Geometry of anisotropic contextual interactions in the visual cortex places fundamental limits on spatial vision.

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ABSTRACT

Crowding, the impaired ability to accurately recognize a target stimulus among distractors, is a major bottleneck in visual perception. The spatial configuration of distractors in relation to the target profoundly influences perceptual fidelity. Notably, when a distractor is placed at a more eccentric point on the radial axis (termed 'radial-out crowding'), it exerts the strongest impairment. Despite the pronounced perceptual anisotropy, the prevalent assumption underlying our understanding of contextual interactions in the visual cortex assumes isotropy. We investigated how distractor stimuli in different spatial configurations impacted the representation of a target stimulus in laminar microcircuits in the primary visual cortex (V1). Our study reveals that radial-out crowding more strongly impacts the ability to decode the target orientation from V1 population activity compared to other spatial configurations. This effect was strongest among putative excitatory neurons in the superficial and input layers, which are the primary neural populations involved in feed-forward information propagation. Remarkably, the feedback pathway involving the deep cortical layers does not exhibit anisotropy. Mechanistically, the anisotropy is explained by a tuned suppression and

untuned facilitation of orientation responses, leading to an anisotropic broadening of tuning curves in the feedforward pathway, but not in the feedback pathway. These results underscore the non-uniform spatial integration of information by neurons in the visual cortex, establishing the presence of anisotropic contextual interactions in the earliest stages of cortical processing. By elucidating the distinct roles of feedforward and feedback pathways in the context of crowding, this study advances our understanding of the intricate interplay between spatial arrangement, neural circuitry, and the constraints on perceptual fidelity during early visual processing.

INTRODUCTION

Our ability to perceive objects in the visual world is profoundly limited by the phenomenon of visual crowding, which decreases our ability to recognize target objects among visual clutter (*1*). Crowding not only limits both perception and visually guided behavior in normally sighted individuals but also impacts patients with conditions ranging from macular degeneration to dyslexia (*2*). The area in visual space over which distractor stimuli impact the perception of a central target is referred to as the crowding zone. A fundamental property of crowding zones is their anisotropy in visual space (for review, see *3*). Psychophysical studies of crowding have identified two major anisotropic characteristics of crowding in perception. First, distractor stimuli positioned on the radial axis exert a larger influence on perception than distractors on the tangential axis (*4*). Second, crowding is asymmetrical along the radial axis, such that distractors that are more eccentric than the target more strongly impair perception than distractors that are less eccentric than the target (*5*). Together, these results indicate that distractor stimuli positioned on the radial axis and more eccentric than the target (radial-out crowding) are more effective at inducing crowding effects than stimuli either on the radial axis but less eccentric than the target (radial-in crowding) or on the tangential axis (tangential crowding).

Psychophysical studies have suggested that crowding emerges in the cortex (*6, 7*), and various models (*8-12*) have been proposed to explain crowding effects based on the anatomy and connectivity within the primary visual cortex (V1). Despite these efforts, very little experimental evidence exists to validate or refute any proposed neural mechanisms. While the perceptual effects of crowding have been studied for many decades (*1, 3, 9, 13-15*), it was only recently that there has emerged direct evidence of

neural correlates underlying the phenomenon (*16, 17*). The question of exactly when and how crowding effects emerge in the visual hierarchy remains unresolved, but recent work has shown that crowding impairs feature representations as early as V1 (*16, 17*). However, the neural mechanisms responsible for how the spatial geometry of stimuli affects the strength of crowding remain poorly understood at the level of cortical microcircuits composed of multiple laminae and cell classes (*18-21*).

We sought to understand how stimuli presented outside the receptive field center could influence stimulus representations in the V1 laminar microcircuit in a spatially anisotropic manner. We hypothesized that radial-out crowding would most strongly impact the representation of target stimuli among excitatory neurons in the output layers of V1. We further hypothesized that these anisotropic contextual interactions might be most prevalent in the subpopulations involved in feed-forward information propagation, particularly excitatory neurons in the input and superficial layers.

RESULTS

To study how the spatial configuration of stimuli influences neural responses in area V1, we trained monkeys to perform a passive fixation task while we presented stimuli in different geometric arrangements. Monkeys fixated on the center of the screen and passively viewed stimuli presented either alone (target-only condition) or along with a distractor in one of four locations (crowding). We defined three crowding conditions based on the spatial position of the distractor relative to the target (Figure 1A, see Methods). The radial-in and radial-out crowding conditions positioned the distractor on the radial axis connecting the target to the fixation point. In the radial-in condition, the distractor was placed between the target and the fixation point, while in the radial-out condition, the

distractor was past the target on the radial axis. For the tangential crowding condition, the distractor was positioned on the tangential axis (the line orthogonal to the radial axis and passing through the target) on either side of the target.

During the task, we performed laminar extracellular recordings (*22, 23*) of single unit activity in V1 (Figure 1B, S1A-E). We positioned the stimuli such that the target stimulus was presented at the center of the aggregate receptive field of the recording sites. During our recordings, we collected data from 905 well-isolated single units (Figure 1B, 511 from monkey M, 394 from monkey D). We used established procedures (*22, 24-28*) to classify these neurons based on their waveform shape into broad-spiking (putative excitatory) and narrow-spiking (putative inhibitory) neurons (Figure 1B-C). Many observed differences between broad- and narrow-spiking neurons suggest they correspond well with excitatory and inhibitory neurons respectively (*22, 25, 26, 28-32*). We used current source density (CSD) analysis to identify the superficial (II/III), input (IV), and deep (V & VI) cortical layers (*22, 33*) (Figure S1D). This allowed us to analyze the different impacts of distractor stimuli based on their spatial location in six subpopulations of the laminar cortical circuit: broad- and narrow-spiking neurons in each of the three layers. Each of these subpopulations was visually responsive and well-tuned to the orientation of the target stimulus (Figure S2A-B).

To examine how contextual interactions among stimuli might impact information coding in V1 in an anisotropic manner, we first determined how well we could decode the identity (orientation and phase) of the target, alone or in each of the crowding conditions, from simultaneously recorded V1 population activity using linear discriminant analysis (Figure 2). All distractor stimuli impaired decoding performance, with radial-out crowding

showing the largest performance decrease (Figure 2).

We next sought to understand how distractor location differentially influences information processing among laminar cortical circuit components. For each subpopulation, we calculated the decoding performance for the target-only and crowding conditions (Figure 3). Most crowding stimuli impair decoding performance compared to the target-only in most subpopulations (Figure 3). In particular, the impairment of decoding performance is worse in the radial-out condition compared to the tangential and radial-in conditions among broad-spiking neurons in the input and superficial layers, the two subpopulations that are key nodes in the feed-forward cortical information flow pathway (Figure 3, middle right and top right). Radial-out crowding also impairs decoding performance more than radial-in crowding in narrow-spiking neurons across all layers, although radial-out crowding has a similar impact compared to tangential crowding in these subpopulations (Figure 3, left column). Consistent with previous reports (*17*), we also found that more effective crowding stimuli (radial-out crowding) most strongly reduced spike-count correlations, and this result was strongest in the feed-forward pathway (Figure S3).

Because distractor location has an anisotropic impact on the ability to decode target orientation from population activity, we investigated whether differential modulation in the tuning properties of V1 neurons could underlie these changes. We normalized the tuning curve for each single unit based on its preferred target orientation (see Methods) and plotted the average tuning curve of each subpopulation in response to the target only and in the crowding conditions (Figure 4). Distractors broaden the tuning curves of V1 neurons in each of the subpopulations (Figure 4). All subpopulations showed substantially

reduced responses when distractors were presented alone (Figure S4).

To quantify how distractor location modulates tuning, we first calculated the firing rates in response to preferred and orthogonal-to-preferred (orthogonal) target orientations. Crowding stimuli reduced firing rates in response to the preferred target orientation and increased the firing rates in response to the orthogonal target orientation (Figure 5). This correspondingly resulted in a similar decrease in orientation selectivity index (OSI) under different crowding conditions in each subpopulation (Figure S2C). Although OSI was similar across conditions and subpopulations, there were distinct differences in how flanker location modulated preferred and orthogonal firing rates. In both narrow and broad-spiking neurons in the input layer, radial-out flankers resulted in less suppression of firing to the preferred orientation, but more effectively facilitated firing in response to the orthogonal orientation (Figure 5, middle row). This pattern was also consistent among broad-spiking neurons in the superficial layers (Figure 5, top right).

To further characterize these results and obtain mechanistic insights into these changes in tuning properties, we quantified the extent to which distractor location induced untuned additive facilitation or tuned divisive suppression (*16, 17*) of V1 tuning curves. We modeled each neuron's tuning curve in the target-only condition and then calculated the extent to which the responses to stimuli under each of the crowding conditions were best explained by additive and multiplicative shifts to the target-only tuning curve (Figure 6 & S5). Input layer neurons under radial-out crowding showed greater additive facilitation compared to tangential or radial-in crowding. (Figure 6A, middle row). The radial-out condition also showed greater divisive suppression in broad-spiking neurons in both the input and superficial layers compared to the tangential and radial-in conditions (Figure

6B, top right and middle right). This effect was similar in narrow-spiking neurons in the input and superficial layers, with radial-out crowding showing more divisive suppression in both subpopulations compared to radial-in crowding and trending towards more suppression compared to tangential crowding (Figure 6B, top left and middle left). Taken together, these results show that radial-out crowding most effectively broadens tuning in the feed-forward pathway through untuned facilitation and tuned suppression.

