

Figure S1. Sample V1 and V4 responses, Related to Figure 2A. Tuning for targets, presented either in isolation (black) or with near (left) or far (right) distractors. Data from two example cells are shown for each area. B. Example spike count distributions used to evaluate single neuron discriminability. Responses for two target stimuli shown either in isolation (left, black) or with near distractors (right; blue for V1 or red for V4) are shown. Examples are provided for two neurons in each area. C. Pairwise correlations for targets alone (left, black) or with distractors (right; blue for V1, red for V4). Z-scored responses are shown for two sample pairs in each area.

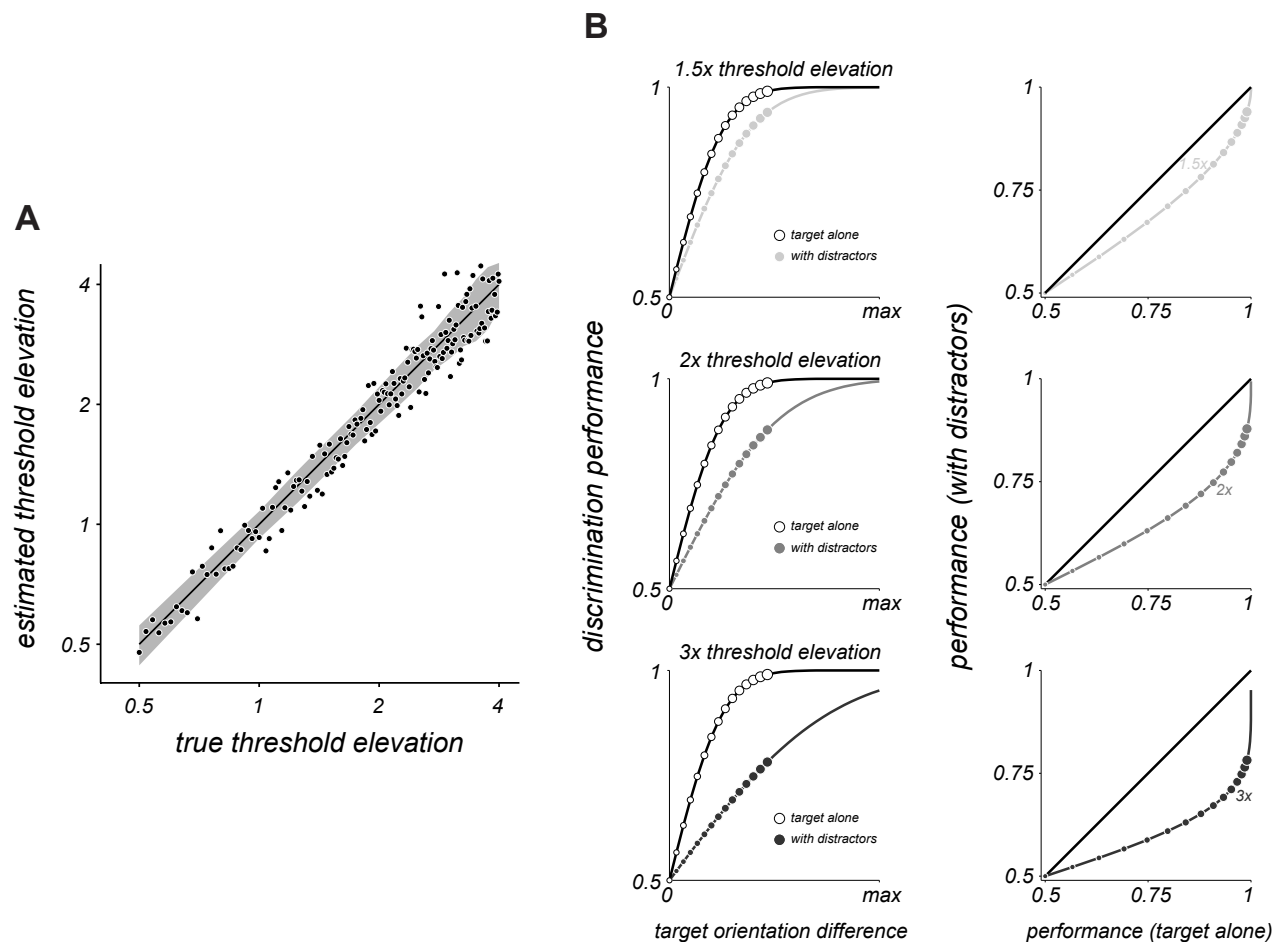


Figure S2. Method to estimate threshold elevation, Related to Figure 2 This figure illustrates our method is effective at recovering ground truth threshold elevation, on synthetic data. (A) We first defined a decoding performance curve for discriminability between targets of varying orientations (white points, black line), as a cumulative Gaussian function with an arbitrary standard deviation (σ) of 3, which defines the slope. We then used the mean performance defined by this curve to generate 40 trials (per stimulus) of responses from a binomial distribution. We generated similar synthetic data for targets with distractors (gray points and line), for which the performance curves were defined by scaling σ by factors of 1.5-3 (top to bottom, respectively). (B) Using the generated trials of binomial responses, we inferred the underlying change in σ by maximum likelihood. Specifically, we sought the σ of the cumulative Gaussian whose performance values maximized the log likelihood of observing the data for a binomial distribution with the success rate specified by the performance curve. The inferred threshold elevations tracked closely the true threshold elevation of the synthetic data. Black line indicates the unity line, shaded gray region represents ± 1 s.e.m.

