes before data collection. The probe was always inserted approximately normal to the brain surface. We advanced the probe into the brain until all the electrode patches were placed in the brain. Real-time spiking data were collected using Trellis and SpikeGLX software for the Plexon and Neuropixels sessions, respectively. The visual stimulus was placed at $1.4\text{--}2.7^\circ$ eccentricity from the fixation point in the lower left quadrant of the visual field.

5. Analysis of electrophysiology data

The electrophysiology data were first spike-sorted automatically into individual single- or multi-unit clusters by Kilosort3. By utilizing the statistical analysis (principal component analysis and autocorrelation analysis of spikes, and distribution of spike amplitudes) generated by Phy, we manually approved or disapproved the automatic sorting of spike clusters. Similar single-unit spike clusters were merged, and dissimilar spikes were either split or excluded.

For each single- or multi-unit in a given trial, we computed the spike counts over 50–250 ms after the onset of each stimulus cycle, scaled them to spike rate (i.e., number of spikes per second). The spike rates were averaged across two stimulus cycles for each trial and averaged across trials for each condition.

The spiking response of each identified single- or multi-unit as a function of stimulus contrast ($R_{spike}(c)$) was fitted independently by the following Naka-Rushton function (Naka and Rushton, 1966; Peirce, 2007):

$$R_{spike}(c) = (R_{max} - SA) \cdot \frac{C^{n_s}}{C^{n_s} + C_{50}^{n_s}} + SA$$

where C_{50} is the semi-saturation constant, n_s is the power exponent, SA is the spontaneous firing rate and R_{max} is the maximum firing rate. The parameters were estimated independently for each unit using maximum-likelihood estimation (MLE). The power exponent, n_s was constrained to be between 0 and 3 and the semi-saturation constant, C_{50} was constrained to be between 0 and 900. Only the units with $R_{max} \geq 5$, $R_{max}/SA \geq 3$, and $R^2 > 0.8$ were included for analysis. R^2 is the coefficient of

determination. The near-saturation contrast (C_{90}) of each unit was estimated from the fitted curve. To compare with the GCaMP data, we averaged the spiking responses across all the selected units and fitted the mean unit spiking response with the same function.

To describe the relationship between C_{50} and n_s across all the selected units, we fitted the following exponential decay function:

$$C_{50} = k_1 \cdot e^{-m \cdot n_s} + k_2$$

where k_1 is the scaling constant, m is the decay rate constant, and k_2 is the additive constant which describes the lower asymptote that the function approaches as n_s increases towards infinity.

6. Calcium imaging

We performed widefield calcium imaging using the procedures described previously (Chen et al., 2022; Seidemann et al., 2016). The imaging system comprised of a PCO Edge CLHS sCMOS camera, a 50 mm fixed-focus objective lens (facing cortex), a dichroic mirror (long-pass at 505 nm) and an 85 mm fixed-focus objective lens. Calcium signals were captured at a frame rate of 100 Hz from an $8.2 \times 8.2 \text{ mm}^2$ cortical area approximately centered on the GCaMP expression site. Images were binned to 512×512 pixels. Excitation light (X-Cite 120 LED) and GCaMP emission were bandpass-filtered at 480 nm and 520 nm, respectively. Data were collected with custom MATLAB-based software. Data acquisition was time-locked to the heartbeat using EKG (HP Patient Monitor) to enable the removal of the heartbeat artifact in offline data analysis. The visual

stimulus was placed in the lower-left visual field at 1.3° eccentricity from the fixation point for Monkey V and 2.3 or 2.7° eccentricity for Monkey S.

7. Analysis of imaging data

The imaging data were downsampled and normalized to compute the physiological signal expressed as $\Delta F/F$. For both monkeys, the average fluorescence over frames 0-300 ms prior to stimulus onset was used as the baseline, F_0 :

$$\frac{\Delta F}{F}(t) = \frac{F(t) - F_0}{F_0}$$

For each trial, the signal was first averaged temporally over frames 100-300 ms after the onset of the first stimulus cycle, and the mean signal from 0-100 ms before the stimulus onset was subtracted to extract the visual-evoked response. The analysis was limited to the first stimulus cycle because the signal did not fully return to baseline before the response to the second stimulus cycle began. The signals were then averaged spatially across the selected ROI ($3.1 \times 2.4 \text{ mm}^2$ cortical area for Monkey V, and $2.3 \times 1.5 \text{ mm}^2$ or $2.8 \times 1.9 \text{ mm}^2$ cortical area for Monkey S) and across trials for each condition. Finally, the mean response in the 0% contrast condition was subtracted from the mean response in each nonzero-contrast condition to remove the heartbeat artifact (i.e., blank subtraction).

For each experiment, the GCaMP response as a function of stimulus contrast ($R_{GCaMP}(c)$) was fitted by the same function used to fit the electrophysiology data; however, the spontaneous firing rate, SA was removed from the equation due to the blank subtraction.

The fitted maximum response, R_{max} allowed the function to account for the variability in the amplitude of signal and imaging quality across recording blocks or sessions due to various factors including, but not limited to, the difference in the GCaMP expression across the animals and over time:

$$R_{GCaMP}(c) = R_{max} \cdot \frac{C^{n_s}}{C^{n_s} + C_{50}^{n_s}}$$

The parameters were estimated using MLE. To fit the GCaMP response in each experiment, the power exponent, n_s and the semi-saturation constant, C_{50} were forced to be shared across blocks, while R_{max} was fitted independently for each block. To compare with the electrophysiology data, we averaged the GCaMP responses across experiments and fitted the mean GCaMP response with the same function.

Results

Initial exploration of the range of local contrasts in natural scenes

To begin exploring the range of local contrasts in natural scenes, we computed what we call the “center-surround contrast” (C_{cs}) at every pixel location in five arbitrarily selected, linear natural scene images by convolving them with a pair of kernels: a center kernel and a surround kernel (**Figure 1A**; see Methods). In each image, C_{cs} at a given image pixel location (x, y) was computed by placing the kernels such that their central pixels aligned with the image pixel, and taking the mean luminance of the image pixels falling within the center ($L_c(x, y)$) and the surround ($L_s(x, y)$) regions as follows:

$$C_{cs}(x,y) (\%) = \frac{L_c(x,y) - L_s(x,y)}{L_s(x,y)} \cdot 100$$

The surround diameter was set to be five times larger than the center diameter to roughly match the large surround receptive field (RF) size of RGCs (Croner and Kaplan, 1995). We chose this definition because it is closer to the contrast signal encoded by neurons in the retina and the lateral geniculate nucleus (LGN) (Enroth-Cugell and Robson, 1966; Hubel and Wiesel, 1961; Kuffler, 1953).