DISCUSSION

Natural vision activates neurons not in isolation, but in the context of other stimuli. The extensive literature on contextual interactions in the visual cortex, particularly surround modulation (*34-42*), has significantly enriched our understanding of visual processing. However, a prevailing assumption in this literature has been the isotropic nature of the surrounding context. This is evident in the experimental design of contextual stimuli typically as annuli or as a circular constellation of flankers (*34, 35, 38, 43*). While several studies (*44-46*) did explore the spatial distribution of contextual interactions and their impact on neural responses, systematic geometrical arrangements of target and flanker objects with respect to the center of gaze were not investigated. Furthermore, it has been shown that intrinsic horizontal connections in V1 are anisotropic in a manner that could facilitate contour processing, enriching connections among neurons with orientation preferences and receptive fields that facilitate the detection of smooth contours (*47, 48*). But here too the spatial geometries alluded to above have not been investigated.

In contrast, perceptual asymmetries in vision have garnered considerable interest in the past several decades(*49-52*). In particular, the polar angle with respect to the center of gaze has been shown to be especially relevant to perceptual performance (see review

by (*53*). Perceptual asymmetries are especially striking in the phenomenology of visual crowding wherein distractors impair target identification over a distinctive elongated zone in visual space. Cortical magnification results in radial-out distractors being represented closer to the target in cortical space compared to radial-in distractors, potentially explaining some of the anisotropy (*9, 10, 54*). However, it has been shown that considerations of cortical magnification alone are not sufficient to explain the marked elongation of the crowding zones along the radial axis defined by the center of gaze and the target stimulus (*8*).

Macaques experience crowding similar to humans, impairing their ability to discriminate the orientation of target stimuli (*15, 16*), and are thus a good model for studying the neural mechanisms of crowding. Experiments in both macaques and humans suggest that crowding can influence neural activity as early as V1 (*16, 55*), including a radial-tangential anisotropy in BOLD responses in V1 (*56*). The present study extends these findings by revealing the impact of distractor location on stimulus representation in the laminar microcircuit of the primary visual cortex and the neural mechanisms underlying these impacted representations.

Notably, the effects of radial-out crowding were more pronounced compared to tangential and radial-in crowding across various measures. These effects included the ability to decode target identity from simultaneously recorded populations, as well as from putative excitatory neurons in the input and superficial layers. Anisotropies were also evident in the modulation of tuning curves in these layers, with radial-out crowding producing stronger broadening of tuning curves through untuned additive facilitation and tuned divisive suppression. Additionally, radial-out distractors exhibited the most

substantial decrease in spike-count correlations in the input and superficial layers. These anisotropies likely contribute to the impaired perception of target stimuli induced by radial-out distractors. Importantly, the decreased ability to decode stimulus orientation from neural activity at the subpopulation level was not solely attributable to changes in spike-count correlations, as correlations were removed across all conditions for those analyses.

Surprisingly, we discovered that contextual interactions exhibit anisotropy even at the earliest stages of processing in V1, specifically within the input layer. This finding suggests a potential sub-cortical origin of the observed anisotropies (*57-61*). Additionally, we observed the presence of anisotropy in the superficial layer of V1, implying that these computations are partially inherited from the input layer. Broad-spiking neurons share electrophysiological characteristics with excitatory pyramidal neurons (*26, 28, 32*). Given that broad-spiking putative excitatory neurons in the superficial layer are likely projection neurons to downstream ventral visual areas (*18, 62-64*), our findings suggest that the anisotropic signaling is propagated along the feedforward pathway and could form the basis of the perceptual anisotropies underlying visual crowding.

In contrast, we did not find the same anisotropy in the deep layers of V1. This intriguing result suggests the emergence of novel contextual computations in the deep layers, indicating that tuning and response properties are not merely inherited from input and superficial layer projections to the deep layers. This is in agreement with previous findings that neurons in the deep layers can have differences in orientation tuning compared to the superficial layers (*65, 66*) and that intrinsic (horizontal) connections in the deep layers are less extensive compared to the superficial layers (*67*). Moreover, as deep-layer broad-spiking putative excitatory neurons are the likely sources of feedback

projections to subcortical areas, these feedback signals are likely not anisotropic. Despite the likely feedforward propagation of anisotropic signals, the absence of anisotropy in the feedback pathway suggests a mechanism of active cancellation in this important modulatory pathway. Speculatively, this might play a role in maintaining a veridical representation of the visual scene in the earliest stages of extra-retinal visual processing.

The implications of our findings extend to the integration of information from outside the classical receptive field in the visual cortex. Orientation tuning properties and their modulation are determined by the balance of excitation and inhibition to cortical neurons (*68, 69*). Recurrent excitation (*70*) and lateral inhibition (*71*) are two key intra-cortical motifs that determine this balance. Cross-orientation suppression (*72*), a form of lateral inhibition likely plays an important role in shaping the cortical activity due to flanker-target interactions examined in this study. Such suppressive activity may operate in several ways according to orientation dependence and the strength of inhibitory connections and have been described in various models of cortical activity including those with attractor dynamics (*73, 74*), recurrence (*70*), balance (*75-77*), push-pull (*78, 79*) and normalization (*80-82*). Our results imply that distractor location differentially impacts the balance of excitation and inhibition in the laminar cortical circuit. Future empirical and computational modeling studies of surround modulation should take this anisotropic and layer-specific integration into account.

In conclusion, this study provides compelling evidence that contextual interactions in the visual cortex exhibit anisotropy at the earliest stages of cortical processing of visual signals. Distractors broaden V1 orientations tuning curves in a spatially anisotropic manner. Radial-out distractors most effectively broaden tuning in the feedforward

pathway through untuned facilitation and tuned suppression. These findings contribute to our understanding of the neural bases of visual crowding and offer mechanistic insights into the processing of contextual signals in the visual cortex.

AUTHOR CONTRIBUTIONS

MPM and ASN conceptualized the project. MPM collected the data, with assistance from SD and NVH. MPM analyzed the data. MPM and ASN wrote the paper.

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FIGURE LEGENDS

Figure 1. Anisotropic contextual interaction task and single-unit recordings.
(**A**) Anisotropic contextual interaction task schematic. Stimuli were presented alone at the receptive field center (target only) or with a distractor at one of the four crowding locations. The radial axis connects the target to the center of gaze, and the tangential axis is orthogonal to it, also passing through the target. The top schematic shows stimuli at all possible locations, while the bottom section shows the possible spatial configurations for the presentation of an individual stimulus array. (**B**) Mean waveforms for all recorded single units (blue=narrow-spiking, orange=broad-spiking). (**C**) Distribution of waveform durations (trough-to-peak time) for all recorded single units across the two monkeys. Neurons with waveform durations less than 350µs were classified as narrow-spiking (blue), and neurons with waveform durations greater than 350µs were classified as broad-spiking (orange).

Figure 2. Distractor stimuli impair decoding performance in simultaneously recorded populations in an anisotropic manner.
Example decoding performance from 4 simultaneously recorded populations (two in each monkey) in the target-only condition and each of the three crowding conditions. Points in the upper section of each plot show the decoding performance for each of the 20 different cross-validations. The lower section for each session shows the bootstrapped estimation of the difference between decoding performance in each crowding condition compared to the target-only condition. Half-violin plots show the bootstrapped distribution of the difference, and black dots and bars represent the mean and 95% confidence intervals of the difference in decoding performance.

Figure 3. Radial-out crowding most strongly impairs decoding in the feed-forward pathway.
Decoding performance from each subpopulation in the target-only condition and each of the three crowding conditions. Points in the upper section of each plot show the decoding performance for each of the 20 different cross-validations. The lower section for each session shows the bootstrapped estimation of the difference between decoding performance in each crowding condition compared to the target-only condition. Half-violin plots show the bootstrapped distribution of the difference, and black dots and bars represent the mean and 95% confidence intervals of the difference in decoding performance.

Figure 4. Crowding stimuli modulate the tuning curves of V1 neurons.
Normalized tuning curves for each subpopulation in the target-only and crowding conditions. Tuning curves are aligned with the preferred orientation at 0 degrees and duplicated to fill the circle. Tuning curves were normalized by the maximum firing rate in the target-only condition. Lines and shading represent mean +/- s.e.m. (black=target only, pink=tangential crowding, green=radial-in crowding, purple=radial-out crowding).

Figure 5. Crowding broadens tuning curves
Difference in firing rate in response to preferred (dark brown) and orthogonal (light tan) stimuli under each crowding condition in the six subpopulations. Colored half-violin plots show the bootstrapped estimation of the paired mean difference in firing rate for a given subpopulation, crowding condition, and stimulus orientation. Black dots and lines represent the mean and 95% confidence interval of the estimated difference.

Figure 6. Radial-out crowding causes stronger additive facilitation and divisive suppression of tuning curves
(**A**) Difference in the modeled (see Methods) untuned additive facilitation caused by each of the crowding conditions. Gray half-violin plots show the bootstrapped estimation of the paired mean difference in the modeled additive component for a given subpopulation and pair of crowding conditions. Black dots and lines represent the mean and 95% confidence interval of the estimated difference. (**B**) Same as (**A**) but for the multiplicative component, reflecting tuned divisive suppression.

Figure S1. Laminar recordings in V1.
(**A**) Section perspective schematic of the artificial dura recording chamber and laminar probe. (**B**) photo of the artificial dura chamber in one monkey. (**C**) Example receptive field contours vertically stacked for each recording site along the depth of each of the two shanks on the laminar probe. (**D**) Example current source density (CSD) map showing the early current sink (red) indicative of the input layer. (**E**) Data recorded from a single trial, including spikes (black vertical ticks) and local field potentials (black traces) collected from each channel on the two shanks. Data is arranged vertically based on the spatial location of the recording channel. Cortical layers are indicated on the left (green=superficial, gray=input, pink=deep). Vertical bars indicate the time of stimulus onsets.

Figure S2. Peri-stimulus time histograms, tuning curves of single units, and orientation selectivity index under crowding.
(**A**) Peri-stimulus time histogram (PSTH) of subpopulations in each condition following the onset of the preferred stimulus. The preferred orientation was calculated separately for each single unit. Spikes were counted in 30ms bins shifted by 5ms. Error bars show mean+/- s.e.m. (**B**) Example single unit tuning curves in the target-only condition. (**C**) Difference in orientation selectivity index (OSI) in each of the crowding conditions compared to the target-only condition. Colored half-violin plots show the bootstrapped estimation of the mean difference in OSI for a given subpopulation and crowding condition. Black dots and lines represent the mean and 95% confidence interval of the estimated difference.

