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Receptive Field Organization in Macaque vIPFC Neurons

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Abstract

While receptive fields (RFs) in ventral and dorsal visual areas are well characterized, their organization in the ventrolateral prefrontal cortex (vIPFC), a region involved in visual processing and cognition, remains largely unexplored. We examined the RFs of 132 vIPFC neurons in macaque monkeys to characterize their spatial response properties, using extracellular recordings with a high-resolution, unbiased random-dot paradigm during passive viewing. Analysis revealed substantial heterogeneity in RF structure, allowing neurons to be classified into three types: uniform, full-field, and nonuniform. More than 85% of neurons exhibited large RFs with multiple high-response regions spanning broad portions of peripheral visual space. These findings reveal the complex organization of vIPFC neurons and provide a foundation for understanding how this region supports flexible visual processing and cognitive computations.

Introduction

In visual neuroscience, a receptive field (RF) is the region of the visual field where a stimulus can alter the firing rate of a neuron [1, 2]. Receptive fields link sensory input to neural representations [3, 4]. Although ventral and dorsal visual areas are well characterized, the organization of receptive fields in the ventrolateral prefrontal cortex (vlPFC) remains less understood. The vlPFC is involved not only in high-level cognitive processes and in integrating visual inputs with task goals and reward signals [5], but also contributes to visual object recognition [6–9]. Understanding its receptive field properties is therefore informative for clarifying how this region contributes to perception and higher cognition.

Receptive field sizes in the ventral visual stream increase progressively along the hierarchy, supporting the transition from fine-grained feature detection to invariant object recognition. In V1, neurons have small, contralaterally confined receptive fields ($\sim 0.25\text{--}5^\circ$) concentrated in the central visual field and exclusively respond to stimuli in the contralateral visual hemifield, enabling high-acuity vision and edge detection. [1, 10–14]. V2 fields expand modestly ($\sim 1\text{--}15^\circ$), aiding contour combination, and are positioned within the contralateral visual field, extending up to 80° eccentricity in a topographically organized map [15]. In contrast, V4 neurons ($\sim 1\text{--}20^\circ$) are located more peripherally, with receptive fields distributed across the contralateral field up to 40° eccentricity, and become selective for complex features such as curvature and shape [13, 14, 16–19]; In these regions RF size scaled as a function of eccentricity from fovea. Further along the ventral stream, inferotemporal neurons have larger receptive fields than those in earlier areas of the ventral visual stream ($\sim 2.8\text{--}39^\circ$). They typically respond most strongly to stimuli at the center of vision and show a preference for the contralateral visual field over the ipsilateral one. However, some neurons also exhibit bilateral receptive fields, responding to stimuli presented in both visual hemifields, supporting object recognition across position and appearance changes [20–23]. Thus, ventral stream receptive fields enlarge and gain complexity while preserving a central bias, enabling detailed yet invariant object perception.

Receptive fields in the dorsal stream are generally large and peripheral, reflecting their role in spatial coordination and visuomotor control. Neurons in the middle temporal (MT) area, primarily responsible for directional motion detection, possess receptive fields of approximately $5\text{--}15^\circ$, with eccentricities ranging from $<1^\circ$ to 18° [24–27]. Similarly, receptive fields in the lateral intraparietal (LIP) area, associated with salience mapping, spatial attention, and saccades, span $1.8\text{--}38.5^\circ$ and extend up to 28° in eccentricity, exhibiting a strong contralateral bias [28]. The anterior intraparietal (AIP) area, which contributes to grasp-related object encoding and contour fragment processing, contains

receptive fields measuring $3\text{--}90^\circ$ and reaching up to 10° in eccentricity, with diverse shapes and a slight contralateral preference [29]. The ventral intraparietal (VIP) area shows comparable receptive field sizes and eccentricities and is implicated in multisensory integration and egocentric spatial mapping [30]. Overall, dorsal stream receptive fields are expansive, eccentric, and contralaterally biased, consistent with their function in spatial attention and visually guided action.

Beyond parietal and temporal regions, receptive fields have also been described in the prefrontal cortex, although evidence remains limited. In the dorsolateral prefrontal cortex (dlPFC), receptive fields range from ~ 3.7 to 13.8° , with eccentricities extending up to 18° and a consistent contralateral bias [30]. These properties are consistent with the dlPFC's role in spatial working memory and goal-directed behavior. By comparison, the vlPFC is implicated in object recognition and broader cognitive functions, yet its receptive field organization remains poorly understood. Neurons in the vlPFC can respond selectively to visual categories and spatial locations even in the absence of explicit task demands [19, 31, 32]. Moreover, this region participates in an integrated network that supports recognition under uncertainty, resolves ambiguous or degraded images, and stabilizes object representations through top-down influences [33, 34]. Only a few studies, however, have examined vlPFC receptive fields directly. They reported sizes of $\sim 4.6\text{--}12.2^\circ$ with eccentricities of $\sim 10\text{--}25^\circ$. [19, 32]. These studies, limited by small sample sizes and a narrow focus on face-selective patches, did not capture the full diversity of receptive field properties in the vlPFC.