A Gaussian stimulus of 100% contrast has the maximal C_{cs} of 70% when convolved with a kernel having a center radius equal to one standard deviation of the Gaussian stimulus (i.e., larger and smaller kernels give a lower C_{cs}). **Figure 1B** highlights the locations in the five natural scene images where C_{cs} exceeds 70%. These high-contrast patches are ubiquitous across the images and occur in diverse locations, including boundaries between trees and the sky, as well as within leaves and rocks (**Figure 1C**). They occupy approximately 5% of the entire distribution of the positive contrasts, with their maximum contrasts exceeding 1,000% (**Figure 1D**). These results are robust to kernel size and demonstrate that high contrasts are common in natural scenes. Building on this result, our next goal was to determine how individual neurons and neural populations in V1 respond to stimuli across such a wide range of contrasts.

Contrast responses of single- and multi-units in V1 show a wide range of nonlinearities

Our main goal was to measure the neural responses in V1 to a range of contrasts that exceed 100% and to understand vision under more natural conditions. To create

Gaussians with such extremely high contrasts, we reduced the mean background luminance of the CRT monitor to 10 cd/m^2 , which was 10% of its maximal luminance. This approach allowed the maximal luminance of the stimulus placed on the background to reach up to ten times larger than the background luminance, achieving the maximal contrast of 900% (**Figure 2A**), while keeping the mean luminance in the photopic range. Our preliminary results from voltage-sensitive dye imaging in V1 show no systematic difference in the amplitude of the response to stimuli of a given contrast for mean background luminance ranging from 10 to 50 cd/m^2 (Y. Chen and E. Seidemann, unpublished observations). We recorded the activity of individual neurons and the activity of neural populations in V1 while two animals performed the fixation task where a small white Gaussian (0.33° FWHM) was flashed briefly over two temporal cycles at the corresponding retinotopic coordinates of the recording site (see Methods; **Figure 2B**). The stimulus contrast varied pseudo-randomly from trial to trial between 0-900% (see Methods).

To characterize the dynamic range of individual neurons, we recorded single- and multi-unit spiking activities using multi-channel probes (a 32-channel Plexon probe and a 384-channel NHP Neuropixels probe). The data were spike-sorted offline and the CRFs of all the identified units were fitted independently with the Naka-Rushton function that has two key free parameters, the power exponent, n_s and the semi-saturation constant, C_{50} (see Methods). We imposed three criteria on the fits of the CRFs to select the units with valid visual-evoked responses to the stimulus. We only included the units that passed the criteria for the analysis below (**Table 1**). However, we later show that our key results hold even without any exclusion (**Figure 7A**). To quantify the contrast where the CRFs

approach response saturation we computed, from the fitted Naka-Rushton curve, the contrast C_{90} where response reached 90% of maximum, R_{max} .

Within our selected pool of single- and multi-units, a subset of the units had a high n_s (> 2) and a low C_{50} (< 100). The spike response in these units started to saturate well below 100% contrast and C_{90} was smaller than 100%. An example of such a unit is shown in **Figure 3A and B**. However, in another subset of units with a low n_s (≤ 1) and a high C_{50} (> 100), the response continued to increase robustly beyond 100% contrast, and in many of these cells, the response continued to increase all the way up to 900% contrast with their C_{90} projected to be greater than 900%. An example of such a unit is shown in **Figure 3E and F**. For the units with a low n_s (< 1) and a low C_{50} (< 100), the response did not start to saturate by 100% contrast but did not necessarily increase robustly beyond 100% contrast either, with their C_{90} estimated to be greater than 100%. An example of such a unit is shown in **Figure 3C and D**. These observations suggest that single- and multi-units in V1 exhibit a wide range of nonlinearities in their contrast responses and that a fraction of V1 neurons respond robustly to contrast above 100%.

Majority of V1 units' responses rise robustly above 100% Weber contrast

Given the variability in the response saturation profiles of our sample of V1 single- and multi-units, we next evaluated the distribution of the three parameters summarizing the shape of the CRFs, n_s , C_{50} , and C_{90} across the population. The two fitted parameters, n and C_{50} show a systematic relationship that can be summarized with an exponential decay function, and their distributions are largely independent of the unit type. For both the

single- and multi-units, the median n was smaller than 2, and the median C_{50} exceeded 100% (**Figure 4A**). With slightly less than 50% of the units estimated to have C_{90} greater than 900%, the median C_{90} exceeded 600% for both groups. Most importantly, cells that approach their response saturation below 100% contrast (i.e., cells with $C_{90} < 100$) occupied less than 10% of our sample of single- and multi-units (**Figure 4B**). The majority of the units had C_{50} and C_{90} greater than 100%, producing CRFs similar to the example units with a low n_s (< 1) or a high C_{50} (> 100) (**Figure 3D and F**).

We binned these units into three groups (grey shaded regions in **Figure 4A**) based on their n_s and C_{50} , each of which includes one of the three example units shown in **Figure 3**. Consistent with the example multi-units, the within-bin average response reached a much higher peak at 900% contrast compared to 100% contrast across the two stimulus cycles for Bin 2 and 3, but not in Bin 1 (**Figure 5A, D and G**). To examine the dynamics of the response across the bins, we focus on the normalized within-bin average responses in the first cycle. The latency of the response increased, and the steepness of the rising phase decreased with increasing bin number (**Figure 5B, E and H**). The latency was shorter at 900% contrast compared to 100% contrast in all the three bins. While the average CRF within Bin 1 had only its C_{90} exceed 100% contrast, the average CRFs within Bins 2 and 3 had both of their C_{50} and C_{90} above 100% (**Figure 5C, F and I**). For Bin 3, with its C_{50} fitted to be larger than 900%, the average response continued to increase through 900% contrast without an immediate sign of saturation. These results indicate that the majority of V1 neurons respond robustly to contrasts above 100%.