Figure S3. Radial-out crowding decreases spike-count correlations in the feed-forward pathway
(**A**) Spike-count correlations from pairs of simultaneously recorded neurons in each subpopulation in the target-only condition and each of the three crowding conditions. In the top panels, error bars represent mean +/- 95% confidence intervals of the spike-count correlation in each condition. In the bottom panels, black dots and lines represent the mean and 95% confidence interval of the estimated difference from the target-only condition, and colored half-violin plots show the bootstrapped estimation of the mean difference in spike-count correlation for a given subpopulation and crowding condition. (**B**) Spike-count correlations for each pair of single units in each subpopulation. Each point represents the spike-count correlations of one pair of simultaneously recorded neurons in the same layer and cell class and each condition.

Figure S4. V1 neurons are not responsive to the distractor alone.
Normalized tuning curves for each subpopulation in the target-only and distractor-only conditions. Tuning curves are aligned with the preferred orientation at 0 degrees and duplicated to fill the circle. Tuning curves were normalized by the maximum firing rate in the target-only condition. The distractor-only condition is plotted relative to the orientation

of the distractor and includes data from all four distractor positions. Lines and shading represent mean +/- s.e.m. (black=target only, gold=distractor only).

Figure S5. Single-unit tuning model parameters in different crowding conditions (**A**) Related to Figure 6A. Value of the fitted additive parameter for each neuron in each crowding condition. Each line represents the additive parameter for a single unit in across the two crowding conditions indicated at the bottom. (**B**) Related to Figure 6B. Same as (**A**) but for the multiplicative component.

MATERIALS & METHODS

Data Collection

Surgical procedures

Surgical procedures were similar to those described previously (*22, 23, 83*). We placed low-profile titanium recording chambers in two rhesus macaques so that the chambers allowed access to area V1 (right hemisphere in monkey D, left hemisphere in monkey M). Chambers were targeted based on sulcus reconstructions created using preoperative structural MRI. After chamber implantation, we removed the native dura mater and replaced it with a transparent silicone artificial dura (AD). The AD allowed for the visualization of cortical sites in V1 for probe targeting. All procedures were approved by the Yale University Institutional Animal Care and Use Committee and conformed to NIH guidelines.

Electrophysiology

Prior to a series of recordings, we electroplated (nanoZ, White Matter LLC) 64-channel electrode arrays (“laminar probes,” NeuroNexus Technologies, Inc., 2 shanks, 32 channels/shank, 70µm spacing between sites, 200µm between shanks) with PEDOT (poly(3,4-ethylene dioxythiophene)). At the beginning of each recording session, we inserted a laminar probe in V1. Laminar probes were attached to a titanium mounting

stage that was screwed into the chamber. We positioned the laminar probes using an electronic micromanipulator (Narishige Inc.) and ensured that the probes were orthogonal to the surface of the cortex by visual inspection through a surgical microscope (Leica Microsystems). To position the probe within the brain, we first penetrated the AD, arachnoid, and pia by moving the probe downward at a high speed (>100µm/s). After the tip of the probe entered the cortex, we inserted the remainder of the probe at a slow speed (2µm/s). Once the entire probe was in the brain, we slowly (2µm/s) relieved the pressure on the brain by retracting the probe upward, relieving pressure on the brain but not moving the probe relative to the cortex.

Electrical signals from the laminar probe were collected at 30kHz and digitized on a 64-channel digital headstage and sent to the recording system (RHD Recording System, Intan Technologies). Action potential waveforms were extracted offline using Kilosort2 (*84, 85*) and manually sorted into single and multi-unit clusters (Phy; *84, 85*). Multi-unit clusters were excluded from further analysis. Single-unit clusters were classified based on their trough-to-peak waveform duration into broad- and narrow-spiking units (*22, 24*). Neurons with waveform durations less than 350µs were classified as narrow-spiking while those with waveform durations longer than 350µs were classified as broad-spiking. Clusters with peaks preceding the trough were identified as axonal spikes and excluded. Recordings were collected over the course of 22 sessions (9 in monkey D, 13 in monkey M) with hundreds of single units recorded in each subject (384 in monkey D, 521 in monkey M).

Behavioral Control and Eye Tracking

We controlled behavioral experiments using NIMH MonkeyLogic (*86*). Eye position and

pupil diameter were sampled at 120Hz (ETL-200, ISCAN Inc.) and sent to the behavioral control system. Stimuli were presented on a monitor positioned 57cm from the monkey with a 60Hz refresh rate. Trials were aborted if the eye position deviated more than 1.2-1.5 degrees of visual angle (dva; 1.2 for monkey D, 1.5 for monkey M) from the central fixation point.

Receptive Field Mapping

We mapped RFs of the column by presenting Gabor patch stimuli (2-4 cycles/degree, 0.25-1 degree Gaussian half-width, 100% luminance contrast) on a square grid spanning the lower visual quadrant of interest (left in monkey D, right in monkey M) while the monkey maintained fixation on the center of the screen. Grid spacing parameters were optimized each session and ranged from 0.25-1 dva. A stimulus was presented at a random location and orientation on the grid during each frame. We calculated the LFP power for each recording channel 40-200ms after stimulus presentation in each location. The LFP power at each location was smoothed using a Gaussian kernel (sigma = 0.75 dva), and the peak location averaged across all recording sites was defined as the RF center. Spatial RF maps for each channel were plotted as stacked contours for each shank for visualization.

Current Source Density Mapping

We used CSD mapping (*33*) to identify laminar boundaries in our recordings. While monkeys maintained fixation on the screen, 100% luminance contrast white annular stimuli were flashed for 32ms, positioned at the center of the RF. The CSD was calculated as the second spatial derivative of the LFP following stimulus onset. CSD traces were spatially smoothed using a Gaussian kernel (sigma = 140µm). The input layer was

identified by the boundaries of the early current sink characterizing feed-forward input into layer IV. Channels above and below this sink were classified as superficial and deep respectively.

Anisotropic Crowding Task

While monkeys maintained fixation, stimulus arrays were flashed on the screen for 100ms and off the screen for 200ms. The arrays consisted of a target stimulus in the RF center either in isolation (target only) or together with a distractor stimulus (crowding). There were four different conditions (target only, tangential crowding, radial-in crowding, and radial-out crowding) of stimulus arrays presented during a trial. This was repeated 4-6 times during each trial depending on the monkey's ability to hold fixation. The stimulus conditions were randomly interleaved from flash to flash. The center of the target stimulus was aligned with the center of the average of the RFs of each recording site. The four distractor locations were positioned on the radial or tangential axes. The radial axis was defined as the axis connecting the target (and RF) center and the fixation point at the center of the monitor. The tangential axis was defined as the line orthogonal to the radial axis and passing through the target center. The tangential crowding condition occurred when the target was presented along with a distractor stimulus on the tangential axis, either in the clockwise or counterclockwise direction. The radial-in crowding condition occurred when the target was presented along with a distractor stimulus on the radial axis and between the target center and the fixation point. The radial-out condition was similar to the radial-in condition, except the distractor stimulus was placed on the radial axis further from the fixation point than the target. Target-distractor spacing was identical across stimulus conditions.

The target-only condition was presented on 10% of flashes. On 80% of flashes, crowding stimuli were presented. In the crowding condition, the distractor stimulus was positioned at a tangential, radial-in, or radial-out location with equal probability. If the distractor was presented tangential to the target, it was positioned clockwise or counterclockwise to the target with equal probability. In the remaining 10% of trials, a stimulus was presented exclusively at one of the four distractor locations. Target stimuli were sine Gabor patches (25% luminance contrast, 3.5 cycles/degree, 0.5-1.0 degree Gaussian half-width) presented at 6 evenly spaced orientations and 2 opposing phases. Flanking stimuli were presented at 100% luminance contrast but were otherwise identical to the target stimuli. There was a 0.1-0.2 degree gap between the edges of the target and flanking stimuli (edge defined as 2 standard deviations from the center of the Gaussian). In the crowding condition, distractors were presented at the same orientation as the target or orthogonal to the target with equal probability. In this study, we focused exclusively on the condition in which the distractor was orthogonal to the target. When distractors were presented alone, they were shown with the same orientation distribution as the targets.

Data Analysis

Wherever possible, we analyzed our data using the estimation statistics framework (*87, 88*) and show bootstrapped estimations of differences between conditions rather than relying on null-hypothesis testing. The estimation statistics framework provides a principled way to measure effect sizes coupled with estimates of uncertainty, yielding interval estimates of uncertainty.

Tuning Curve Visualization

To visualize the modulation of tuning curves of each subpopulation by distractor stimuli, we calculated the number of spikes for each neuron 0-300ms following stimulus onset in each orientation and condition, collapsing across phases, and subtracted the baseline firing rate (0-100ms before stimulus onset). For each neuron, we identified the orientation with the highest firing rate in the target-only condition as the preferred orientation and shifted the tuning curves to set this orientation to 0 degrees in each condition. We then normalized the turning curves by dividing each neuron's response to each orientation and condition by the firing rate for the preferred target-only orientation. For visualization, the tuning curve was duplicated and rotated 180 degrees to completely fit around a circle. We excluded neurons that did not respond in the target-only condition. To visualize the tuning curves of individual single units, we followed the same procedure but did not average across phases, instead plotting the response to each phase as the opposite orientation. Additionally, single-unit tuning curves were not rotated based on the preferred orientation.