To address this gap, we investigated receptive fields in the ventrolateral prefrontal cortex of two macaque monkeys during passive viewing. Unlike earlier studies limited to small samples or restricted subregions, we recorded from 132 neurons across different vlPFC sites. Receptive fields were mapped using an unbiased random-dot stimulation method and classified into three types, nonuniform, uniform, and full field. More than 85% of neurons exhibited large receptive fields, often multi-peaked and extending into peripheral vision. These findings reveal substantial heterogeneity within the vlPFC and underscore its role in linking visual processing with flexible behavior.

Results

To investigate the spatial properties of receptive fields (RFs) in the ventrolateral prefrontal cortex (vlPFC), we recorded single-unit activity from two macaque monkeys during a passive visual fixation task optimized for RF mapping. Although the vlPFC is recognized as a node for visual object recognition, either directly or via feedback and recurrent processing [8, 9, 32, 34, 35].

Random-dot stimuli were sequentially presented across a 13×25 grid covering $50^\circ \times 26^\circ$ of visual space, while monkeys maintained fixation on a central cross. The spike-triggered averaging (STA) method was applied to map the RFs of 132 visually responsive vIPFC neurons; RFs were clearly observed when the STA window was set to $\tau = -90$ ms, whereas maps generated at $\tau = -300$ ms appeared diffuse and lacked spatial structure, suggesting that receptive field mapping in vIPFC depends on a temporally specific integration window. (Figure 1b). RF maps were normalized, interpolated, and smoothed before contour extraction, and neurons were classified based on RF structure and spatial localization (see Methods).

This task is suitable for mapping vIPFC RFs because it provides high spatial resolution across a large visual field, while passive fixation minimizes confounding effects of eye movements or active task engagement. By systematically sampling a dense grid of visual locations, the task allows precise estimation of both RF size and structure, which is required for understanding how vIPFC neurons integrate visual space. Figure 1a illustrates the experimental setup and the stimulus grid used.

Across the population, RFs exhibited considerable diversity in structure, size, and spatial position, reflecting multiple modes of spatial integration in this higher-order visual area. Using a split-half validation procedure, 57% of neurons demonstrated significant RF reliability ($p < 0.05$), indicating robust map estimation. All recorded neurons are included in the analyses; comparisons between the full dataset and the validated subset revealed qualitatively consistent patterns, supporting the reliability of our findings.