Population response in V1 and comparison with average unit spiking response

Understanding the neural basis of perception requires studying neural activity not only at single-neuron resolution, but also at coarser, population-level. Although our high-density electrophysiological recordings provided access to the activity of hundreds of neurons, this still represents only a small fraction of the neural population activated by the stimulus, which comprises millions of neurons (Seidemann and Geisler, 2018). To capture this larger population response, we performed widefield calcium imaging in V1 across the cortical area encompassing the GCaMP expression site while the two animals viewed Gaussian stimuli across the same wide range of visual contrasts as in the electrophysiological recordings (see Methods). The stimuli were presented at the corresponding retinotopic coordinates of the GCaMP expression site.

Additionally, it is important to examine how the response properties of individual neurons translate to population-level activity patterns. In a previous study, we found that GCaMP signals in V1 are approximately linearly related to the local spiking activity of the underlying neural population, modelled as the pooled activity of individual neurons (Seidemann et al., 2016). Our next goal, therefore, was to determine whether the wide dynamic range of contrast-encoding in V1 empirically observed with extracellular electrophysiology extends to measures of population responses captured by widefield calcium imaging in the same animals.

To examine the dynamics and magnitude of the GCaMP response, we pooled the GCaMP signals over an approximately $3 \times 2 \text{ mm}^2$ region at the center of the cortical area

activated by the Gaussian stimuli (see Methods). **Figure 6A and C** show the GCaMP responses to 100% and 900% contrast Gaussians in two example experiments. Consistent with our electrophysiological results, the GCaMP response to 900% contrast is much higher than the response to 100% contrast Gaussian.

To quantify the CRF of these responses, we computed the average amplitude of the GCaMP responses as a function of contrast (**Figure 6B and D**). Unlike the single- and multi-unit activity, the calcium signal did not fully return to baseline before the response to the second stimulus cycle began (**Figure 6A and C**). Therefore, we restricted the analysis of the imaging data to the first stimulus cycle. The population GCaMP response continued to increase robustly beyond 100% contrast. Because we did not observe large variations in the shape of the CRF across experiments and monkeys, we fit all the GCaMP CRFs with a Naka-Rushton function with shared n_s and C_{50} while allowing R_{max} to vary (to account for the varying imaging quality between experiments). The GCaMP CRFs had a small n_s and a large C_{50} , similar to one of our multi-unit examples (**Figure 3F**).

To compare the GCaMP and electrophysiology CRFs more directly, **Figure 7A** shows the average normalized CRF across all the selected units and the average CRF across all the calcium imaging experiments. Here, the Naka-Rushton function was fitted to the mean spiking response across all the single- and multi-units or to the mean GCaMP responses across all the experiments. On average, the spiking response of the single- and multi-units reached approximately 50% of its saturation at 100% contrast (when the data was normalized by the mean response at 900% contrast) and continued to increase robustly up to near 500% contrast where it reached approximately 90% of its saturation (**Figure 7A, red**). To examine whether our selection criteria biased our observed CRF, we

repeated the analysis without excluding any units. The average CRF of all units (**Figure 7A, black**) was indistinguishable from that of the selected subset, indicating that our results are robust to the selection criteria of the electrophysiology data set.

The increase in the visual response above 100% contrast was even more pronounced in the GCaMP signals (**Figure 7A, blue**). The average GCaMP response reached approximately 30% of its saturation at 100% contrast, creating a significant deviation from the average unit spiking response. This result differs from our previous study, which showed that widefield GCaMP signals are approximately linearly related to the locally pooled spiking activity (Seidemann et al., 2016). Several factors may contribute to this difference. First, widefield imaging predominantly captures neural activity in superficial layers of the cortex (up to the depth of $\sim 500\ \mu\text{m}$) due to the limited penetration depth of the blue excitation light (Yizhar et al., 2011), whereas laminar probes used in the present study record activity from all layers. To determine whether this could account for the observed discrepancy, we divided the selected single- and multi-units into two groups according to their cortical depths and compared their average CRFs to the GCaMP data. The analysis was limited to the Neuropixels recordings ($N = 14$) where we had a more accurate estimate of the depth of each recorded unit. The average CRF of units recorded at depths of 0–500 μm indeed had a higher C_{50} and aligned more closely with the GCaMP data than the average CRF of units recorded at 500–2000 μm (**Figure 7B**). These results further suggest that the neuronal pool in superficial layers (L1 and L2/3) is dominated by neurons with a high C_{50} , while the pool in deeper layers contains a higher proportion of neurons with a low C_{50} .

Other contributing factors may include the difference in the cell types recorded by the two methods (i.e., both excitatory and inhibitory neurons for electrophysiology and only the excitatory for calcium imaging, as targeted with the $\text{CaMKII}\alpha$ promoter) and the nonlinear relationship between spiking of single neurons and GCaMP fluorescence (Akerboom et al., 2012; Chen et al., 2013; Scheuss et al., 2006; Zhang et al., 2023; Zhang and Looger, 2023), which may have persisted despite the pooling of heterogeneous neurons. Overall, our electrophysiological and GCaMP results show that V1 neural populations have a wide dynamic range of contrast encoding.

We repeated the analysis of the electrophysiology data using only the response to the first stimulus cycle, as was done for the imaging data. The key results at the population level remained largely unchanged. There was a slightly larger number of units ($n = 594$) meeting the selection criterion, 60% of the units had C_{50} larger than 100%, and only 7% of the units had C_{90} smaller than 100%. The average CRF across the units was fitted with $n_s = 1.00$ and $C_{50} = 107$.

Discussion

The dynamic range of contrast-encoding in V1 has been investigated extensively using oriented stimuli such as gratings and Gabor patches (Albrecht and Geisler, 1991; Albrecht and Hamilton, 1982; Albrecht et al., 2002; Geisler and Albrecht, 1997; Palmer et al., 2017; Seidemann et al., 2016; Sit et al., 2009). These studies show that most V1 neurons begin to saturate at low contrasts. Unoriented broadband stimuli such as Gaussians are common in natural scenes. Moreover, Gabors and Gaussians of equivalent size and contrast produce similar magnitudes of V1 population response and are equally detectable by macaques (Chen et al., 2012), and by humans (Watson and Ahumada, 2005). Given the saturating behavior of V1 to oriented stimuli and the similarity of V1 population responses to Gabors and Gaussians, one may expect similar saturating contrast response functions (CRF) for unoriented stimuli such as Gaussians. Yet V1 responses to such stimuli have rarely been studied.