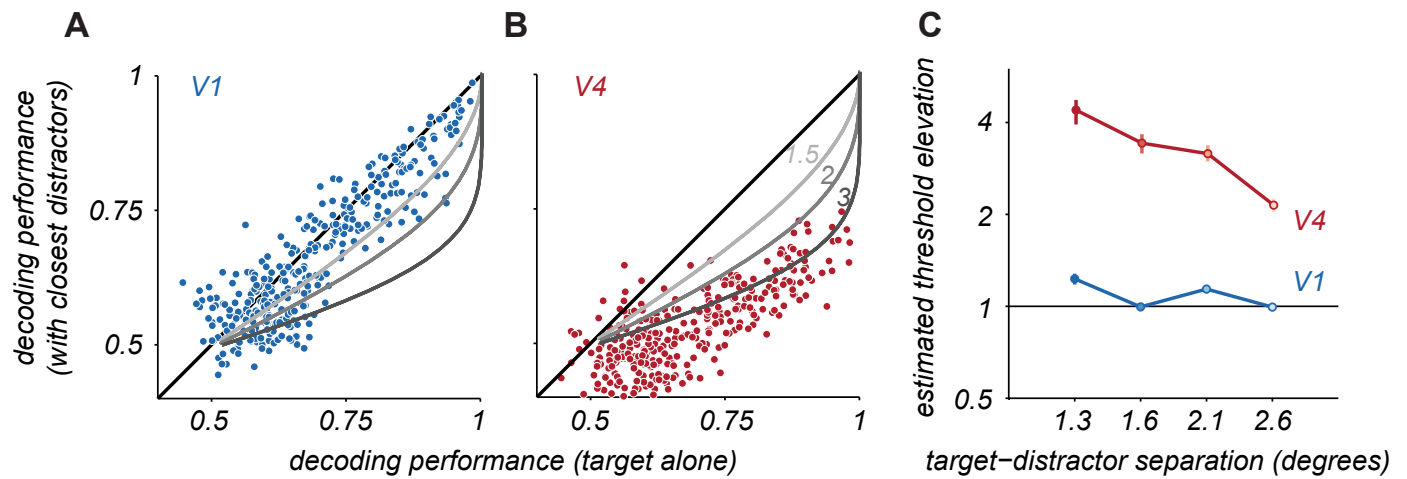


Figure S3. Target discriminability in pseudo-populations, Related to Figure 2A. Pseudo-population responses were created for a range of population sizes by resampling from neuronal responses (across animals and sessions). Cross-validated V1 pseudo-population decoding performance for targets alone (abscissa) and targets with closest distractors (ordinate). Each point represents a single pairing of two target stimuli. Gray lines indicate expected performance for the indicated threshold elevations. B. Same as in A, but for V4 pseudo-populations. C. Threshold elevation as a function of target-distractor separation. Points and error bars represent the mean \pm s.e.m. estimated via bootstrapped resampling of the data for V1 (blue) and V4 (red) pseudo-populations.