Preferred and Orthogonal Firing Rate and OSI

OSI was calculated using the following equation:

$$OSI = \frac{FR_{pref} - FR_{orth}}{FR_{pref} + FR_{orth}}$$

Where FR_{pref} is the firing rate in response to the preferred orientation and FR_{orth} is the firing rate in response to the stimulus orthogonal to the preferred orientation. Firing rates were calculated 0-300ms following stimulus onset. The preferred orientation was identified as the orientation with the highest firing rate. FR_{pref}, FR_{orth} , and OSI were compared between the target-only condition and the crowding conditions by calculating the bootstrapped estimation of the mean difference.

Modeling Tuning Curve Modulation

We investigated the components of single-unit tuning curve modulation using a previously published approach to identify additive and multiplicative changes to tuning curves (*17*). Briefly, we fit a Poisson model based on spike counts from 0-300ms after stimulus onset in the target-only condition for each orientation. We then calculated the untuned additive and tuned multiplicative modulation of the fitted target-only tuning curve that would best account for the observed spike counts independently for each crowding condition (*17*). We then compared the additive and multiplicative parameters for each neuron across conditions by calculating a bootstrapped estimation of the paired mean difference of the components.

Decoding Analysis

We trained a decoder using linear discriminant analysis (LDA) to determine the identity (orientation and phase) of a target stimulus from simultaneously recorded single-unit activity. Spike counts were calculated from 0-300ms following stimulus onset. The decoder performance was determined using 20-fold cross-validation. The decoder was trained on stimuli presented in the target-only condition and tested on neural responses in each of the crowding conditions. This procedure was repeated for each recording session. Performance in the tangential crowding condition was calculated separately for the two tangential locations and averaged.

To calculate decoding performance at the subpopulation level, we first generated a database of pseudo-population activity for each neuron in every combination of conditions and target orientations. Spike counts were calculated from 0-300ms following stimulus onset. To train the decoder for each subpopulation, we generated pseudo-

population activity by randomly drawing samples from this database, independently for each neuron. We trained separate decoders for each subpopulation, training and testing on responses from every neuron in each cell class and layer across all recording sessions. Decoders were trained by sampling from data in the target-only condition. 20% of each neuron's responses to each orientation were held out (the subset was independent for each neuron) for cross-validation. This procedure was repeated 20 times with a different random subset of responses used for cross-validation in the target-only condition. The decoding performance on this 20% of left-out data was considered the decoding performance in the target-only condition. We then tested each decoder on pseudo-population activity generated from responses in the crowding conditions.

Peri-stimulus time histograms (PSTH)

PSTHs were generated based on spike counts in 30ms bins shifted by 5ms. PSTHs are shown only for the preferred orientation as defined previously. The PSTH for each neuron was calculated separately for each condition, and the average PSTH for each subpopulation was plotted in Figure S2A. All times are relative to stimulus onset.

Spike-count correlations

Spike-count correlations were calculated for each pair of simultaneously recorded neurons in the same layer and broad- or narrow-spiking cell class. Spike counts were extracted from 100-300ms after stimulus onset and normalized by Z-score for each stimulus orientation and condition. For each condition, the spike-count correlation was calculated separately for each orientation from the normalized spike counts and was then averaged across orientations. Thus, each pair of neurons had a single spike-count correlation number for each stimulus condition.

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Figure 1

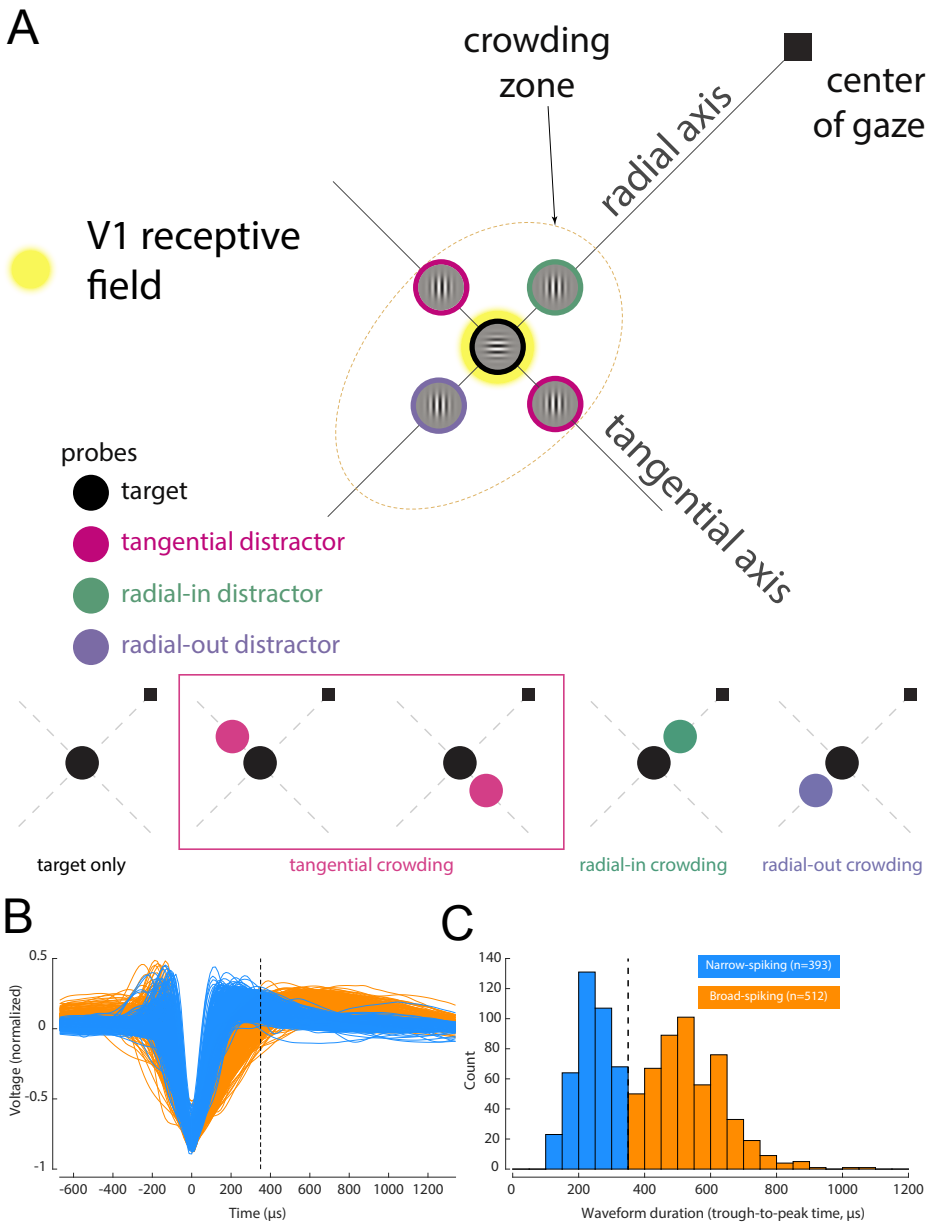

Figure 1. Anisotropic contextual interaction task and single-unit recordings.
(**A**) Anisotropic contextual interaction task schematic. Stimuli were presented alone at the receptive field center (target only) or with a distractor at one of the four crowding locations. The radial axis connects the target to the center of gaze, and the tangential axis is orthogonal to it, also passing through the target. The top schematic shows stimuli at all possible locations, while the bottom section shows the possible spatial configurations for the presentation of an individual stimulus array. (**B**) Mean waveforms for all recorded single-units (blue=narrow-spiking, orange=broad-spiking). (**C**) Distribution of waveform durations (trough-to-peak time) for all recorded single-units across the two monkeys. Neurons with waveform durations less than 350µs were classified as narrow-spiking (blue), and neurons with waveform durations greater than 350µs were classified as broad-spiking (orange).

