

Current Biology

Prefrontal Control of Visual Distraction

Highlights

- Monkeys performed a search task where salient distractors appeared on some trials
- Neurons in FEF and extrastriate ERPs were recorded simultaneously
- Distractor suppression manifested in FEF prior to emerging in extrastriate ERPs
- This suggests that FEF may control distractor processing in extrastriate cortex

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In Brief

Cosman et al. simultaneously record neurons in FEF and ERPs over extrastriate cortex in monkeys performing a distraction task, showing that behavioral control over distraction results from suppressed processing of distractor items. Suppression in FEF precedes that in extrastriate cortex, suggesting a prefrontal source of distraction control.



Prefrontal Control of Visual Distraction

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SUMMARY

Avoiding distraction by conspicuous but irrelevant stimuli is critical to accomplishing daily tasks. Regions of prefrontal cortex control attention by enhancing the representation of task-relevant information in sensory cortex, which can be measured in modulation of both single neurons and event-related electrical potentials (ERPs) on the cranial surface [1, 2]. When irrelevant information is particularly conspicuous, it can distract attention and interfere with the selection of behaviorally relevant information. Such distraction can be minimized via top-down control [3–5], but the cognitive and neural mechanisms giving rise to this control over distraction remain uncertain and debated [6–9]. Bridging neurophysiology to electrophysiology, we simultaneously recorded neurons in prefrontal cortex and ERPs over extrastriate visual cortex to track the processing of salient distractors during a visual search task. Critically, when the salient distractor was successfully ignored, but not otherwise, we observed robust suppression of salient distractor representations. Like target selection, the distractor suppression was observed in prefrontal cortex before it appeared over extrastriate cortical areas. Furthermore, all prefrontal neurons that showed suppression of the task-irrelevant distractor also contributed to selecting the target. This suggests a common prefrontal mechanism is responsible for both selecting task-relevant and suppressing task-irrelevant information in sensory cortex. Taken together, our results resolve a long-standing debate over the mechanisms that prevent distraction, and provide the first evidence directly linking suppressed neural firing in prefrontal cortex with surface ERP measures of distractor suppression.

RESULTS

Neurons in prefrontal cortex show attention-related enhancements in firing rates to visual targets that precede similar enhancements in extrastriate visual areas and temporal cortex

[10, 11]. Furthermore, causal manipulations of prefrontal cortex recapitulate this attention effect [12, 13]. This suggests that input from prefrontal cortex provides an attentional control signal that gates visual processing in early sensory areas, enabling the selection of information that is relevant in a given context. However, a long-standing debate concerns how distracting, task-irrelevant information is processed within this system. On the one hand, stimulus-driven hypotheses propose that salient distractors automatically “capture” attention and prefrontal control signals then re-direct attention to task-relevant items [6]. On the other hand, signal-suppression hypotheses propose that prefrontal control signals proactively suppress the representation of salient distractors before they capture attention and interfere with the selection of task-relevant information [14, 15].

This debate persists because the measures used to study distraction have been restricted to human performance and noninvasive electrophysiology that lack the sensitivity and specificity to resolve the dynamics of distraction control in neural systems. For example, much of this debate has played out in tasks in which observers show little or no behavioral evidence of distraction [3–5, 7, 8]. Bypassing the ambiguities of behavioral evidence, electrophysiological work has sought to characterize covert responses to task-irrelevant distractors during visual search by measuring event-related potential (ERP) components putatively related to either attentional selection (the *N2pc*) or suppression (the *Pd*). However, these studies have produced mixed results, with some conditions supporting the stimulus-driven hypothesis and some supporting the signal-suppression hypothesis [16–19]. One reason for these conflicting results is that the noninvasive ERP signals arise from as-yet-unspecified, large-scale neuronal ensembles, so the signatures of processes such as selection and suppression might overlap and mask one another. Given that top-down input from prefrontal cortex modulates processing in the extrastriate regions thought to generate the *N2pc* and *Pd* components, pairing prefrontal single-unit recordings with extrastriate ERPs can resolve conflicting views of distraction control by directly measuring neuronal responses to distracting information.