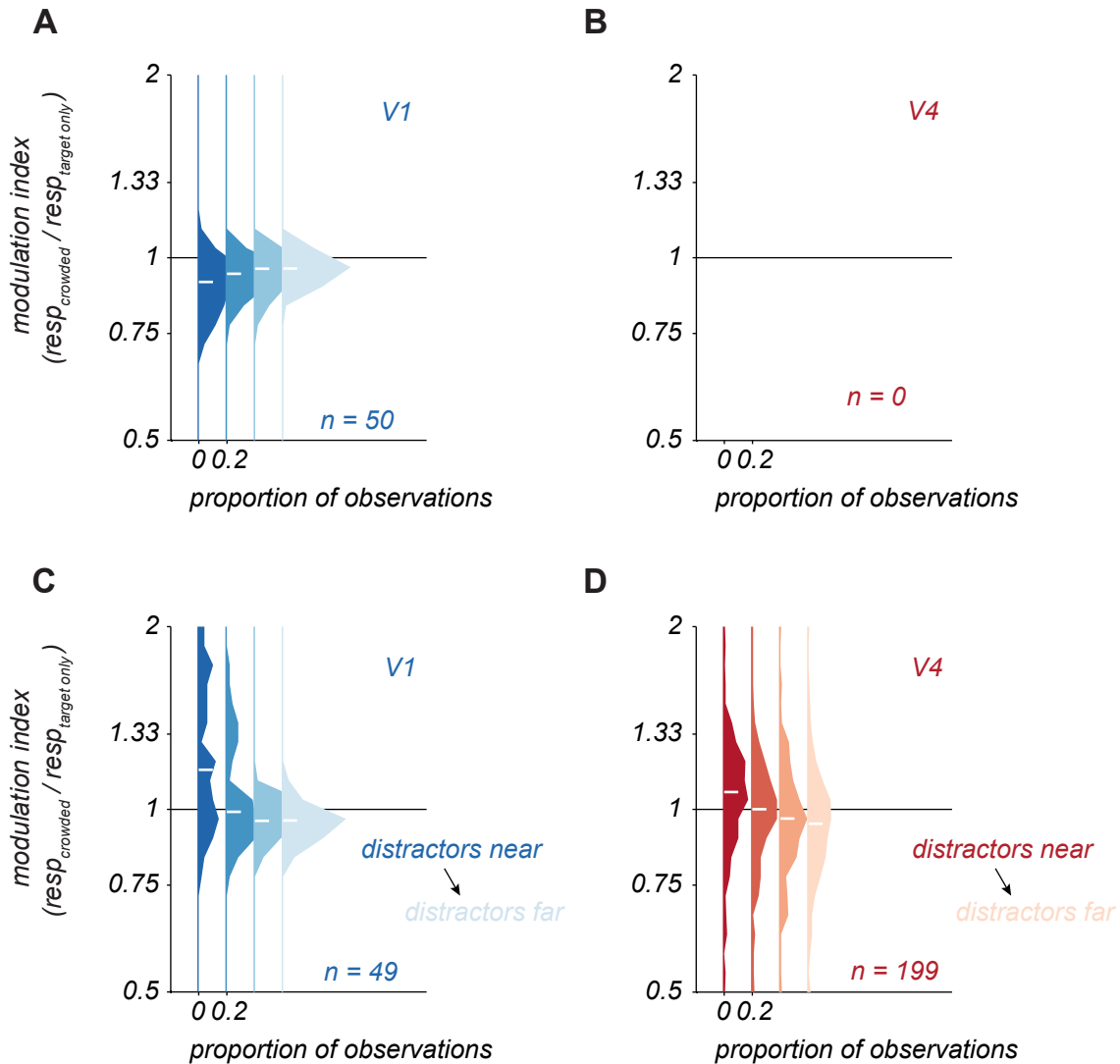


Figure S4. Response modulation with distractors, conditioned on the spatial receptive fields of each neuron, Related to Figure 4A, B. Modulation indices for neurons whose spatial receptive fields overlapped the target location, plotted with the conventions of Figure 4. At the beginning of each session, we conducted a brief, coarse mapping measurements, in which we presented targets and each distractor in isolation. The neurons plotted here had responses to a target stimulus which $>95\%$ of the maximum measured response, and a response to each distractor which did not exceed 30% of the maximum response. The modulation indices show that V1 neurons were suppressed by distractors, with the nearest distractors causing the greatest suppression (A). No V4 neurons were driven solely by the target stimuli (B). C,D Modulation indices for V1 (C) and V4 (D) neurons driven by both targets and targets presented in isolation. Specifically, these neurons responded to the target at $>95\%$ of the maximum measured response and to at least one distractor at $>80\%$ of the maximum response. V1 neurons whose receptive fields straddled both target and distractor stimuli showed robust facilitation for nearby distractors and suppression for more distant distractors (C). Similar trends were evident for V4 neurons (D).