Previous measurements of responses to Gaussians or similar broadband stimuli in V1 have been constrained to Weber contrasts up to 100% (Chen et al., 2022; Kumar et al., 2019; Xing, Yeh and Shapley, 2010; Yeh, Xing and Shapley, 2009). This range may not adequately reflect the statistics of contrast in natural scenes: indeed, we found that a substantial percentage of patches had contrasts exceeding that of a 100% contrast Gaussian (**Figure 1**). Given the prevalence of high contrasts in natural scenes, we hypothesized that V1 neurons will continue to encode Weber contrasts of Gaussian stimuli well above 100%. To test this hypothesis, we measured single-unit, multi-unit, and GCaMP responses to small Gaussian targets, for contrasts up to 900%.

Our sample of single- and multi-units in V1 exhibited a range of CRF shapes, which were quantified by the semi-saturation constant C_{50} and exponent n_s of the Naka-Rushton function. While some units reached 90% of their maximum response at a contrast (C_{90}) below 100%, the vast majority of units did not saturate until the contrast substantially exceeded 100%, consistent with our hypothesis.

Our results show that neurons that continue to respond robustly to contrasts above 100% (i.e., high C_{50} neurons) tend to have exponents n_s closer to 1, which means that their fitted Naka-Rushton curves are relatively linear in the low contrast range (i.e., below 100%). However, it is important to note that the typical accelerating rise often observed in the low contrast range might be missed when fitting such a wide contrast range (i.e., Naka-Rushton function may not be a sufficiently accurate description over the full dynamic range).

We estimated population activity in V1 from the spiking activity of neurons by averaging the CRFs across our selected sample of single- and multi-units. Consistent with the fact that most single- and multi-units had a C_{90} greater than 100%, the average unit response continued increasing above 100%. Also, the exponent of the average unit response is 1.01, and hence the population contrast response is approximately linear over the lower range of contrasts.

We then compared the average spiking to the average widefield GCaMP response, which measures neural activity over a much larger population of neurons. The average GCaMP response continued to increase robustly across the high-contrast range, to an even greater extent than the average spiking response. This discrepancy, however, diminished

when the analysis of the electrophysiology data was restricted to units in the superficial layers, which dominate the imaging signal.

In previous work (Chen et al., 2022), we found that direct optogenetic stimulation in V1 can produce population responses substantially greater than those produced by 100% contrast Gaussian stimuli. One hypothesis for this finding is that the optogenetic stimulation was pushing the neural population response beyond its normal operating range. However, the current findings suggest that this may not be true. Further testing with higher contrast visual stimuli will be required to compare the population dynamic ranges of visual and optogenetic stimulation.

A couple of behavioral studies in humans have measured contrast discrimination under conditions similar to those tested here (Cornsweet and Pinsker, 1965; Kortum and Geisler, 1995). They found that Weber's law holds over the ranges of transient luminance and contrast tested here, a result consistent with weak saturation (very large values of C_{90}).

What can explain the very high C_{90} values that we observed? One possible explanation follows from a study in cats that measured contrast response functions of simple and complex cells to randomly interleaved transient changes in background luminance and Gabor target contrast (Geisler, Albrecht and Crane, 2007). It was found that the shape of the contrast response function is invariant to changes in transient luminance, but is scaled multiplicatively (i.e., there are changes in R_{max}) depending on the transient luminance. There are individual differences across cells but on average R_{max} increases with transient luminance. The important insight is that unlike Gabor targets, Gaussian

targets produce a transient increase in both contrast and luminance. In other words, the R_{max} should increase with increasing Gaussian Weber contrast, which could explain the continuous increases in response at high Weber contrast. Indeed, simulations of units with both contrast and luminance gain control suggest that these continuous increases are expected for changes in R_{max} like those observed in cats. This hypothesis could be tested with similar experiments in primates.

A dynamic range from 0% to 900% would allow the primate visual system to be sensitive to the differences between very high contrasts. Why would that be useful? In our sample of natural scene images, high contrasts exist where materials and objects are backlit by the sky and also within materials and objects themselves. Encoding of the high-contrast backlit regions could support foraging in primates. Similarly, specular reflections from smooth surfaces, which also tend to have high contrast, could serve as a cue for discriminating materials that differ in their glossiness and as a cue for locating water droplets. These are all examples of tasks that may have important survival value.

Future directions

Here, we find that the dynamic range of contrast-encoding in V1 population responses to localized stimuli extends beyond the commonly assumed range. Previous studies typically used Gabor or grating stimuli optimized for each neuron's preferred orientation and spatial frequency, whereas the Gaussian stimulus used here is suboptimal for driving individual neurons. Future studies should therefore compare single-neuron responses to Gabor and Gaussian stimuli, testing whether Gabor responses saturate below 100% Michelson contrast in neurons with a wide dynamic range for Weber contrast and whether

a very high-contrast Gaussian evokes stronger responses in these neurons than an optimized Gabor of 100% Michelson contrast. Composite “increment-Gabor” stimuli, formed by summing a Gaussian and a Gabor of equal amplitude (Kortum and Geisler, 1995), could further help isolate the contributions of contrast, orientation and spatial frequency to single-neuron and population responses in V1. Furthermore, a comparison of responses to these laboratory stimuli and natural scene patches of various contrasts and sizes will be required to more completely determine the relevance of our findings for natural vision. Also important is testing whether the broad dynamic range persists across a wider range of background luminance.

Previous studies reported black-dominant responses in macaque V1 using a limited range of contrasts that was symmetrical (i.e., $\pm 100\%$) for black and white stimuli (Xing, Yeh and Shapley, 2010; Yeh, Xing and Shapley, 2009; Benvenuti et al., 2018). Our study, however, shows that white contrasts can extend well beyond this previously tested range in both natural and experimental settings. This raises the possibility that the earlier studies underestimated the full dynamic range of responses to white stimuli and consequently may have overestimated the prevalence of black-dominant responses. This can be tested by redefining black contrasts such that its magnitude could exceed 100%, as is possible for the white contrasts, and comparing neural responses to high-contrast black and white stimuli. However, it is worth noting that our analysis of the natural images revealed that the majority of the patches have a negative contrast (i.e., dark contrast; see **Figure 1D** legend), and this was consistent across both images and kernel sizes. This imbalance may have created a computational advantage for black dominance in V1.

Finally, the present study has only focused on the neural representation of contrast encoding in V1. Behavioral measurements of discrimination should be compared with thresholds derived from these population responses to determine whether perceptual performance is consistent with the observed neural encoding.