To this end, three monkeys (*Macaca radiata*) performed a visual form search task in the presence or absence of a salient color singleton distractor (Figure 1A). We tracked responses to both task-relevant target items and task-irrelevant distractors across areas and measurement scales in real time by simultaneously recording neuronal discharges in frontal eye field (FEF) (Figure 1B) and ERPs from electrodes embedded in the cranial surface over occipital lobe. Monkeys were trained to search for a T or L target among homogeneous non-targets in the presence



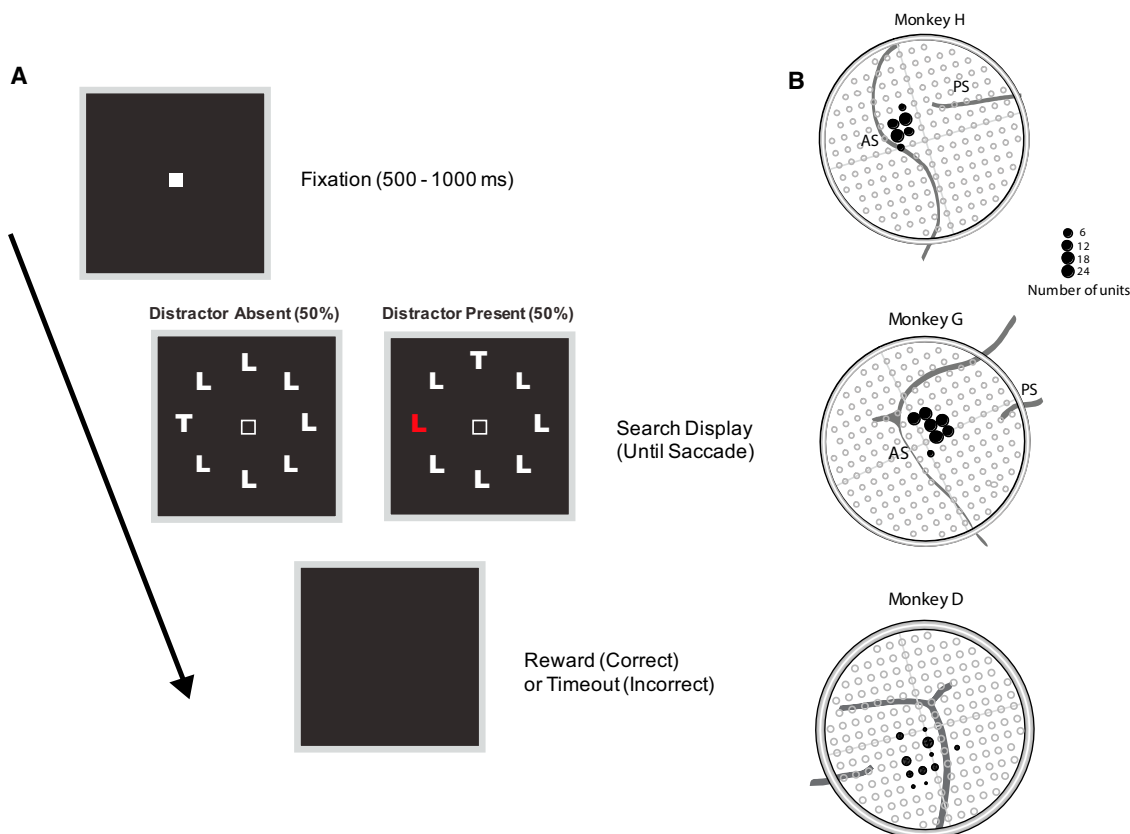


Figure 1. Task and Electrode Penetration Maps

(A) Visual search task. Monkeys fixated for a variable duration (500–1,000 ms), at which point the fixation point extinguished and the search array appeared. Monkeys were trained to covertly search for the target, and were rewarded for a first saccade to the target item. A salient, irrelevant distractor appeared unpredictably on half of all trials, which monkeys were trained to ignore.