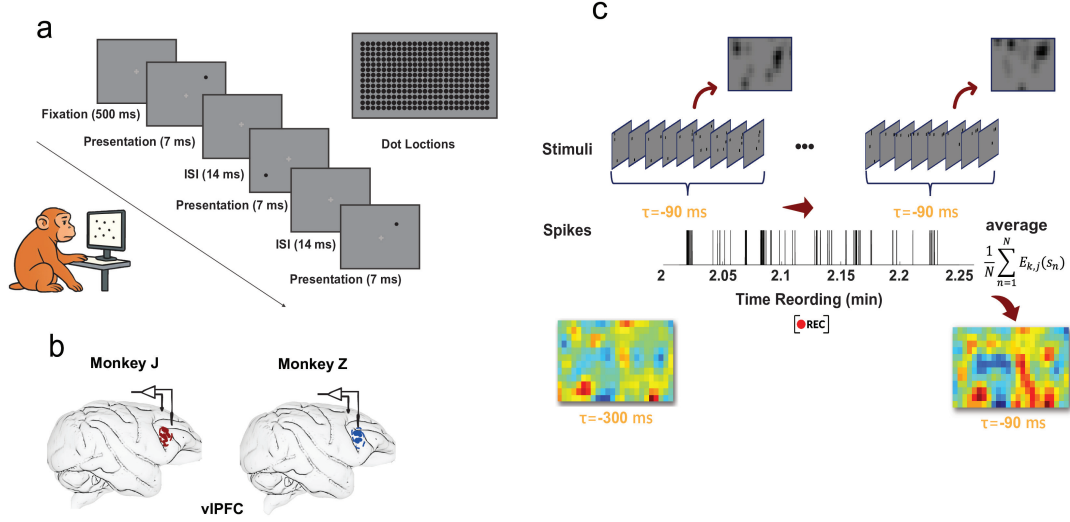


Figure 1. Experimental Setup and Receptive Field Mapping Paradigm. (a) Schematic of the RF mapping task. Monkeys maintained fixation on a central grayscale cross displayed on a monitor. Visual stimuli consisted of brief dots, randomly positioned (7 ms duration), sequentially flashed across a 13×25 grid, with 14 ms Interstimulus intervals. (b) Location of the vIPFC in Monkey J (red) and Monkey Z (blue), indicating the electrode placement for neuronal recordings in each monkey. (c) Schematic of the STA procedure used to estimate vIPFC receptive fields. Random-dot frames were presented while spikes were recorded. For each spike, the stimulus frames in a fixed pre-spike window at lag $\tau = -90$ ms were selected and aligned to spike time. The STA was computed as the mean event count per spatial bin across N spikes, $\frac{1}{N} \sum_{n=1}^N E_{k,j}(s_n)$. Heat maps illustrate STAs at $\tau = -300$ ms and $\tau = -90$ ms, with warmer colors indicating stronger normalized responses. The resulting map was taken as the spatial receptive field for subsequent analyses.

Classification of Receptive Fields

To characterize the spatial properties of vIPFC neurons, we applied spike-triggered averaging to responses elicited by brief random-dot stimuli presented across a broad visual grid. RF maps were baseline-subtracted, normalized, interpolated, and smoothed to reveal spatial response patterns. Based on their shape and spatial distribution, neurons were classified into three main categories, uniform, non-uniform, and full-field.

Uniform RFs, defined by a single contiguous region of elevated activity, were rare and observed in 9 of 132 neurons (6.8%; Figures 2a-b). Non-uniform RFs, characterized by multiple local peaks exceeding 98% of the maximal response, were the most common,

comprising 113 neurons (85.6%; Figure 2c). Full-field RFs, which spanned more than 75% of the stimulus area, were observed in 10 neurons (7.6%; Figure 2d). The overall distribution is summarized in Figure 2e. We further classified uniform RFs based on their spatial location relative to the fixation point. RFs with centroids within 5° of fixation, covering foveal and parafoveal regions, were labeled central [36–38]. RFs with centroids beyond 5° were classified as contralateral (opposite the recording hemisphere) or ipsilateral (same side). This finer analysis identified three contralateral neurons (2.3%) and six ipsilateral neurons (4.5%), with no central RFs detected.

These results demonstrate that vlPFC neurons predominantly exhibit large, multi-peaked non-uniform RFs that often extend into peripheral visual space.