Conclusions

In conclusion, our results strongly suggest that the dynamic range of single-neuron and population responses to localized stimuli in V1 are substantially wider than previously assumed.

The broad dynamic range also aligns more closely with the distributions of contrast in natural scenes, suggesting that there is evolutionary value in encoding the high contrasts found in the natural environment.

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Legends

Figure 1. Distribution of center-surround contrasts in natural scenes. **A**, Contrasts in natural scene images (50 px/deg) are computed by convolving them with a center kernel and a surround kernel (see Methods). **B**, Natural scene images that were analyzed. Images are gamma-compressed for visualization. Pink circles mark the spots with a center-surround contrast, C_{cs} , greater than 70% when the images were convolved with kernels having d_c and d_s values of 15 and 71 pixels, respectively. **C**, Example high-contrast (> 300%) patches from image 3 in **B**. Magenta outlines indicate the kernels. **D**, Distribution of the positive contrasts (i.e., $L_c > L_s$) pooled across all the images in **B**, computed by kernels of different sizes. Insets show the kernels used to convolve the image (d_c and d_s : 7 and 35 px, 15 and 71 px, and 29 and 141 px, respectively, from left to right). The majority of contrasts are negative (i.e., $L_c < L_s$) for all the three kernel sizes, with the same proportion observed for each kernel size ($P(C_{cs} < 0) = 0.56$). Vertical dashed lines indicate 70% contrast.

Figure 2. Stimulus and behavioral paradigm. **A**, *Left*, a small white Gaussian stimulus (0.33° FWHM; 50 px/deg) of 100% Weber contrast placed on a uniform grey background (50 cd/m²). *Right*, a Gaussian stimulus of 900% Weber contrast placed on a uniform dark grey background (10 cd/m²). **B**, Fixation task. Following the initial fixation period, a Gaussian stimulus is presented at the receptive field (RF) of the electrode's penetration site or the imaging site for two cycles. The monkeys maintain fixation at the central dot over two cycles of stimulus presentation to receive a reward.

Figure 3. Example multi-unit responses in V1 across a wide range of visual contrasts. **A**, Trial-averaged peristimulus time histogram (PSTH) of an example multi-unit with a low C_{50} for 100% and 900% contrast stimuli, aligned to the first stimulus onset. Spike count in the preceding 50 ms window is scaled to spike rate (number of spikes per second) for every 10 ms for visualization. Vertical dashed lines indicate the stimulus onsets. Shaded regions indicate the time windows (50–250 ms after each stimulus onset) over which the spike rate is computed for each trial to generate the CRF shown in **B**. **B**, Trial-averaged CRF of the multi-unit shown in **A**, fitted by a Naka-Rushton curve. Error bars indicate SE across trials ($n = 20$). Dashed light and dark green lines indicate the responses at C_{50} and C_{90} , respectively. Horizontal solid line indicates the fitted spontaneous firing rate, SA . **C-D**, Same as **A-B** for a multi-unit with a mid C_{50} . **E-F**, Same as **A-B** for a multi-unit with a high C_{50} .

Figure 4. Summary of single- and multi-unit data. **A**, C_{50} as a function of n_s for the selected single- (red) and multi-units (black) is fitted by an exponential decay function (blue curve; $k_1 = 2290.65$, $k_2 = 97.16$, $m = 2.68$; see Methods). Markers on the marginal histograms indicate medians for single- (red; $n_s = 1.26$, $C_{50} = 149$) and multi-units (black; $n_s = 1.22$, $C_{50} = 130$). Horizontal bars indicate 95% bootstrap CIs of the median. Decimals on the top and the right edges of the figure indicate the proportion of units in each trisected subpopulation of n_s and C_{50} for single- (red) and multi-units (black). Yellow stars indicate the three example units shown in Figure 3, each drawn from one of the three bins (grey shaded regions). **B**, Distribution of C_{90} derived from the CRFs fitted to the selected single- and multi-units. Markers indicate medians for single- (red; $C_{90} = 669$) and multi-units (black; $C_{90} = 754$). Horizontal bars indicate 95% bootstrap CIs of the median.

Figure 5. Average PSTH and CRF across subpopulations of single- and multi-units.

A, Normalized average PSTHs across single- and multi-units in Bin 1 shown in Figure 4A. Same convention as Figure 3A. Spike count in the preceding 10 ms window is scaled to spike rate for every 10 ms and averaged across the units. The average PSTHs are normalized by the mean response between 100–300 ms after each stimulus onset at 900% contrast. **B**, Same as **A**, displayed over the first response cycle (0–400 ms) and normalized independently for each contrast level. **C**, Average CRF across the units in Bin 1. Error bars indicate SE across units. Same convention as Figure 3B. **D-F**, Same as **A-C** for Bin 2. **G-I**, Same as **A-C** for Bin 3.

Figure 6. Example calcium population responses in V1 across a wide range of

visual contrasts. A, Trial-averaged time courses of GCaMP responses to 100% and 900% contrast stimuli from an example experiment in Monkey V, aligned to the first stimulus onset. Same convention as Figure 3. The response is averaged over 100–300 ms after the first stimulus onset to generate the CRF shown in **B**. **B**, Trial-averaged CRF from the example experiment shown in **A**, fitted by a Naka-Rushton curve ($n_s = 0.98$, $C_{50} = 277$, $C_{90} > 900$). Error bars indicate SE across trials ($n = 20$). Dashed lines indicate the responses at C_{50} . **C-D**, Same as **A-B** for an example experiment in Monkey S. The fitted curve in **D** shares the same parameters as the curve in **B** (see Methods).

Figure 7. Comparison of electrophysiology data and imaging data. A, Spike rate or

$\Delta F/F$ data is averaged across units or experiments and normalized by the mean response at 900% contrast. Curves are fitted to the mean responses across all the identified units (black; $n_s = 1.00$, $C_{50} = 113$), the selected units (red; $n_s = 1.01$, $C_{50} = 106$), and the imaging

experiments (blue; $n_s = 1.01$, $C_{50} = 275$). Error bars indicate SE across units or imaging experiments. **B**, Among the selected units, those recorded with Neuropixels probes are divided into two groups according to the cortical depths at which they were identified (solid red; $n_s = 1.37$, $C_{50} = 172$; dashed red; $n_s = 0.98$, $C_{50} = 110$).