(B) Penetration maps for recordings in each monkey including the total number of units isolated at each location, regardless of task-related modulation. AS, arcuate sulcus; PS, principal sulcus.

or absence of a salient distractor. The color distractor was introduced relatively early in training of two monkeys (Ga and He) and after many months of visual search expertise by a third monkey (Da). The first two monkeys gained the capacity to ignore the color distractor (Figure 2A), mirroring the learned control over distraction observed in human studies using a similar task [20, 21]. Neurophysiological data were collected in eight sessions from monkey Ga and eight sessions from monkey He. During recordings from Ga and He, the presence of a salient distractor had no effect on saccade latency (distractor present: 206 ms; distractor absent: 207 ms; $t(15) < 1$) or accuracy (distractor present: 82.4%; distractor absent: 81.8%; $t(15) < 1$) in these monkeys. During recordings from Da, though, the presence of a salient distractor reduced accuracy. The behavioral effect of the salient distractor diminished but never disappeared over the course of training. During training, performance was significantly affected by the presence of a salient distractor (distractor present accuracy: 74.6%; distractor absent accuracy: 79.6%; $t(12) = 2.82$, $p = 0.015$). Neural data were sampled during 6 early sessions when performance was affected more by the salient distractor (distractor present accuracy: 90%; distractor absent accuracy: 95%; $t(5) = 14.1$, $p < 0.001$) and during 11 later ses-

sions when it was affected less (distractor present accuracy: 83.0%; distractor absent accuracy: 84.5%; $t(10) = 3.0$, $p = 0.004$). Lower accuracy in the later sessions was due to a hiatus in performance testing on this task. The persistent effect of the salient distractor on task performance in monkey Da provided the opportunity to examine neural responses to the salient distractor in a case where it negatively impacted task performance, allowing a comparison with the data from the other two monkeys. Although it is not entirely clear why monkey Da did not show the same ability to overcome distraction as monkeys Ga and He, such a result is not entirely unexpected given previous work in humans demonstrating individual variation in the ability to overcome distraction by salient distractors [22].

Contingent Suppression of Salient Distractors by FEF

FEF has been proposed as a source of attention control, acting as a salience map that integrates information about stimulus properties and task goals to bias attention in favor of relevant information [2, 23]. Visually responsive neurons in FEF show enhanced processing through elevated discharge rates for attended targets and suppressed discharge rates for unattended distractors [24–27], even when the target item “pops out” of the display on