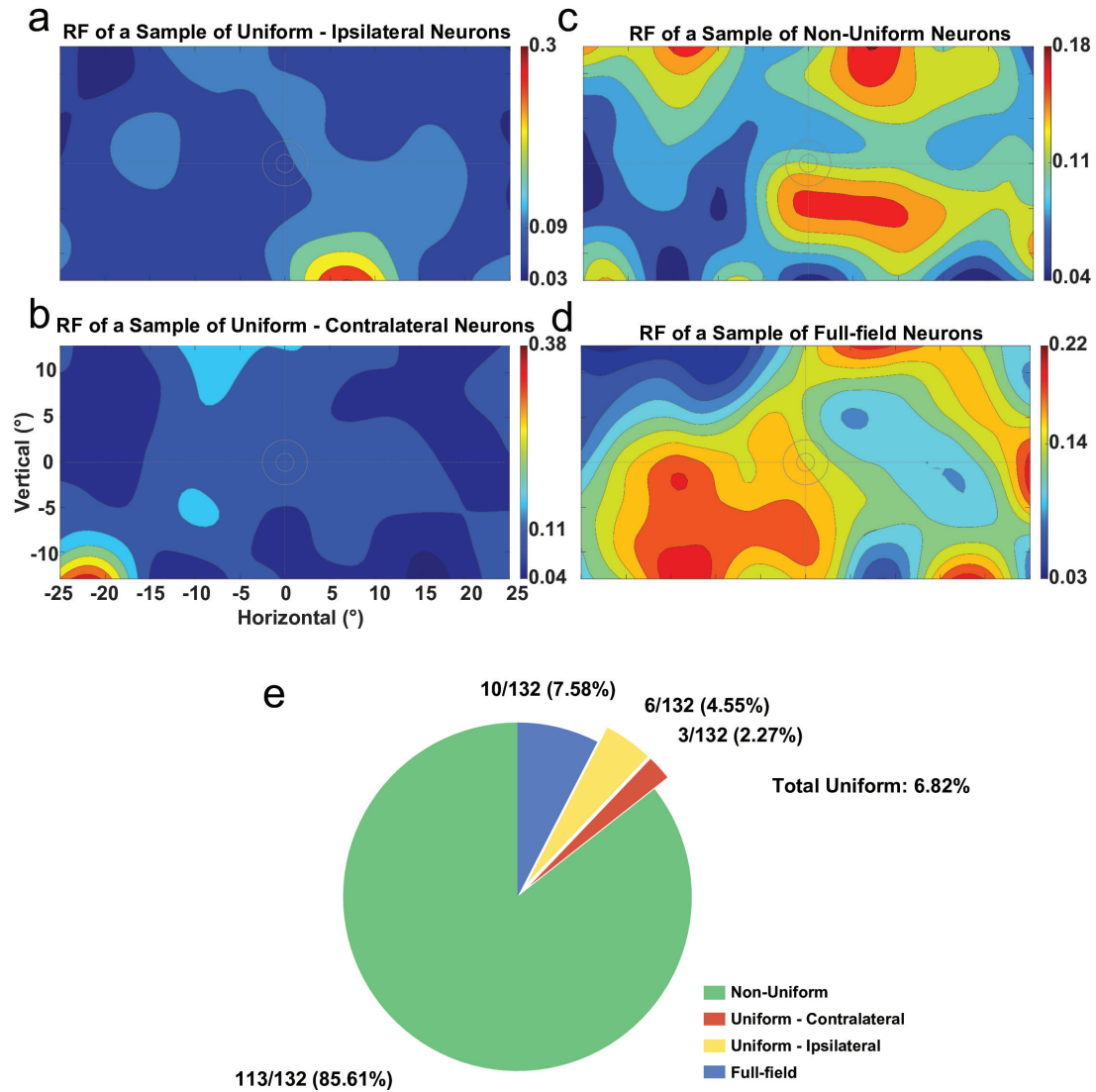


Figure 2. Classification of vLPFC receptive fields. (a–d) Example maps showing different receptive field categories: (a) ipsilateral uniform RF with a single contiguous activation area, (b) contralateral uniform RF, (c) non-uniform RF with multiple local maxima, and (d) full-field RF covering more than 75% of the stimulus area. (e) Pie chart showing the distribution of RF types across 132 neurons: multi-lake RFs (86.61%), uniform RFs (6.82%), and full-field RFs (7.58%).

Receptive Field Size and Area Coverage

To understand how vIPFC neurons map visual field and integrate central and peripheral information, we quantified RF size and area. RFs were measured by extracting contours at 50% of each neuron's peak response. Figure 3a shows an example RF from a single neuron, with the purple region indicating areas above the 50% threshold and the surrounding white area representing subthreshold activity.

The distribution of RF sizes across the population ranged from approximately 2° to 36° , with a median of 22.1° (Figure 3b). Some neurons were labeled “underestimated” because their RFs extended beyond the monitor boundaries, which may have limited accurate size estimation.

RF sizes are grouped by classification into uniform, non-uniform, and full-field categories uniform, non-uniform, and full-field, based on the number and spatial arrangement of local maxima. Median sizes were 3.64° for uniform RFs, 21.94° for non-uniform RFs, and 34.19° for full-field RFs. Bootstrap confidence intervals were 3.30° – 6.18° for uniform, 19.13° – 23.62° for non-uniform, and 33.21° – 35.27° for full-field RFs (Figure 3c).