Figure 2

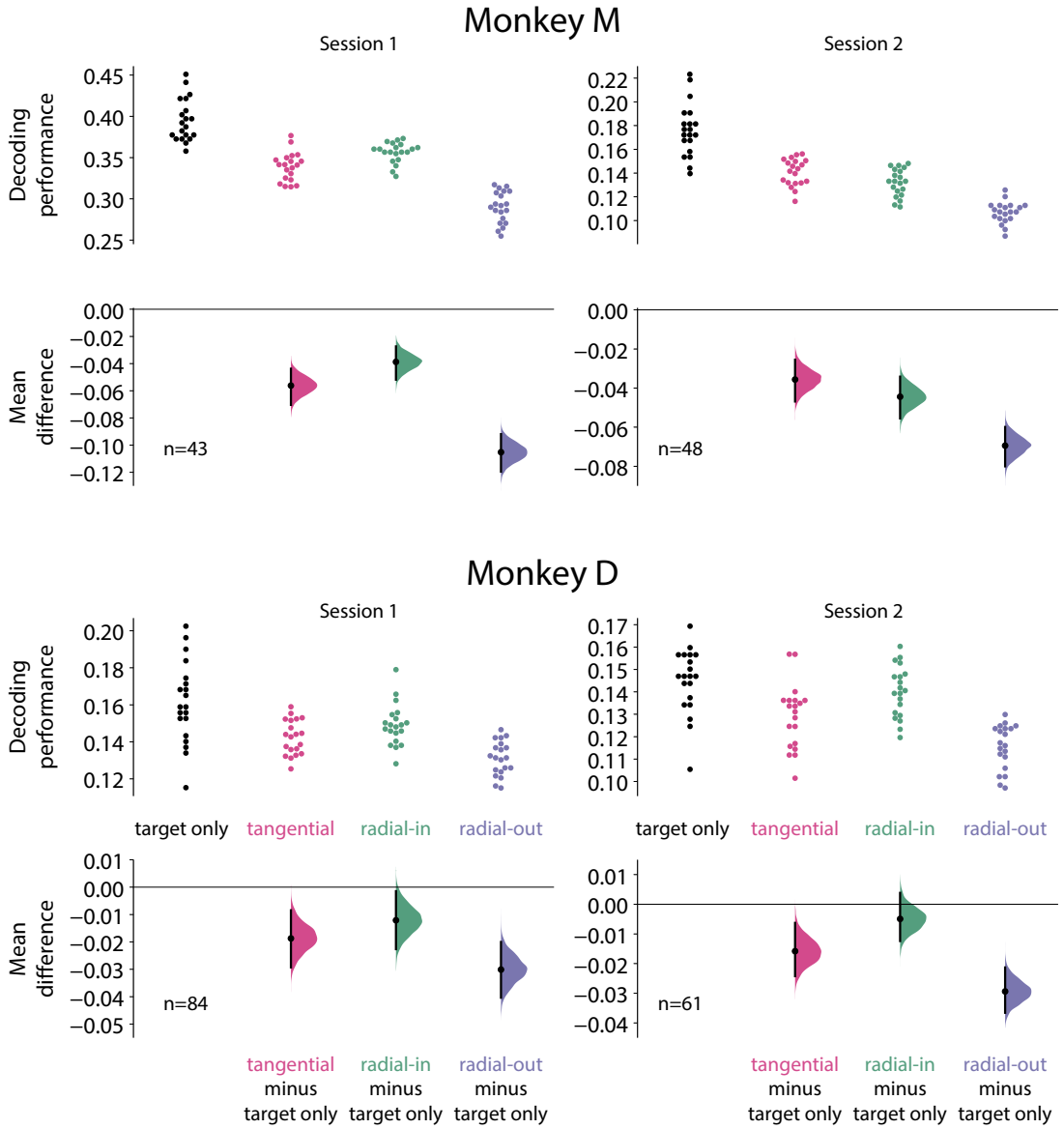

Figure 2. Distractor stimuli impair decoding performance in simultaneously recorded populations in an anisotropic manner.

Example decoding performance from 4 simultaneously recorded populations (two in each monkey) in the target-only condition and each of the three crowding conditions. Points in the upper section of each plot show the decoding performance for each of the 20 different cross-validations. The lower section for each session shows the bootstrapped estimation of the difference between decoding performance in each crowding condition compared to the target only condition. Half-violin plots show bootstrapped distribution of the difference, and black dots and bars represent the mean and 95% confidence intervals of the difference in decoding performance.

Figure 3

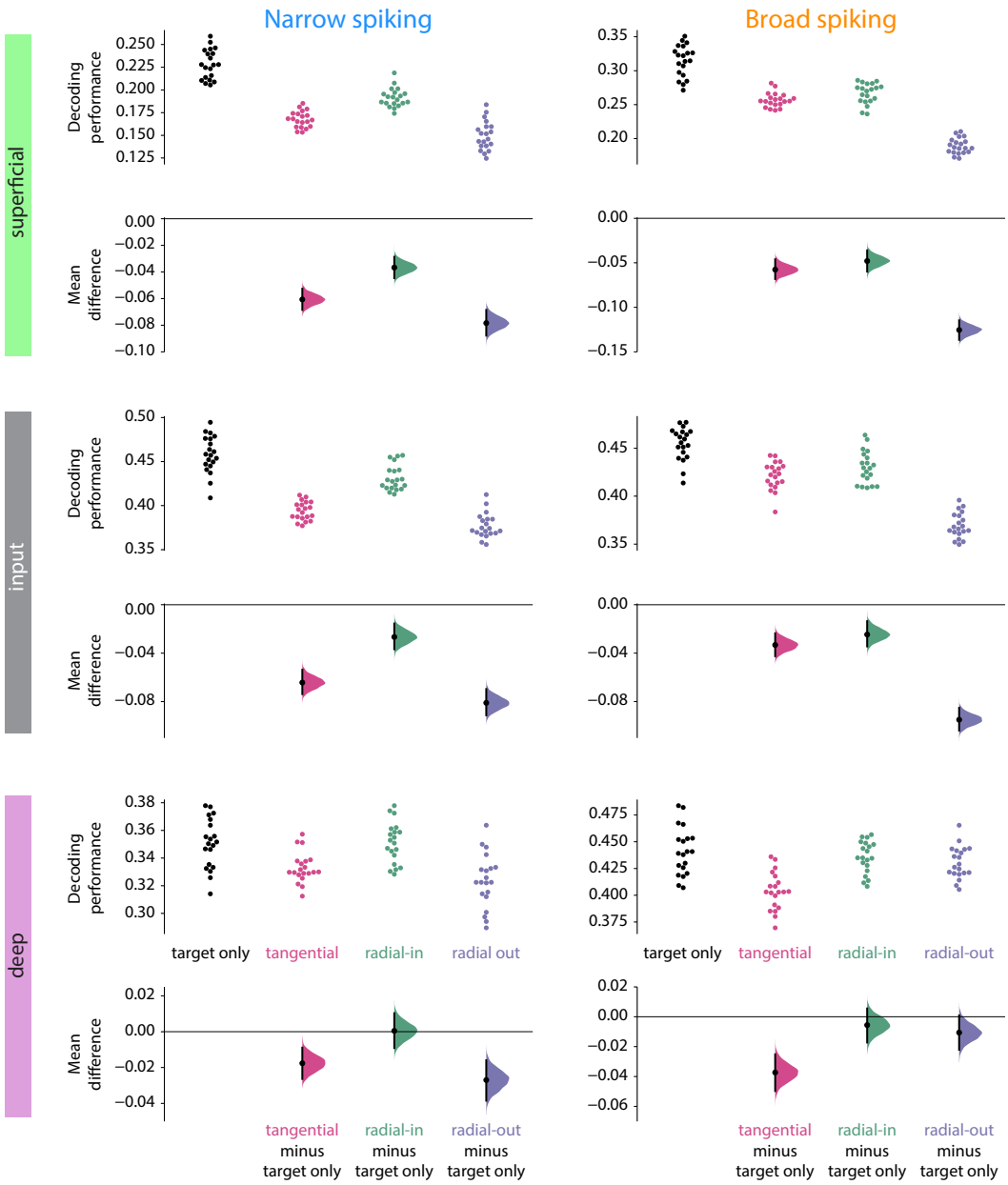

Figure 3. Radial-out crowding most strongly impairs decoding in the feed-forward pathway.
Decoding performance from each subpopulation in the target-only condition and each of the three crowding conditions. Points in the upper section of each plot show the decoding performance for each of the 20 different cross-validations. The lower section for each session shows the bootstrapped estimation of the difference between decoding performance in each crowding condition compared to the target only condition. Half-violin plots show bootstrapped distribution of the difference, and black dots and bars represent the mean and 95% confidence intervals of the difference in decoding performance.

Figure 4

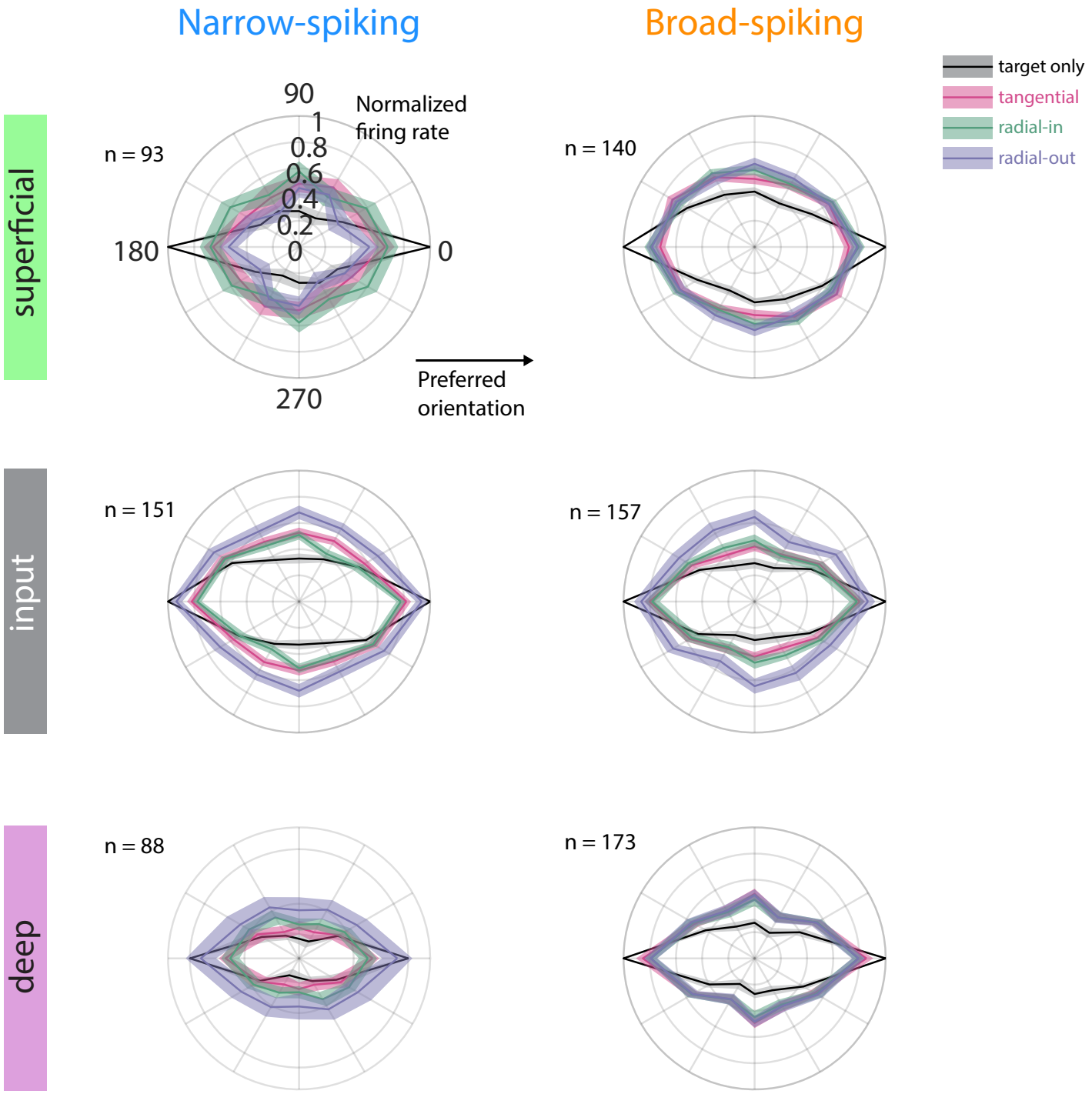

Figure 4. Crowding stimuli modulate the tuning curves of V1 neurons.
Normalized tuning curves for each subpopulation in the target-only and crowding conditions. Tuning curves are aligned with the preferred orientation at 0 degrees and duplicated to fill the circle. Tuning curves were normalized by the maximum firing rate in the target-only condition. Lines and shading represent mean +/- s.e.m. (black=target only, pink=tangential crowding, green=radial-in crowding, purple=radial-out crowding).