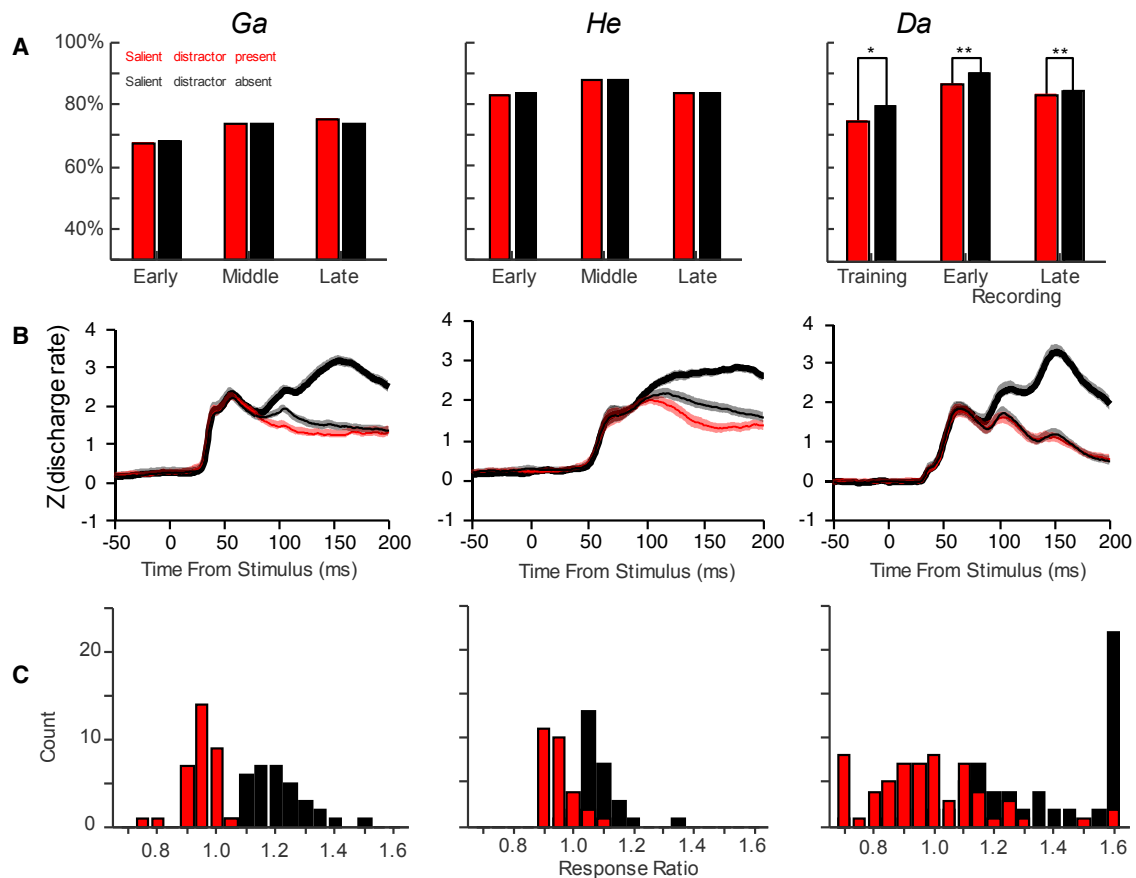


Figure 2. Salient Distractor Processing in Behavior and Prefrontal Neurons

(A) Effects of the salient distractor on visual search accuracy when the color singleton distractor was present (red) relative to absent (black). Monkeys Ga and He were exposed to the color singleton distractor early in training, and learned to avoid distraction. Monkey Da performed the visual form search task for many months before exposure to the color singleton distractor, and subsequently suffered distraction when the distractor was introduced. As training progressed, behavioral distraction decreased but never disappeared. The salient distractor exerted a significant influence on behavior during early and late periods of neurophysiological data collection for this monkey. * $p < 0.05$, ** $p < 0.01$.

(B) Mean (\pm SEM error bars) population responses of FEF neurons when the target (thick), non-salient distractor (black), or salient distractor (red) appeared within the receptive field for each monkey. The target was selected through elevated discharge rates relative to the non-salient distractor in all monkeys. The salient distractor was suppressed by reduced discharge rates relative to the non-salient distractor only in the monkeys that did not exhibit behavioral distraction.

(C) Distribution of target selection and distractor suppression for all neurons with a significant visual response. The response ratio was calculated by dividing the magnitude of responses to targets or salient distractors by responses to non-salient distractors in the interval 50–150 ms following presentation of the search array. Values greater than 1.0 indicate enhancement, and values less than 1 indicate suppression. Both target enhancement and distractor suppression were consistent features in FEF of the monkeys that were not distracted. Only target enhancement was observed in FEF of the monkey that was distracted by the color singleton.

the basis of its bottom-up salience [28, 29]. Nonetheless, how visually responsive FEF neurons respond to salient but irrelevant items during visual search is unknown. We contrasted neural responses to task-relevant target items and non-salient distractors with responses to salient, irrelevant color singleton distractors. If salient distractors automatically draw attention, FEF responses to salient distractor items should be enhanced relative to non-salient distractor items, paralleling the enhancement observed during selection of task-relevant targets.