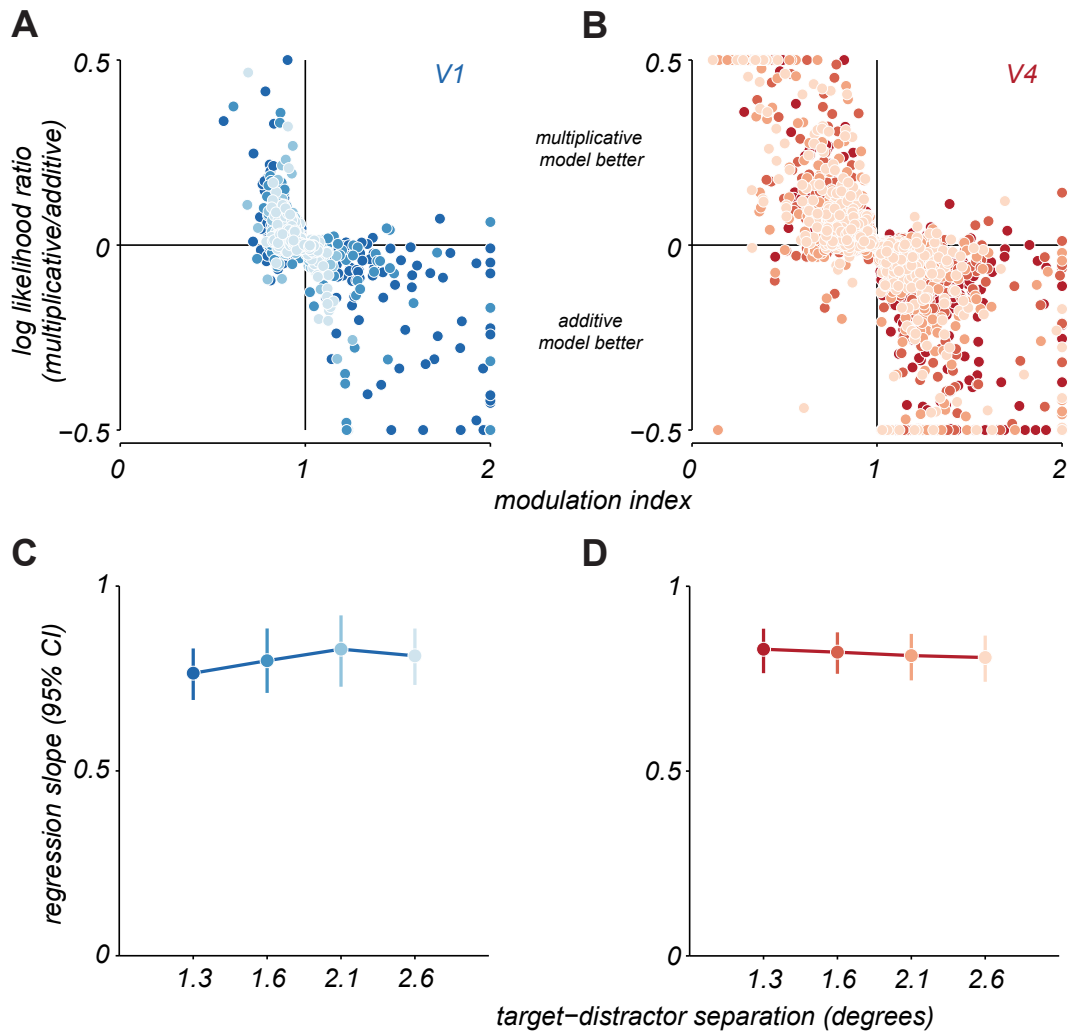


Figure S5. Comparison of additive and multiplicative modulation of responses to targets by distractors, Related to Figure 5. We repeated an analysis from our prior study (Henry and Kohn, 2020) to determine whether the orientation tuning for targets amid distractors was better characterized as an additive or multiplicative change of the tuning for isolated targets. Responses under crowding were fit by inclusion of either an additive or multiplicative scaling term c , applied to the responses to targets alone. Model responses were rectified at 0. Models were fit by choosing parameters that maximized the likelihood of observing the data given the model predictions (as in the model fitting considered in the main text).

Model comparison was performed using the log-likelihood of each model given the data, assuming Poisson variability of neuronal responses (El-Shamayleh and Movshon, 2011). Note that our definition of additive modulation of tuning does not require that responses to targets and distractors strictly add. Sublinear (e.g. due to normalization, Carandini and Heeger, 2011) or supralinear (e.g. due to thresholding or exponentiation, Carandini et al., 2005) summation would also result in an additive modulation of tuning, so long as the degree of non-linear summation was constant across target orientations.