Figure 5

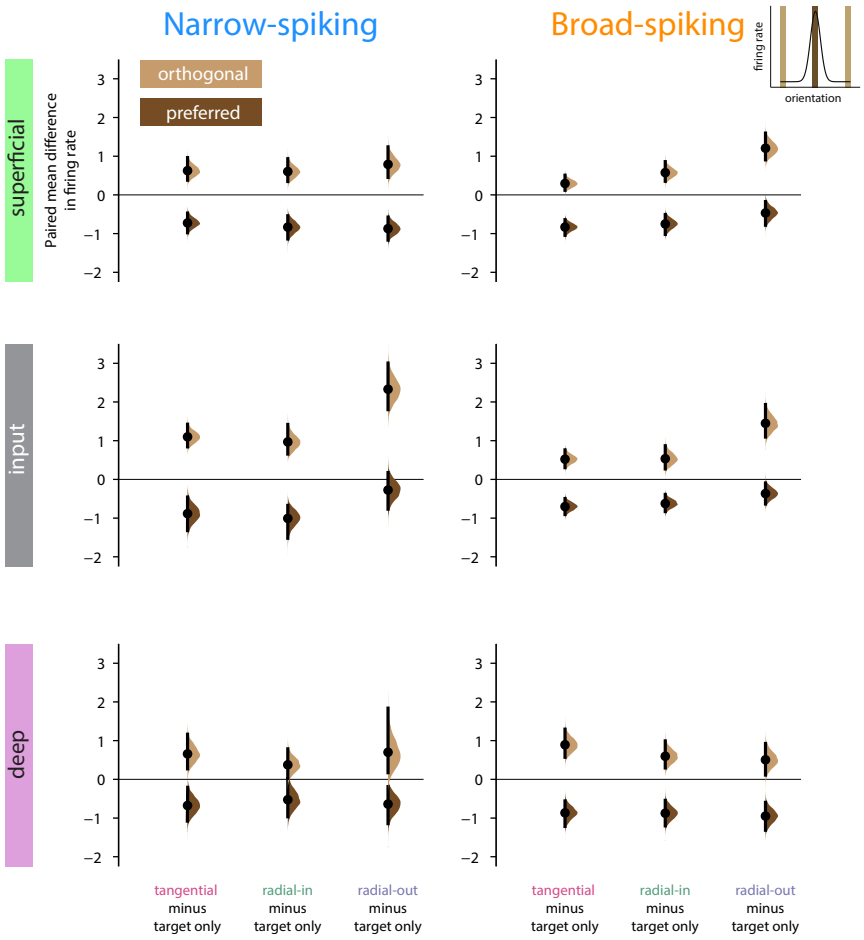

Figure 5. Crowding broadens tuning curves
Difference in firing rate in response to preferred (dark brown) and orthogonal (light tan) stimuli under each crowding condition in the six subpopulations. Colored half-violin plots show the bootstrapped estimation of the paired mean difference in firing rate for a given subpopulation, crowding condition, and stimulus orientation. Black dots and lines represent the mean and 95% confidence interval of the estimated difference.

Figure 6

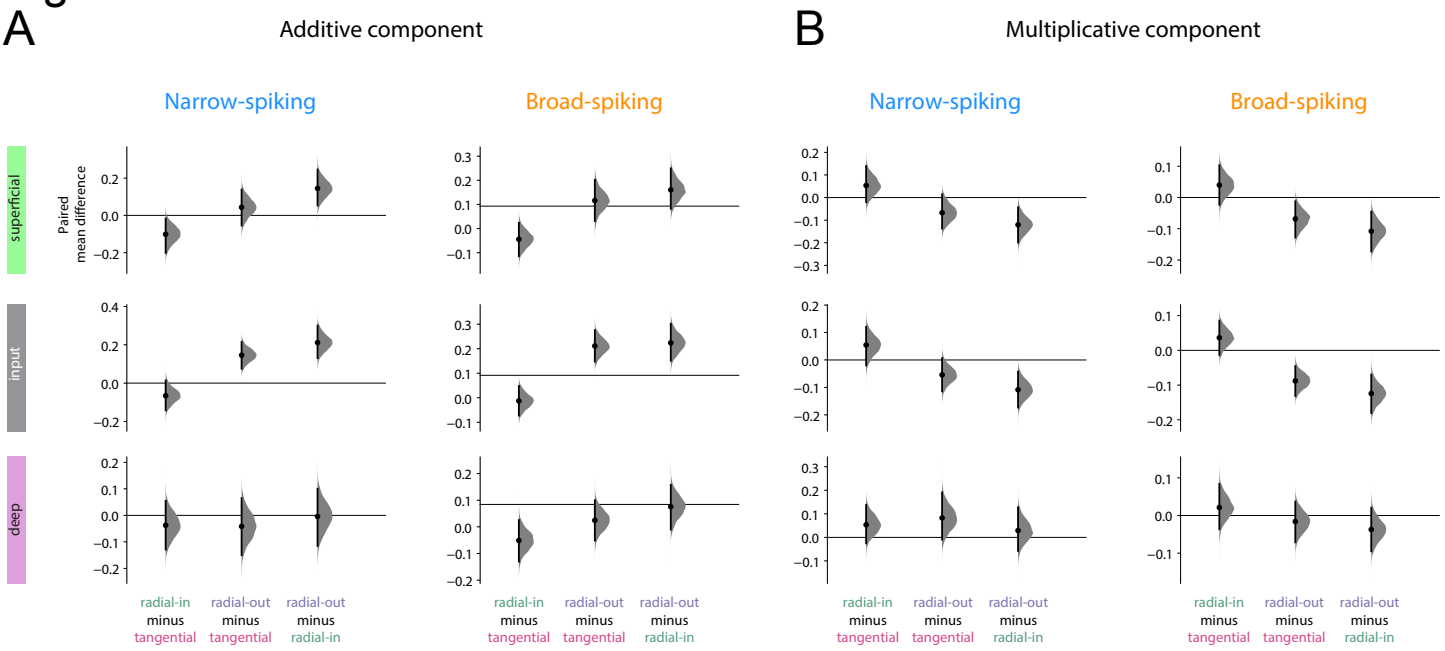

Figure 6. Radial-out crowding causes stronger additive facilitation and divisive suppression of tuning curves
(**A**) Difference in the modeled (see Methods) untuned additive facilitation caused by each of the crowding conditions. Gray half-violin plots show the bootstrapped estimation of the paired mean difference in the modeled additive component for a given subpopulation and pair of crowding conditions. Black dots and lines represent the mean and 95% confidence interval of the estimated difference. (**B**) Same as (**A**) but for the multiplicative component, reflecting tuned divisive suppression.