We observed robust selection of task-relevant targets through enhanced responses to target items relative to non-salient distractors in all three monkeys (Figure 2B). Critically, we observed no enhancement of responses to salient distractor items. Instead, in the two monkeys who overcame distraction (Ga and He), we observed suppression of the responses relative to

both target and non-salient distractor items. The contrast of this observation with previous reports [26], and its absence in the third monkey (Da), even in later recording sessions, suggests that the selection of salient stimuli by prefrontal neurons is not automatic. Instead, prefrontal cortex can be configured to select or suppress salient stimuli according to task demands.

We examined the latency of these suppression effects through millisecond-resolution Wilcoxon rank-sum tests to determine when neural responses to a search target or salient distractor significantly differed from responses to a non-salient distractor when these items fell within or without the preferred receptive field ($p < 0.01$ for 10 consecutive milliseconds). For monkeys Ga and He, this analysis revealed enhancement of the target 90 ± 15 ms after the onset of the search display, effectively simultaneous with suppression of the salient distractor at 86 ± 17 ms (Figure 3).

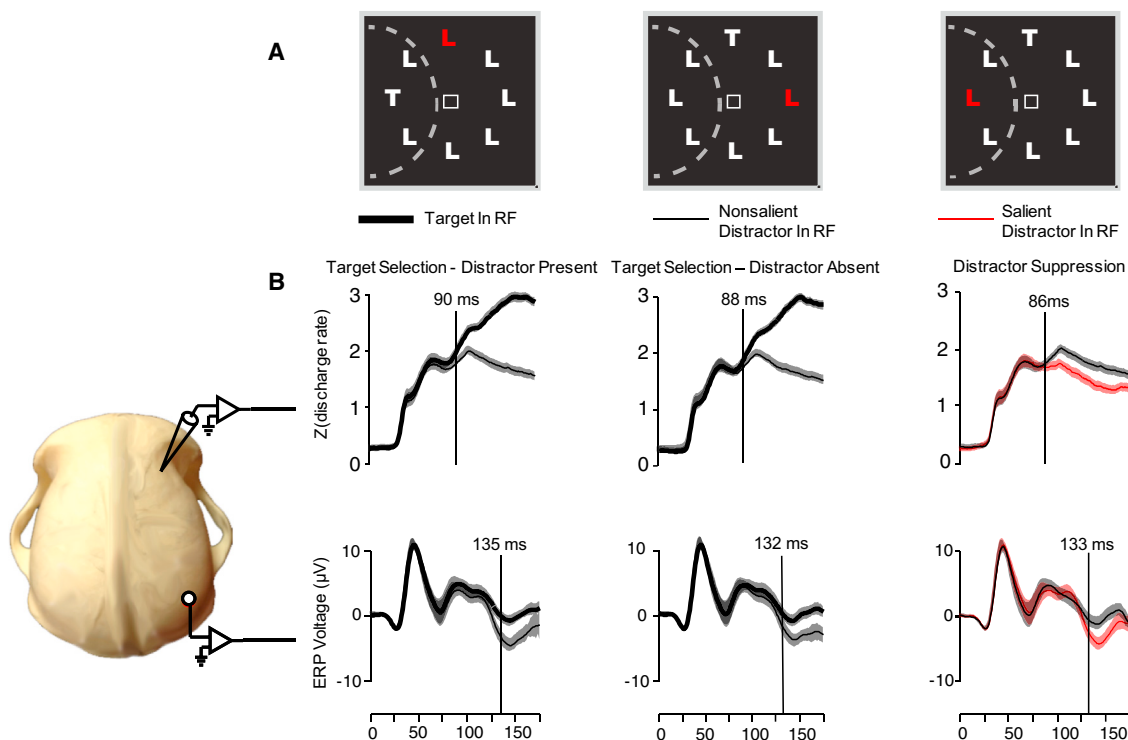


Figure 3. Salient Distractor Processing in Prefrontal Neurons and Extrastriate ERPs

(A) Configurations of the search array used for analyses. Dashed lines indicate the receptive field of FEF neurons in the visual hemifield contralateral to the cranial electrode. RF, receptive field.