Log-likelihood model comparison for whether V1 tuning with distractors was better explained by an additive or multiplicative change in tuning for targets alone. Response modulation index is shown on the abscissa; values less than 1 indicate suppression, greater than 1 indicate facilitation. Each point represents a single V1 neuron and distractor spacing condition (near distractors: dark blue, far: light blue). B. Model comparison for V4 neurons, same conventions as in A. In both areas, an increase in responsivity (modulation index > 1) was better described as an additive modulation; a loss of responsivity (modulation index < 1) was better described as a multiplicative modulation. C. Both additive facilitation and multiplicative suppression would be expected to reduce discriminability (Henry and Kohn, 2020). To determine how strongly discriminability would be affected, we simulated responses for each neuron using a model where facilitation acts additively and suppression divisively. This panel shows the expected change in V1 discriminability as a function of target-distractor spacing. The change in discriminability was quantified using the slope of the regression line relating discriminability for target only and crowded conditions, as in Figures 2 and 6. Error bars indicate 95% confidence interval. D. Same as in C, but for V4 discriminability. Thus, panels C and D show that allowing for either additive facilitation or divisive suppression reduces discriminability in both areas, but not as strongly as in the measured responses. Only by including both forms of modulation together (Figure 6) can we accurately capture the observed change in discriminability.