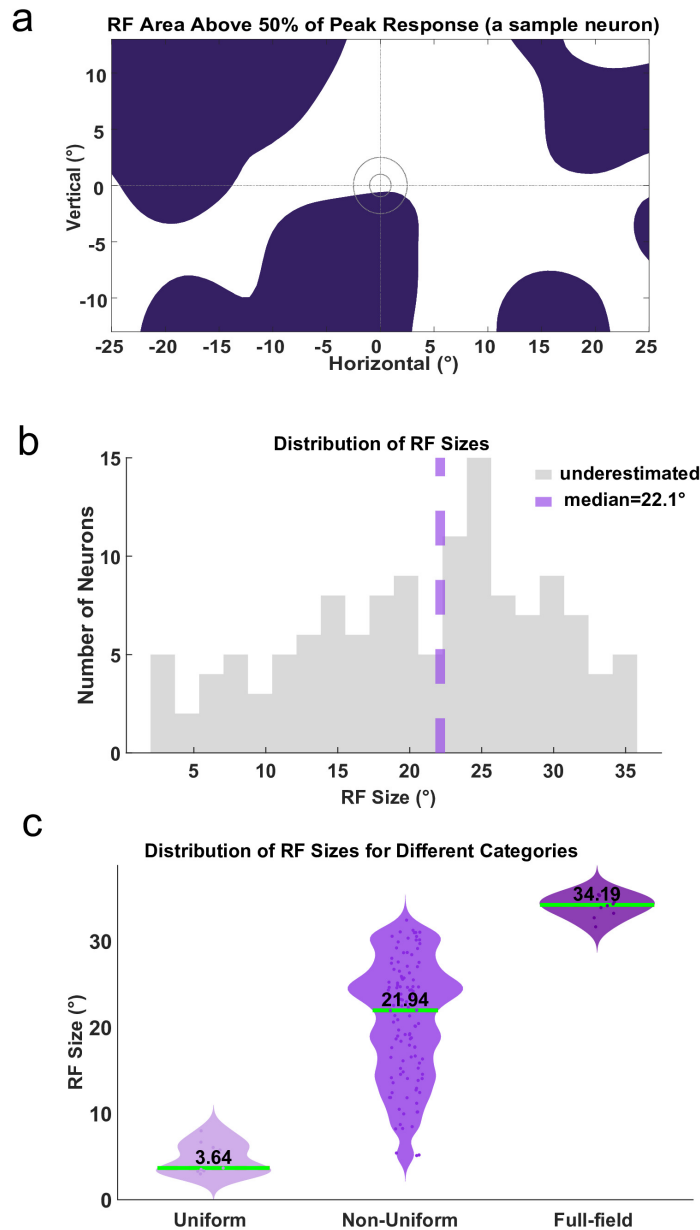


Figure 3. Receptive Field Size and Area Coverage. (a) Example of a receptive field from a single neuron, with the purple region indicating the area above the 50% peak response threshold and the white area representing subthreshold activity. (b) Histogram showing the distribution of RF sizes across the population, with sizes ranging from $\sim 2^\circ$ to 36° and a median of 22.1° . The “underestimated” label highlights neurons with RF contours extending beyond the screen, potentially resulting in size underestimation. (c) RF sizes grouped by classification into uniform, non-uniform, and full-field categories. Violin plots show the distribution of RF sizes within each category, with individual data points shown. Median RF sizes were 3.64° for uniform, 21.94° for non-uniform, and 34.19° for full-field RFs.

Spatial Distribution of Receptive Field Peaks in vLPFC Neurons

To characterize the spatial properties of receptive fields in vLPFC neurons, we extracted peak locations from 132 neurons, yielding a total of 181 peaks. Peaks were defined as regions where RF activity exceeded 98% of each neuron's maximum firing rate.

Peak positions were mapped onto a $5^\circ \times 5^\circ$ spatial grid spanning the visual field. The number of peaks within each bin was visualized using circle size and color intensity (Figure 4a). Of the total peaks, 92 (50.8%) were located in the contralateral hemifield, 85 (47.0%) in the ipsilateral hemifield, and 4 (2.2%) within the central region ($\pm 2.5^\circ$ of fixation). Although contralateral peaks slightly outnumbered ipsilateral peaks, a chi-square test indicated no significant difference between the distributions ($\chi^2 = 0.28$, $p = 0.5988$).

To quantify eccentricity, the Euclidean distance of each peak from the screen center was calculated. The resulting distribution (Figure 4b) showed a median distance of 15° , indicating that most peaks were located in peripheral regions of the visual field.