(B) Mean (\pm SEM error bars) discharge rates (top) and voltage (bottom) combined for monkeys Ga and He. Neural signals are aligned on the presentation of the search array, and responses were truncated 10 ms prior to the saccade. The response to the target (thick) becomes elevated relative to the response to a non-salient distractor (thin black) whether the salient distractor was present (left) or absent (center). The response to the salient distractor (red) becomes suppressed relative to the response to a non-salient distractor. Vertical lines indicate the time at which responses deviated significantly from one another. Both target selection and distractor suppression emerged earlier in FEF and later in extrastriate ERP responses.

The stimulus-driven capture hypothesis posits that attention is drawn first to the distractor item and then redirected to the target. This would be observed as delayed target selection in the presence of the salient distractor. We therefore compared when the target was discriminated from non-salient distractors in the presence and absence of the salient distractor appearing outside of the receptive field for the first two monkeys. We observed no influence of the salient distractor on the latency of target selection by FEF neurons (distractor present: 90 ± 18 ms; distractor absent: 88 ± 13 ms; $t(78) = 1.20$, $p = 0.23$). In the third monkey, we found a similar result (distractor present: 118 ± 34 ms; distractor absent: 119 ± 39 ms; $t(41) = 0.28$, $p = 0.78$). Results were not different for the early or late recording sessions. The absence of salient distractor effects on monkeys' behavioral performance or on FEF responses contradicts the stimulus-driven hypotheses but is consistent with the signal-suppression hypothesis. Hence, the representation of a salient distractor item is proactively suppressed before it can influence neural selection processes and subsequent behavior.

Target Selection and Distractor Suppression in FEF Are Accomplished by Overlapping Neuronal Populations

To determine whether functionally overlapping or segregated populations of neurons implement target enhancement and dis-

tractor suppression, we examined the firing characteristics of individual attention-related FEF neurons in response to targets and salient distractors. Of the 119 units with significant visual responses in monkeys Ga and He, 79 (66%) showed significant target selection, 51 (42%) showed salient distractor suppression, and none (0%) showed significant salient distractor enhancement. Both target selection and distractor suppression were consistent features of visually responsive FEF neurons. Indeed, of the 51 neurons showing significant salient distractor suppression, all also showed target enhancement. Thus, a subclass of neurons within FEF participates in both processes, providing evidence that only neurons that encode information about task-relevant targets contribute to the suppression of salient distractors. This finding underscores the benefit of the resolution provided by single-neuron recordings, as scalp electrophysiological studies cannot provide such an insight into the neural mechanisms of distraction control.

Extrastriate ERP Responses to Salient Distractors

Human ERP studies using a task like that employed here have played a central role in the debate over the neural mechanisms of distraction control during visual search tasks, providing covert measures of attention in the absence of behavioral distraction. These studies have taken advantage of two lateralized ERP

components conjectured to index the selection (*N2pc*) and suppression (*Pd*) of visual information in extrastriate cortex [16, 30, 31]. A primary goal of the current work was to provide evidence that a putative suppression-related ERP signal, the *Pd*, parallels the operation of neural suppression processes implemented by FEF. By placing the salient distractor item at a position contralateral to the recording electrode and placing the target on the vertical midline, or vice versa, we isolated the lateralized responses to the different items at extrastriate electrode sites [14, 16, 32]. To determine the relationship between FEF neuronal responses and extrastriate ERPs, we analyzed trials in which the hemifield contralateral to the extrastriate electrode (electrode site OR) overlapped the receptive field of the population of FEF neurons included in the discharge rate analyses, allowing us to directly compare responses across areas and recording modalities (see STAR Methods). We compared ERP responses to the target or salient distractor items with those to the non-salient distractor item when each appeared in the hemifield contralateral to the recording electrode.

The ERP response to the target in the presence of a salient distractor item consisted of a positive deflection in the ERP response (Figure 3) relative to the non-salient distractor occurring 135 ± 25 ms after the search array appeared. This was observed in each monkey, replicating previous work with other monkeys [31–33]. This is the monkey homolog of the human *N2pc* [33–35]. This response arose 45 ms later than the target selection signal observed in FEF single neurons. This delay is consistent with previous work indicating prefrontal cortex as the source of attentional modulation in extrastriate single-unit and associated ERP responses [12, 29, 34, 35].