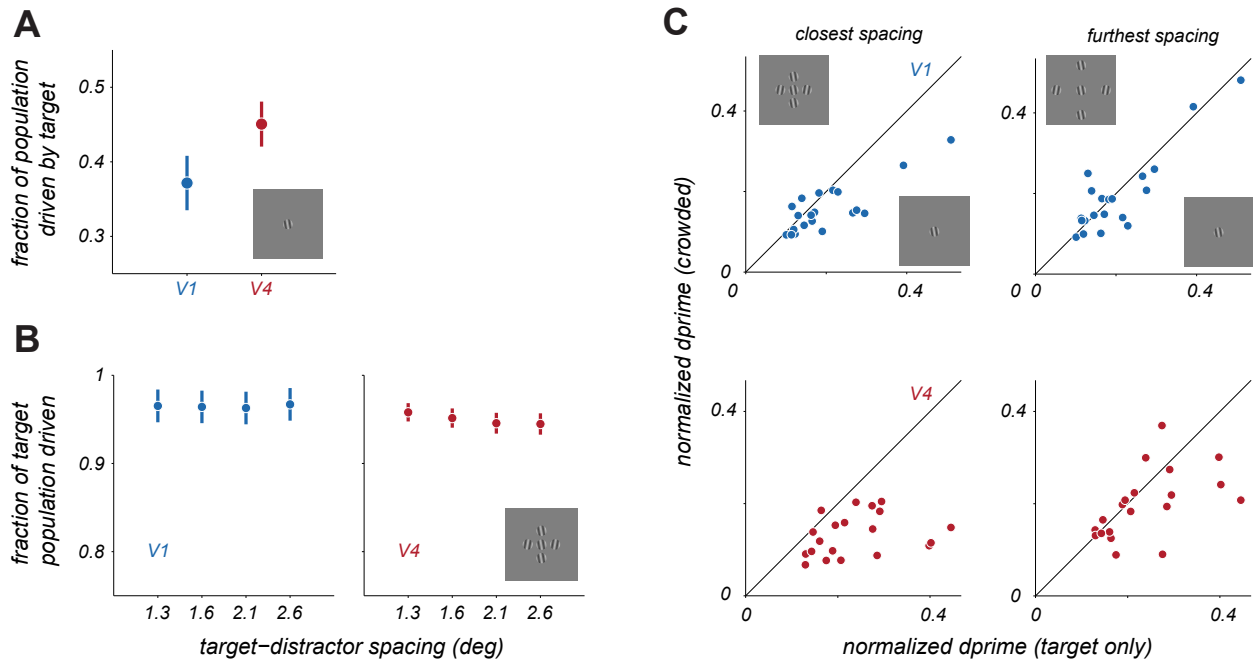


Figure S6. Informative populations across conditions of crowding, Related to Figure 7A. Average fraction of neuronal population that was significantly driven by target stimuli (defined as a response greater than the baseline rate and 1 SD of that rate), for V1 (blue) and V4 (red). Points represent mean \pm s.e.m. B. Average fraction of those target-responsive populations that remained driven in the presence of distractors, at various target-distractor spacings. C. For each population, the contribution of the most informative neuron for targets alone (abscissa) compared to the informativeness of that neuron for targets with distractors (ordinate). Dprime values were calculated for the two most extreme targets shown, and then normalized by the summed dprime value of the recorded population. Left column represents comparison between targets alone and with near distractors; right column represents comparison between targets alone and with far distractors.