Table 1. Number and proportion of excluded single- and multi-units by criterion.

Three criteria were imposed on the fitted CRFs of all the single- and multi-units identified by spike-sorting, based on the fitted maximum firing rate, R_{max} and spontaneous firing rate, SA , and the coefficient of determination, R^2 , to select units with reliable visual-evoked responses for analysis (see Methods). Numbers in the brackets indicate the proportion with respect to the multi-, single- or all-unit category.

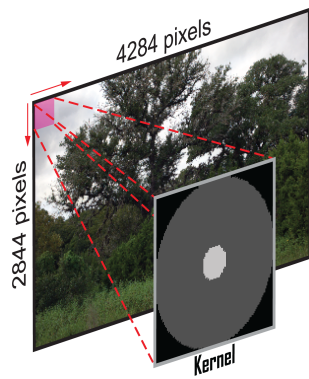
Table 1

	nUnits	Total excl.	R_{max}	R_{max}/SA	R^2
Multi-unit	1904	1461 (0.77)	426 (0.22)	1364 (0.72)	1066 (0.56)
Single-unit	692	608 (0.88)	443 (0.64)	495 (0.72)	486 (0.70)
All-unit	2596	2069 (0.80)	869 (0.33)	1859 (0.72)	1552 (0.60)

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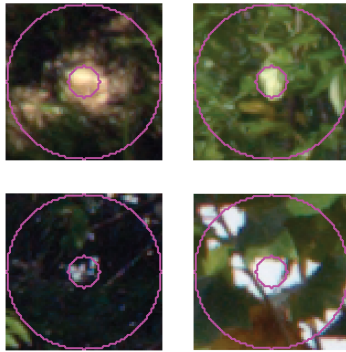
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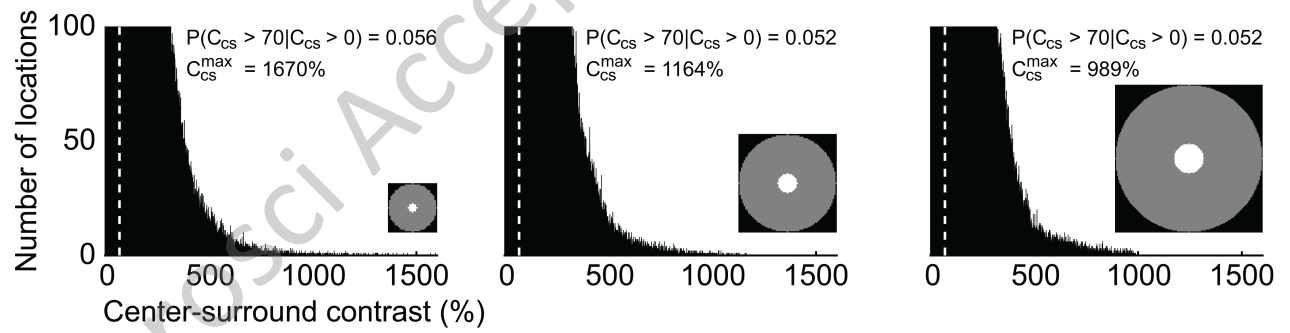