Figure S1

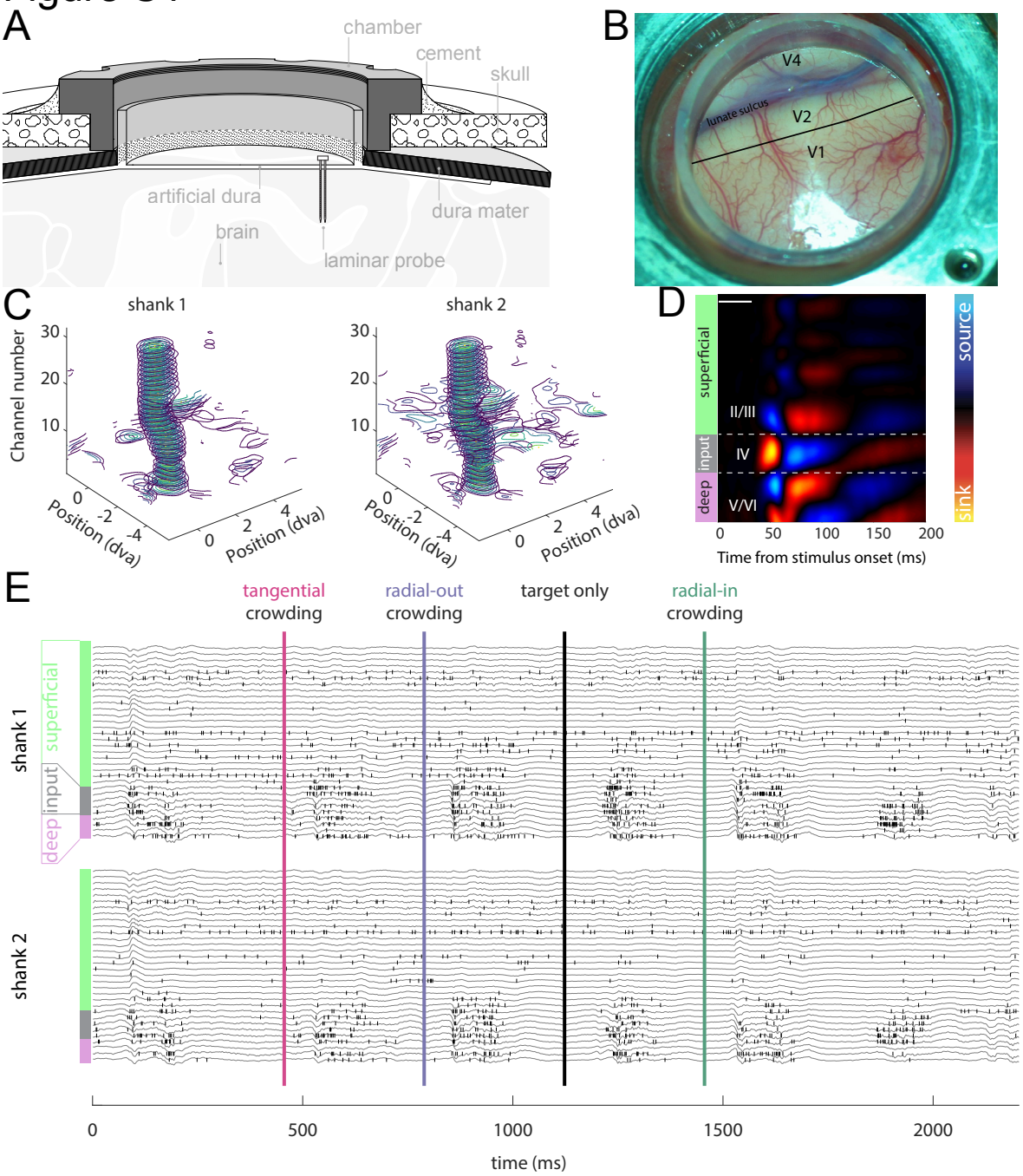

Figure S1. Laminar recordings in V1.
(**A**) Section perspective schematic of the artificial dura recording chamber and laminar probe. (**B**) photo of the artificial dura chamber in one monkey. (**C**) Example receptive field contours vertically stacked for each recording site along the depth of each of the two shanks on the laminar probe. (**D**) Example current source density (CSD) map showing the early current sink (red) indicative of the input layer. (**E**) Data recorded from a single trial, including spikes (black vertical ticks) and local field potentials (black traces) collected from each channel on the two shanks. Data is arranged vertically based on the spatial location of the recording channel. Cortical layers are indicated on the left (green=superficial, gray=input, pink=deep). Vertical bars indicate the time of stimulus onsets.

Figure S2

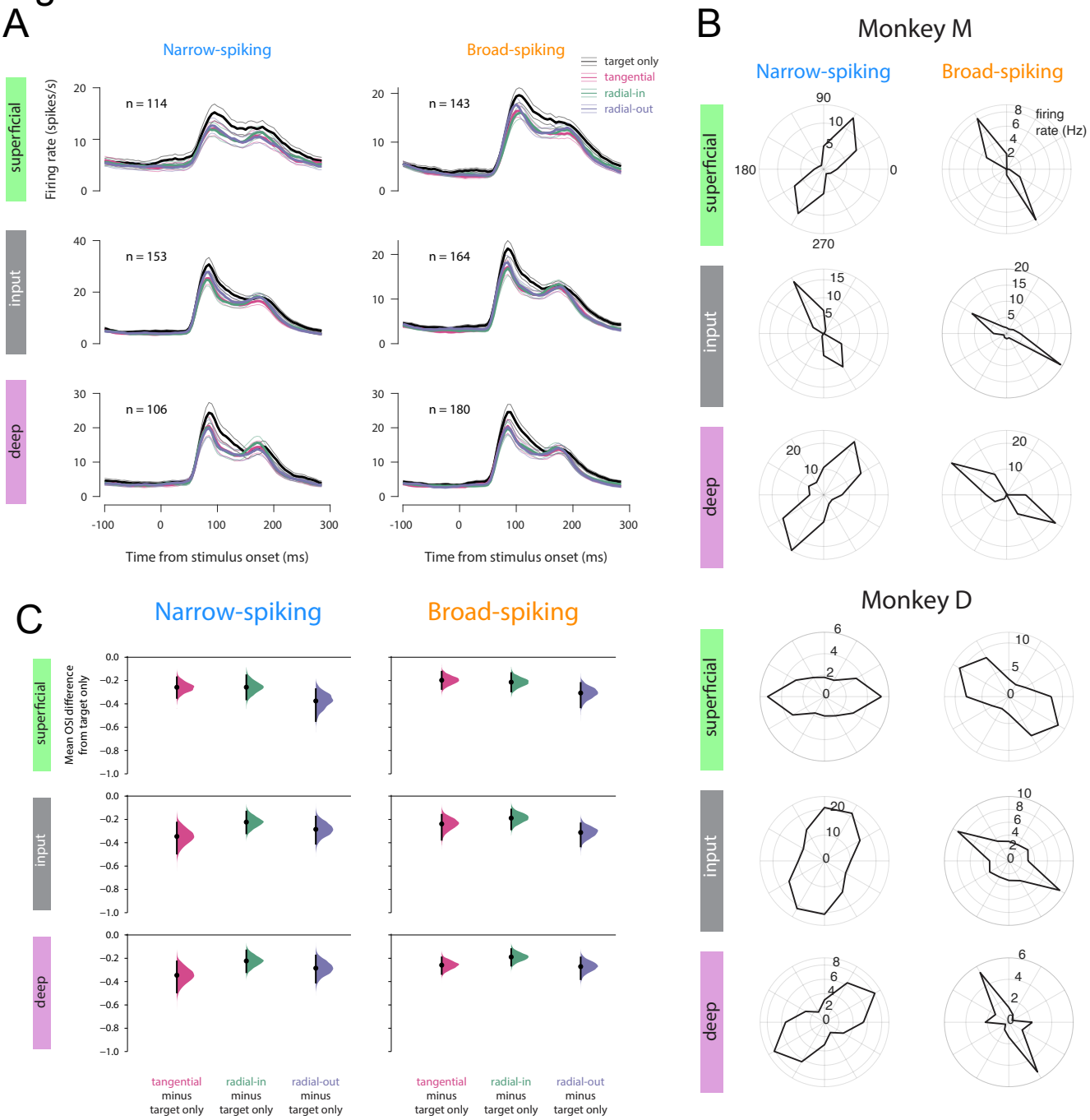

Figure S2. Peri-stimulus time histograms, tuning curves of single units, and orientation selectivity index under crowding.
(**A**) Peri-stimulus time histogram (PSTH) of subpopulations in each condition following the onset of the preferred stimulus. The preferred orientation was calculated separately for each single unit. Spikes were counted in 30ms bins shifted by 5ms. Error bars show mean+/- s.e.m. (**B**) Example single unit tuning curves in the target-only condition. (**C**) Difference in orientation selectivity index (OSI) in each of the crowding conditions compared to the target-only condition. Colored half-violin plots show the bootstrapped estimation of the mean difference in OSI for a given subpopulation and crowding condition. Black dots and lines represent the mean and 95% confidence interval of the estimated difference.

Figure S3

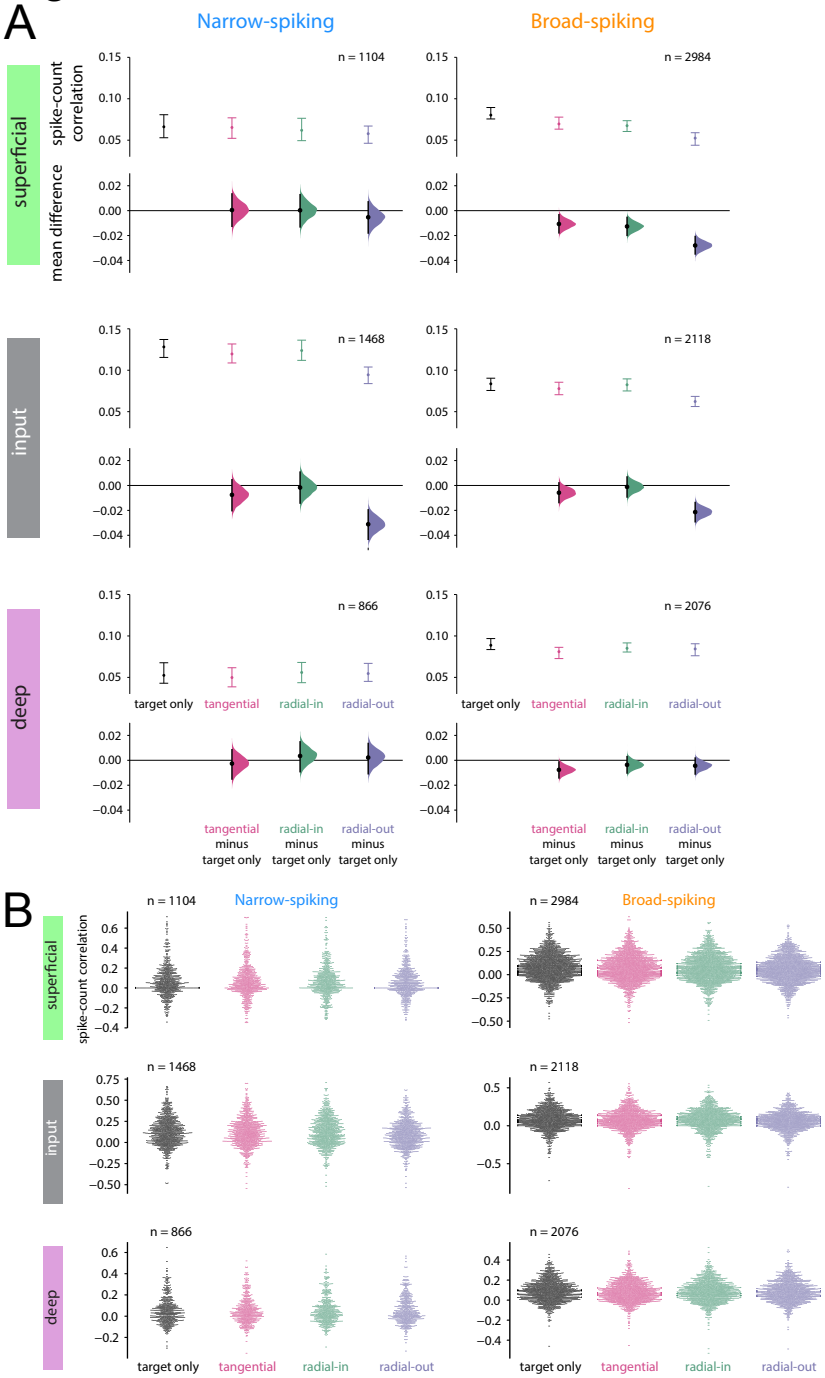

Figure S3. Radial-out crowding decreases spike-count correlations in the feed-forward pathway
(**A**) Spike-count correlations from pairs of simultaneously recorded neurons in each subpopulation in the target-only condition and each of the three crowding conditions. In the top panels, error bars represent mean +/- 95% confidence intervals of the spike-count correlation in each condition. In the bottom panels, black dots and lines represent the mean and 95% confidence interval of the estimated difference from the target only condition, and colored half-violin plots show the bootstrapped estimation of the mean difference in spike-count correlation for a given subpopulation and crowding condition. (**B**) Spike-count correlations for each pair of single-units in each subpopulation. Each point represents the spike-count correlations of one pair of simultaneously recorded neurons in the same layer and cell class and in each condition.