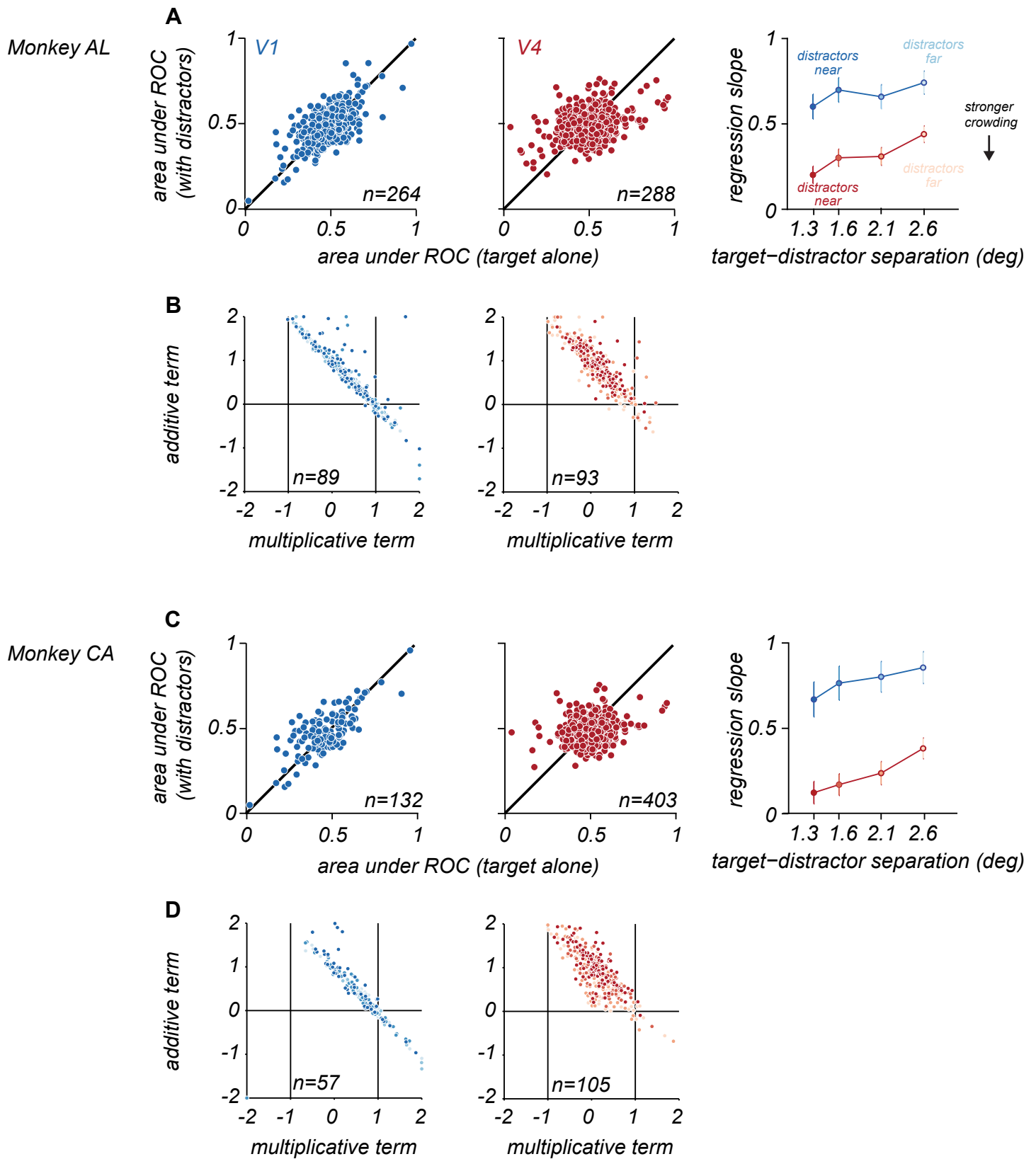


Figure S7. Effects of distractors on single-neuron discriminability and tuning, shown separately for each animal, Related to Figures 2 and 5A. Discriminability afforded by single-neuron responses in V1 (left) and V4 (center), for monkey AL. Each plot compares the area under the ROC, for spike count distributions elicited by target stimuli differing in orientation by 18 degrees. Reduction in discriminability is quantified as the slope of the regression line relating performance for targets alone (abscissa) and targets with distractors (ordinate). All conventions as in Figure 2A-C. B. Additive and multiplicative changes in target tuning with distractors, for monkey AL. Each point represents one neuron and distractor spacing condition, darker shades indicate closer distractor spacing. Conventions as in Figure 5. C,D Corresponding data from monkey CA.