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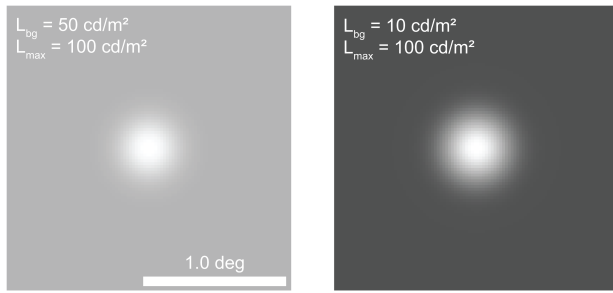
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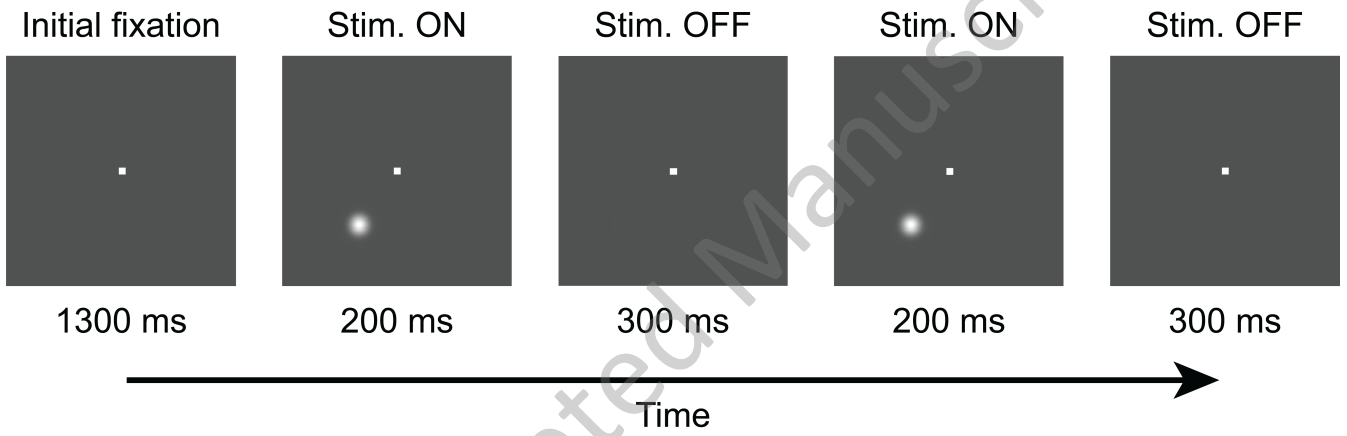
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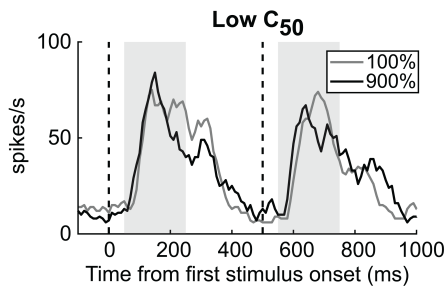
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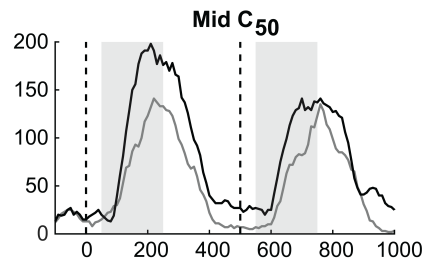
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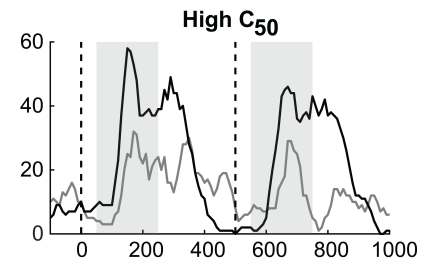
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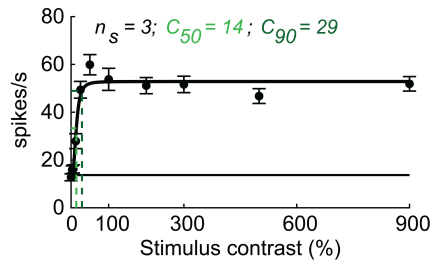
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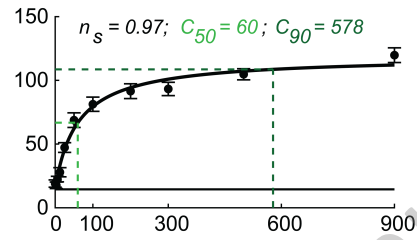
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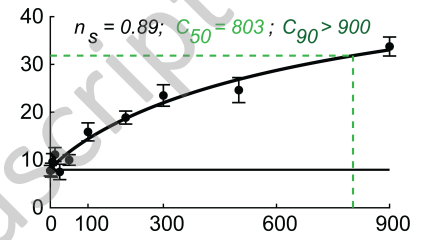
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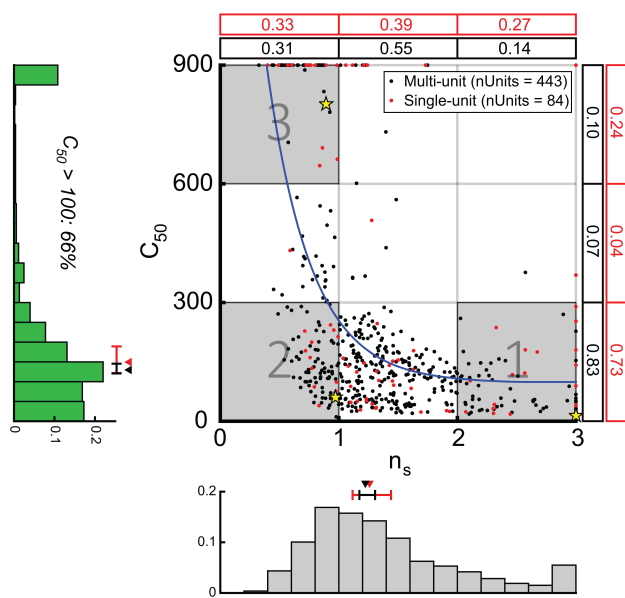
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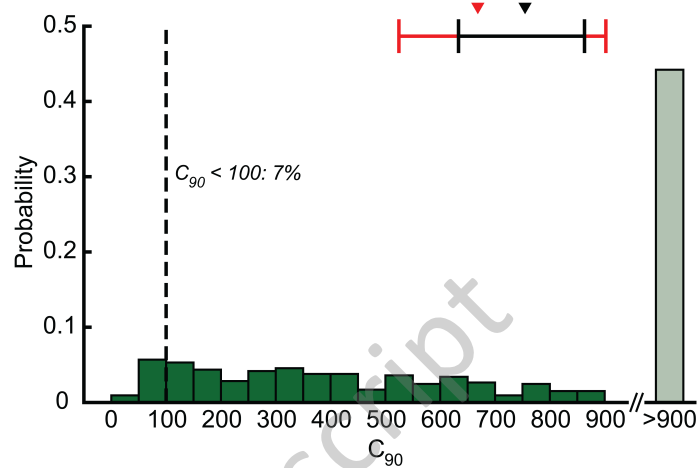
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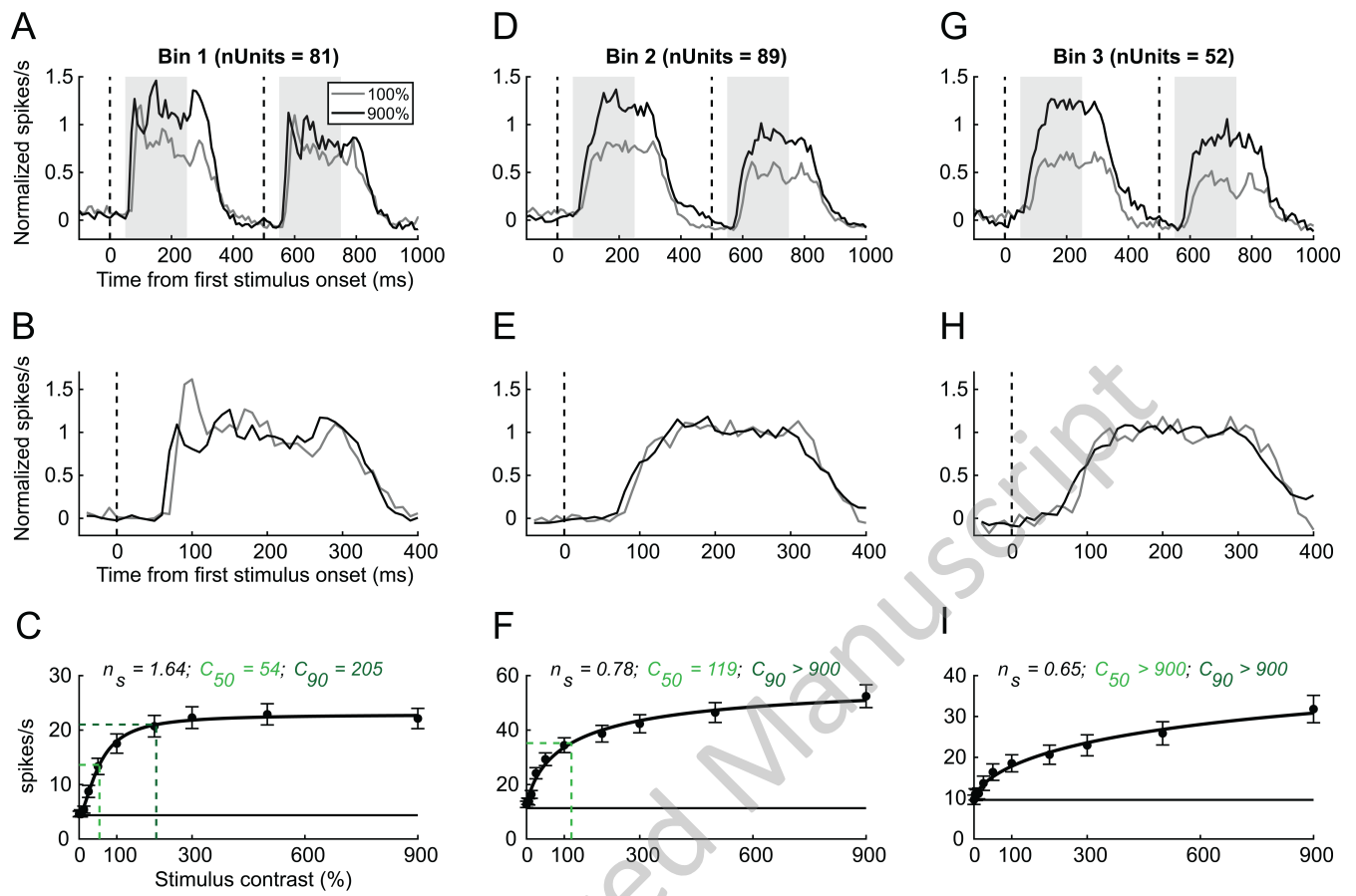