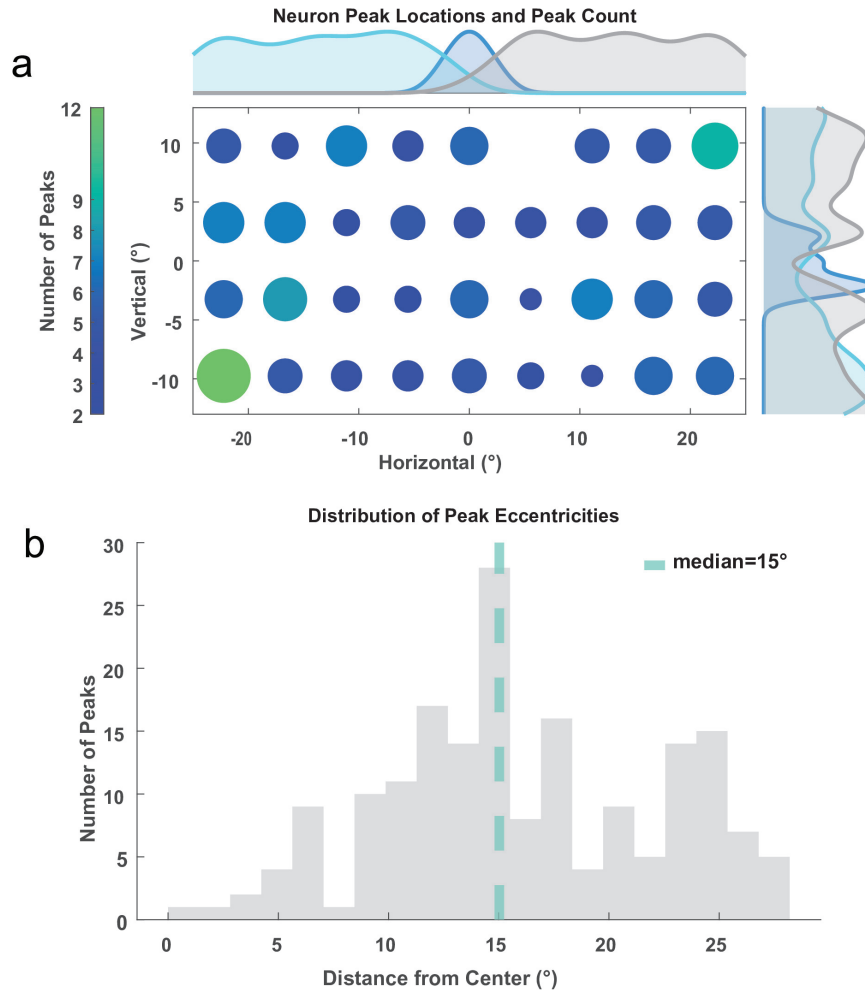


Figure 4. Spatial Distribution of Neuronal Peak Responses Across the Visual Field. (a) Peaks from 132 neurons (totaling 181 due to multiple high-response regions per neuron) were mapped across the screen using $5^\circ \times 5^\circ$ bins. Each circle's size and color intensity represent the number of peaks within that bin. Larger and greener circles indicate greater peak density. Peaks were further classified as central (2.21%, 4/181), ipsilateral (46.96%, 85/181), or contralateral (50.83%, 92/181) based on their distance from screen center. (b) Histogram of Euclidean distances between each peak and the screen center, illustrating spatial distribution. The dashed line marks the median distance of 15° , indicating that most peaks were located in peripheral regions.

Discussion

This study reveals how neurons in the ventrolateral prefrontal cortex (vLPFC) respond to visual space. We mapped receptive fields (RFs) using spike-triggered averaging with random dot stimuli and found substantial variation in RF structure and size. Based on their spatial patterns, RFs were classified as nonuniform, uniform, or full field [30, 39]. RF size, calculated as the square root of the area exceeding 50% of peak response, ranged from 2.9° to 35.7° , with a median of 22.1° , indicating diverse spatial sensitivity across vLPFC neurons [30, 32, 39]. We analyzed the spatial distribution by computing eccentricity from the 98% peak response locations. The median eccentricity was 15° , showing that most neurons responded to peripheral rather than central visual inputs.

In the ventral stream, receptive field size increases progressively from V1 through IT, scaling with eccentricity and enabling a shift from detailed feature analysis to stable object recognition across changes in position and appearance.[15–17, 20, 21, 23]. V1 neurons have small, centrally biased RFs ($\sim 0.25\text{--}5^\circ$), V2 neurons expand modestly ($\sim 1\text{--}15^\circ$) and V4 neurons ($\sim 1\text{--}20^\circ$) become selective for features such as curvature and shape with topographic maps extending far into the periphery. IT neurons then reach larger sizes ($\sim 2.8\text{--}39^\circ$) while typically maintaining a strong foveal preference. In our dataset, only 2% of RF peaks (4 out of 132 neurons) were foveal, and these centrally responsive vLPFC neurons may serve a function similar to ventral stream cells, supporting object-related evaluation in working memory and decision making [1, 6–9, 11–14, 18, 19, 21–23].

Comparing visual streams, ventral areas like IT show homogeneous, foveal biased RFs optimized for object recognition, receptive fields in dorsal stream areas are expansive, eccentric, and contralaterally biased, reflecting their roles in spatial coordination and visuomotor control. MT neurons ($5\text{--}15^\circ$) are tuned for motion and concentrated in the periphery, LIP neurons (up to 38°) support spatial attention and saccades, and AIP and VIP show similarly large, multi-peaked fields supporting grasping and multisensory integration [24, 25, 27–30]. In this respect, the eccentric and heterogeneous RFs of vLPFC resemble dorsal stream organization more than the ventral, suggesting a contribution to rapid, spatially distributed processing rather than purely foveal object recognition.

Our findings align with recent reports on visual responses in vLPFC. [19] showed that some neurons in this region respond to coarse shapes with eccentric receptive fields, and [32] reported that frontal face patches can respond to low-spatial-frequency facial information with very short latencies, consistent with models of top-down facilitation where coarse input rapidly engages prefrontal circuits to guide recognition in visual cortex [40]. Together, these findings and the predominance of eccentric and heterogeneous receptive fields in our results, along with the scarcity of foveal responses, suggest that vLPFC is particularly engaged by peripheral and coarse visual input. Such properties may

enable rapid detection of salient features, while the integration of these signals with task demands supports higher-order cognitive functions.

The diversity of RFs observed in vIPFC, including nonuniform and spatially distributed structures, likely provides a functional advantage. This arrangement may allow vIPFC neurons to integrate inputs from both dorsal and ventral visual streams, as well as other sensory modalities, supporting complex perceptual and cognitive functions [41–43].