Figure S4

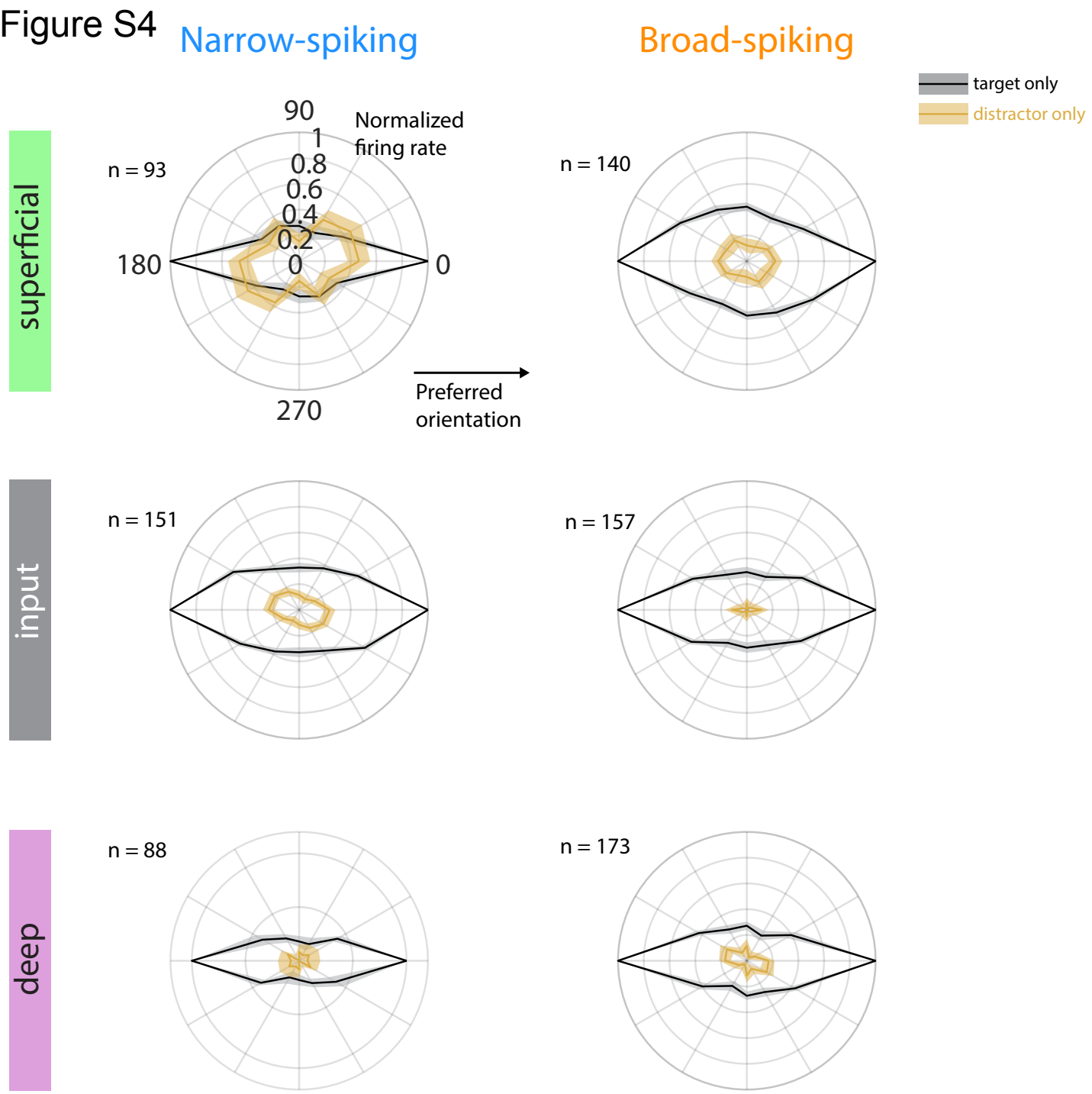

Figure S4. V1 neurons are not responsive to the distractor alone.
Normalized tuning curves for each subpopulation in the target-only and distractor-only conditions. Tuning curves are aligned with the preferred orientation at 0 degrees and duplicated to fill the circle. Tuning curves were normalized by the maximum firing rate in the target-only condition. The distractor-only condition is plotted relative to the orientation of the distractor, and includes data from all four distractor positions. Lines and shading represent mean +/- s.e.m. (black=target only, gold=distractor only).

Figure S5

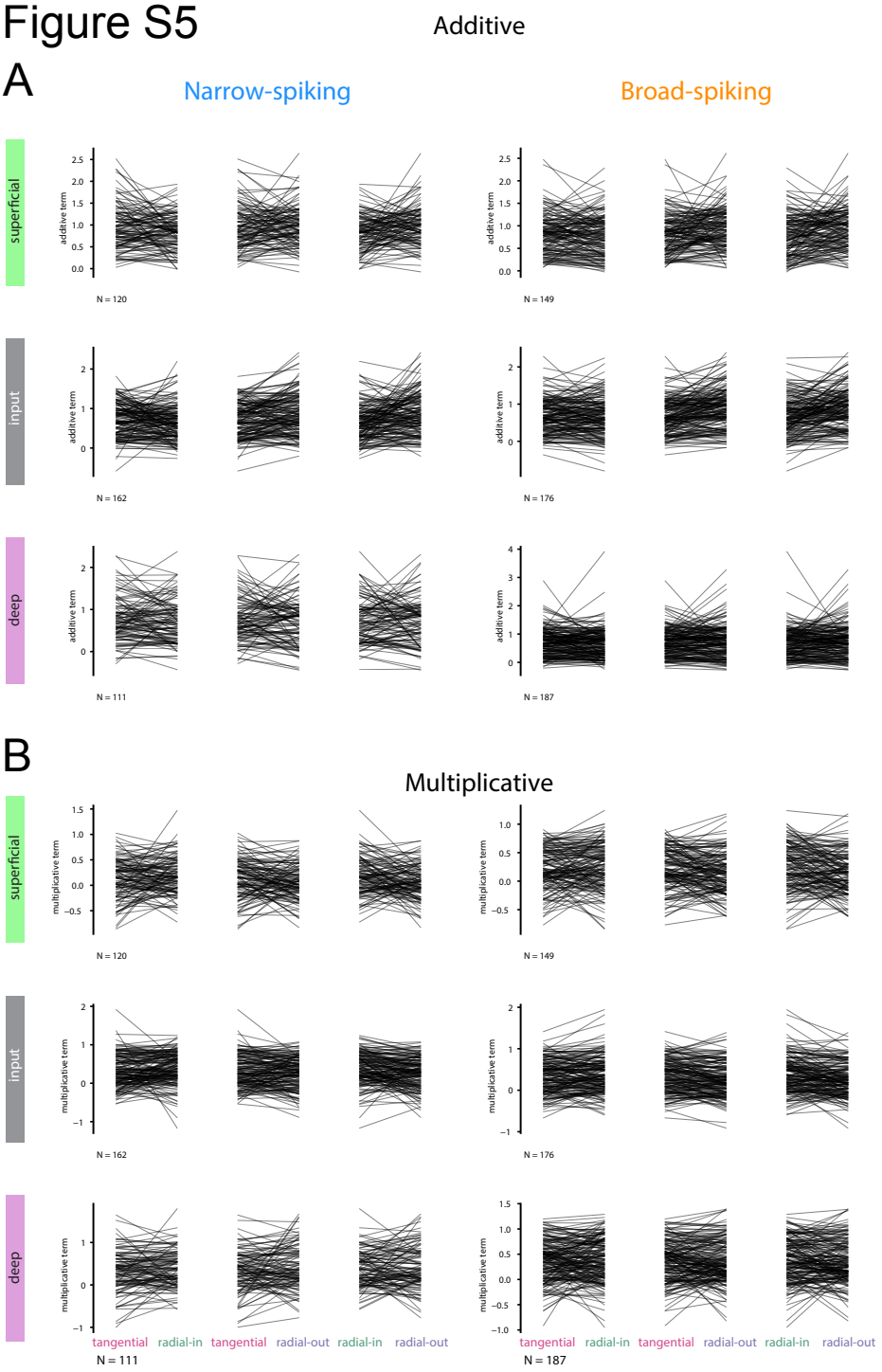

Figure S5. Single-unit tuning model parameters in different crowding conditions
(**A**) Related to Figure 6A. Value of the model fit additive parameter for each neuron in each crowding condition. Each line represents the additive parameter for a single unit in across the two crowding conditions indicated at the bottom. (**B**) Related to Figure 6B. Same as (**A**) but for the multiplicative component.