In monkeys Ga and He, but not Da, the ERP response to the salient distractor was a negative polarization relative to the non-salient distractor voltage, arising 133 ± 21 ms after search array presentation. This negativity is the monkey homolog of the *Pd* component observed in the human ERP under similar task conditions. The *Pd* is proposed to index attentional suppression processes [14, 16, 32]. Critically, the distractor suppression polarization emerged on average 47 ms after the suppression observed in FEF neurons. Thus, like the *N2pc*, this component reflects the operation of attention control processes driven by prefrontal cortex. We have shown previously that such timing differences do not arise from differences in the signal-to-noise ratio across measures and so can be interpreted as the timing of cognitive operations across regions [32, 33]. This observation provides the first evidence linking a putative attentional-suppression-related ERP component with suppression of neuronal firing in prefrontal cortex, establishing the scalp-recorded *Pd* component as an indirect, noninvasive readout of prefrontal attentional suppression processes.

It is worth noting that in humans, the *N2pc* and *Pd* components occur with a similar time course and scalp distribution but are opposite in polarity—the *N2pc* manifests as a negativity at electrode sites contralateral to task-relevant targets, whereas the *Pd* appears as a positivity contralateral to a salient distractor. We have previously demonstrated that the monkey homolog of the *N2pc* is inverted in polarity relative to humans, which we believe is due to differences in the cortical folding of extrastriate cortex across species [33, 34].

Accordingly, the monkey homolog of the *Pd* was also inverted in polarity relative to humans. This complementarity indicates that both components originate from a common anatomical source, manifesting attentional modulation in one or more extrastriate cortical areas [31].

DISCUSSION

Our data are the first to demonstrate FEF contributions to distractor suppression, complementing its well-described role in target selection. This corroborates previous work showing target selection and distractor suppression in parietal cortex [36], providing further evidence for a mechanistic overlap in the systems responsible for these processes. We also provide the first demonstration linking this suppression to a nonhuman primate ERP signal of distractor suppression, indicating a homology in extrastriate ERP markers of attentional suppression processes across humans and macaques. The finding that target selection and salient distractor suppression in FEF neurons preceded ERP responses related to these processes elaborates on previous claims that FEF is responsible for modulating processing in extrastriate visual areas [3, 5, 6, 32, 33].

However, because FEF neurons are not inherently feature selective, it is unclear how FEF can register where the target and color singleton are located in the display. Previous work has shown that during visual search, V4 neuron responses to color singletons falling within their receptive field are initially equivalent whether the singleton is a task-relevant target or a task-irrelevant distractor. However, this initial undifferentiated response is followed by a selective suppression of responses to the task-irrelevant distractor singleton, whereas firing rates to task-relevant target singletons remain high, paralleling the target-selective signals typically observed in FEF [37].

Thus, it is possible that during an initial feedforward sweep of visual processing, undifferentiated color signals from V4 feed into FEF in a spatiotopic manner [38], where they are combined with top-down information about target features and used to modulate perceptual processing and shift attention to task-relevant items [39]. This conjecture is consistent with the target selection and distractor suppression effects we observed in FEF neurons and reinforces the hypothesis that FEF acts as a salience map, integrating bottom-up stimulus features and task goals to enable goal-directed processing. Further, although FEF neurons are not inherently feature selective, extensive training in a fixed context induces feature selectivity [40]. This demonstrates that FEF has access to the location of specific features in the visual field.