In summary, vIPFC neurons exhibit diverse receptive field properties that combine features of both dorsal and ventral visual pathways. This organization may enable vIPFC to support integrative, higher-order cognitive and perceptual functions. At the same time, several limitations of the present study should be acknowledged. Recordings were obtained during passive fixation, which does not capture how RF properties in vIPFC may change under active task conditions such as attention, decision-making, or working memory. While this passive design limited behavioral context, it also allowed us to focus on the intrinsic RF mapping of vIPFC neurons without the confounds of task-related modulation. Moreover, RF mapping was conducted with simple random-dot stimuli. While this unbiased approach allowed precise spatial sampling, it may not fully represent how vIPFC neurons respond to more complex or naturalistic stimuli such as faces, objects, or scenes. The stimulus display was also limited to a fixed monitor size, meaning that RFs extending beyond screen boundaries were likely underestimated, particularly for the largest fields. Finally, our analyses emphasized spatial RF organization and did not address temporal dynamics, which could be critical given reports of rapid vIPFC responses to coarse visual input.

Together, these considerations highlight opportunities for future research. Expanding stimulus sets to include behaviorally relevant categories, examining RF dynamics during active tasks, and conducting larger-scale or multi-area recordings will provide a more comprehensive understanding of how vIPFC contributes to visual perception and higher cognition.

Materials and Methods

Subjects

Two adult male rhesus macaques (*Macaca mulatta*), Monkey J (7y old, 10kg) and Monkey Z (14y old, 12kg), participated in this study. All procedures were approved by the Institute's Fundamental Science Committee (Approval Code: 99/60/1/160/1). Structural MRI and CT imaging were used prior to surgery to guide the placement of titanium recording chambers targeting the ventrolateral prefrontal cortex (vIPFC) (Figure 1a). In total, 84 sessions and 132 vIPFC neurons were recorded (67 from Monkey J and 65 from

Monkey Z).

Surgical Procedures

Animals were fasted for approximately 8 hours prior to surgery to minimize anesthetic risk and ensure gastric clearance. Recording chambers were implanted under general isoflurane anesthesia using aseptic techniques. Titanium cylinders were anchored with orthopedic screws and dental acrylic. For Monkey J, the chamber covered anterior-posterior coordinates from ~28 mm to ~48 mm; for Monkey Z, it spanned ~2 mm to ~42 mm. Electrodes were inserted through guide tubes passing through the dura mater to access cortical sites.

Anesthesia was initiated via intramuscular injection of ketamine (10 mg/kg) and xylazine (2 mg/kg). Upon confirmation of sedation, unconsciousness and reflexes, animals were transferred to the operating room and placed under general anesthesia using isoflurane gas (vaporizer setting: 0.2), delivered via endotracheal intubation and mechanical ventilation with oxygen at a flow rate of 3 L/min. Neuromuscular blockade was maintained with intravenous atracurium, beginning with a 10 mg dose followed by 5 mg every 30 minutes. Nesdonal (thiopental sodium, 150 mg) was administered intravenously to deepen anesthesia. Intravenous fluids consisting of normal saline and a one-third/two-thirds glucose-saline solution were administered throughout the procedure to maintain hydration and metabolic stability.

Following surgery, animals were monitored closely and allowed to recover for 60 days before the onset of experimental procedures. During this recovery period, animals received daily veterinary assessments and supportive care to ensure full healing and acclimatization. After recovery, a craniotomy was performed to expose cortical regions of interest, and electrophysiological recordings commenced using varnish-coated tungsten microelectrodes.

Euthanasia

At the conclusion of the study, one animal remained alive (Monkey Z), while another (Monkey J) was euthanized in accordance with the AVMA Guidelines for the Euthanasia of Animals: 2020 Edition and the ARRIVE guidelines (<https://arriveguidelines.org>). Deep sedation was first induced via intramuscular injection of ketamine (10 mg/kg) and xylazine (2 mg/kg). Upon confirmation of unresponsiveness and loss of reflexes, euthanasia was performed via intravenous administration of pentobarbital sodium (100 mg/kg), resulting in rapid loss of consciousness, respiratory arrest, and cardiac cessation. Death was confirmed by the

absence of heartbeat, respiration, and corneal reflex. All procedures were conducted by trained personnel in a controlled environment to ensure humane treatment and full compliance with ethical standards.

Ethical Compliance

All procedures involving animals were approved by the Institute's Fundamental Science Committee (Approval Code: 99/60/1/160/1) and were conducted in accordance with relevant institutional and national guidelines and regulations. This study is reported in accordance with the ARRIVE guidelines (<https://arriveguidelines.org>). Anesthesia and euthanasia protocols followed veterinary best practices as outlined in the AVMA Guidelines for the Euthanasia of Animals: 2020 Edition.

Electrophysiological Recording

Single-unit activity was recorded extracellularly using varnish-coated tungsten microelectrodes (FHC; impedance 0.2–1 M Ω). Signals were amplified, filtered (300 Hz–5 kHz), and digitized at 40 kHz. Spike sorting was performed offline using the ROSS toolbox [44].