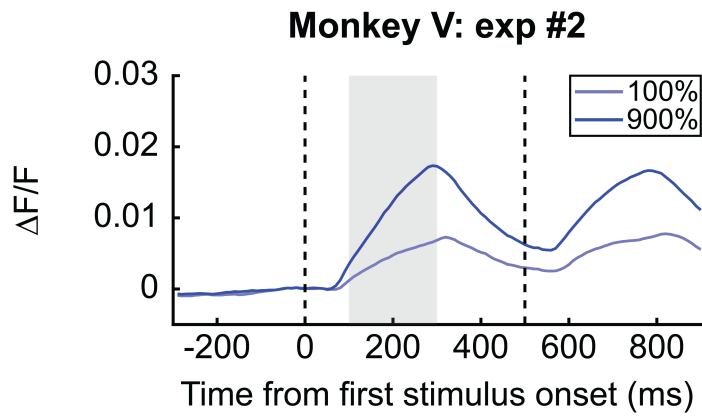
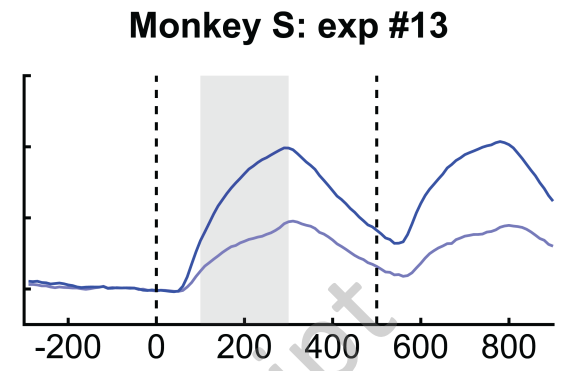
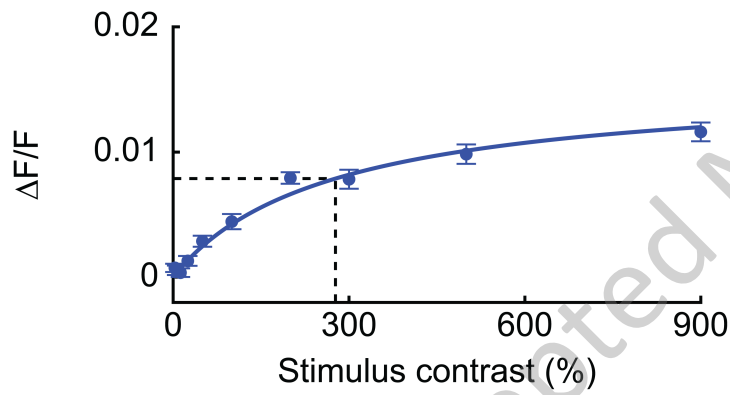
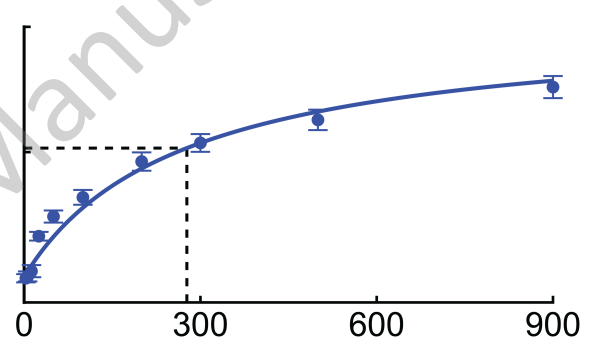
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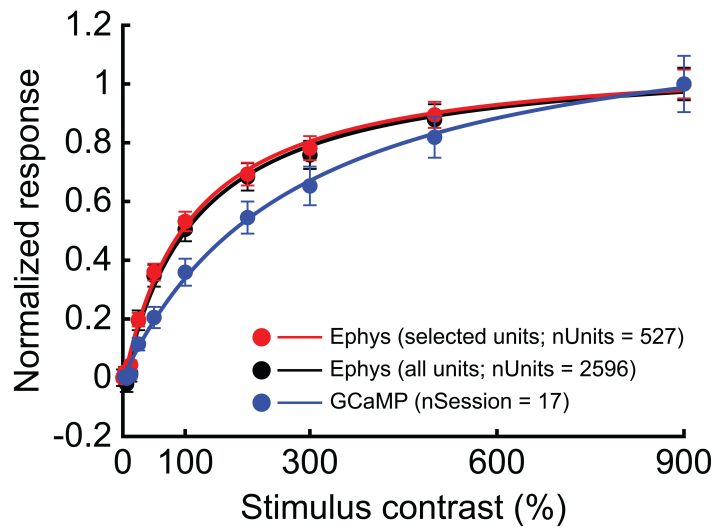


B





A**C****B****D**

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