Neuronal Localization

Recording sites were identified using structural landmarks, stereotaxic coordinates, and depth profiles. Microstimulation of the frontal eye field (FEF) was used to evoke saccades or facial twitches, confirming electrode placement near the arcuate sulcus and vIPFC boundaries.

Behavioral Setup

Monkeys were seated in primate chairs with head fixation. Stimuli were displayed on a 24-inch LED monitor (Asus VG248QE; 1920 $\times$ 1080 resolution; 144 Hz refresh rate) positioned 65.5 cm from the eyes. A grayscale fixation cross (0.25° visual angle) was displayed at the screen center. Eye position was monitored using an EyeLink 1000 Plus infrared system (sampling rate: 2 kHz; precision <0.01° RMS). Stimuli and rewards were controlled using MATLAB and Psychtoolbox.

Visual Stimuli and Task Design

Stimulus Set

The visual stimulus set consisted of 165 grayscale images (500×500 pixels; $\sim 5^\circ$ visual angle), displayed centrally on a mid-gray background (luminance = 0.5). Categories included animal and human faces and bodies, man-made objects, and natural scenes. Each image was presented for 50 ms, followed by a 450 ms interstimulus interval. Monkeys were required to maintain fixation within a 2° window. Juice rewards were delivered every 1.5–2 seconds.

Responsiveness Screening

Prior to receptive field (RF) mapping, neuronal responsiveness was assessed using a sliding window approach. Spike rates during a 30 ms baseline window (-30 to 0 ms) were compared to successive 30 ms post-stimulus windows, advanced in 1 ms steps. A neuron was considered responsive if it showed a statistically significant increase in firing in five consecutive windows post-stimulus (Wilcoxon signed-rank test, $p < 0.05$).

Receptive Field Mapping Procedure

RFs were mapped using brief random-dot stimuli presented across a 13×25 grid (325 locations), covering 26° horizontally and 50° vertically, with 2° spacing. Each dot was shown for 7 ms, followed by a 14 ms blank interval. Mapping sequences lasted several minutes per neuron (Figure 1).

Analysis

RF Estimation and Preprocessing

RFs were estimated using spike-triggered averaging (STA). For each neuron, stimulus frames preceding each spike were averaged across trials. The analysis window began 90 ms post-stimulus onset, determined via 500 bootstrap iterations (median latency = 70 ms + 20 ms buffer). RF maps were median-subtracted, rectified, normalized to peak response, interpolated to a 39×75 grid, and smoothed with a Gaussian filter ($\sigma = 5$) (Figure 1c).

RF Mapping and Classification

Neurons were categorized into three classes based on the structure of their RFs. Neurons exhibiting a single local maximum within a contiguous region of activation were classified as *uniform*. Those displaying multiple local maxima exceeding 98% of peak were labeled as *non-uniform* [29]. A subset of neurons with RFs spanning 75% or more of the screen area, despite minor local minima, were designated as *full-field* [30] (Figure 2).

Boundaries were extracted using MATLAB’s `contourf` at a 50% peak-response threshold [29, 30, 32, 39, 45]. Zero-padding (`padarray`) enclosed contours extending beyond the visual field. RF area was computed using `polyarea`, and size was defined as the square root of this area (Figure 3).

Distribution of Peak Locations

From 132 neurons, 181 peak locations were identified. Coordinates were baseline-subtracted, normalized, and binned into $5^\circ \times 5^\circ$ grids. Bubble plots visualized peak density. Peaks were categorized as central ($\leq 2.5^\circ$), ipsilateral, or contralateral. Eccentricities were computed as Euclidean distances from $(0^\circ, 0^\circ)$ and summarized via histograms. Chi-square (χ^2) tests assessed distribution differences (Figure 4).

RF Map Validation

RF map reliability was evaluated using split-half correlations. Each neuron’s spike train was randomly divided into two halves 1,000 times. STA maps were generated for each half, and similarity was quantified using the Pearson correlation coefficient:

$$r = \frac{\sum_h \sum_v (\text{Half}_1 - \overline{\text{Half}_1})(\text{Half}_2 - \overline{\text{Half}_2})}{\sqrt{[\sum_h \sum_v (\text{Half}_1 - \overline{\text{Half}_1})^2] [\sum_h \sum_v (\text{Half}_2 - \overline{\text{Half}_2})^2]}} \quad (1)$$

A null distribution was generated by shuffling spike trains 1,000 times while preserving spike count. The observed statistic was the mean correlation across real splits. Neurons were considered reliable if their true correlation exceeded the 95th percentile of the shuffled distribution (one-tailed, $p < 0.05$).

Data Availability

The datasets generated during and/or analysed during the current study are available from the corresponding author upon reasonable request.

Author Contributions Statement

Y.A. wrote and edited the manuscript and performed the analyses.

J.N. supervised the study, managed data collection, reviewed and edited the manuscript.

M.R.A.D. supervised the project and critically reviewed the manuscript.

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