Taken together, our results are consistent with the signal-suppression hypothesis, proposing an active suppression of distracting information before it can capture attention [9, 14, 15]. Thus, when distraction control is successful, the same prefrontal-extrastriate circuit responsible for enhancing task-relevant visual information also contributes to the suppression of task-irrelevant information. Consequently, electrophysiological markers of attention suppression in humans may reflect the effectiveness of distractor control processes implemented by prefrontal cortex, providing a tool for understanding prefrontal control over distraction in both the healthy and disordered brain.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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AUTHOR CONTRIBUTIONS

Conceptualization, J.D.C., J.D.S., and G.F.W.; Methodology, J.D.C., J.D.S., and G.F.W.; Investigation, J.D.C., K.A.L., W.Z., and J.D.S.; Writing – Original Draft, J.D.C., J.D.S., and G.F.W.; Writing – Review & Editing, J.D.C., K.A.L., W.Z., G.F.W., and J.D.S.; Funding Acquisition, J.D.S. and G.F.W.; Resources, J.D.S.; Supervision, J.D.S. and G.F.W.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
<i>Maccaca radiata</i>	Wake Forest University School of Medicine	Monkey Ga, Monkey He, Monkey Da
Software and Algorithms		
TEMPO stimulus control software	Reflective Computing	TEMPO-VIDEOSYNCH
Eye Tracking System	SR Research	Eyelink 1000, http://www.sr-research.com/EL_1000.html
MAP Data Acquisition System	Plexon	Rasputin v2 HLK3, https://plexon.com/products/map-data-acquisition-system-plexon/
MATLAB R2016b	MathWorks	RRID: SCR_001622
Other		
Cement	Patterson Dental Supply	Ortho-jet
Orthopedic Screws	Thomas Recording	Ceramic screw type SA06
Headpost	Custom fabrication	PEEK material
Recording Chamber	Crist Instrument Company	6-ICO-J0
Amphenol Pins	Fine Science Tools	Gold wire contact
Linear Multichannel Arrays	Neuronexus	Vector Array, https://neuronexus.com/products/primate/vector
Linear Multichannel Arrays	Plexon	Uprobe, https://plexon.com/products/plexon-u-probe/

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Jeffrey D. Schall (jeffrey.d.schall@vanderbilt.edu).

EXPERIMENTAL MODELS AND SUBJECT DETAILS

Nonhuman Primates

Data from three pair-housed, male rhesus monkeys (*Macaca radiata*) were included in the current study. At the time of recording, monkey Da was 9 years, monkey Ga was 8 years, and monkey He was 7 years. All experimental procedures were in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals, the Society for Neuroscience Guidelines and Policies, and approved by the Vanderbilt University Institutional Animal Care and Use Committee.

METHOD DETAILS

Surgical preparation

Monkeys were surgically implanted with EEG electrodes and recording chambers under aseptic conditions with isoflurane anesthesia. Antibiotics and analgesics were administered postoperatively. EEG implants consisted of Teflon-coated braided stainless steel wire and solid-gold male and female terminals. Implanted wires were cut to 6.5 cm, the wire ends exposed, and gold amphenol pins were crimped to both ends. The female pin was inserted into a plastic connector, whereas the male pin on the opposite end of the wire was sanded until approximately 1 mm of the pin remained. During surgery, 1-mm holes were drilled into the surface of the skull (2–3 mm thick), allowing the terminal end of the electrode to be tightly inserted. The inserted gold pin was then covered with a small amount of acrylic cement. After all EEG electrodes were implanted, the plastic connector was attached to exposed acrylic, allowing the leads to be plugged into a headstage. A Crist CILUX chamber was placed over FEF and a craniotomy was made, allowing recording access to the periarculate area, and a headpost was affixed to the skull via ceramic screws. The implant was built out to cover the locations of the EEG electrodes and secure the recording chamber. Monkeys were allowed 6 weeks to recover following surgery before being placed back on task.

Behavioral tasks

Monkeys performed both the primary visual search task as well as a memory guided saccade task, which was used to classify the response properties of FEF single units [41].

Memory-guided Saccade Task

In the memory guided saccade task, monkeys fixated the center of the screen to initiate the trial, and then a single target box was presented for 70ms. Monkeys maintained fixation for 300–700ms after target offset, and when the fixation point extinguished made a saccade to the remembered location. FEF single unit activity during the memory guided saccade task was used to distinguish between neurons with visual, movement, or visual and movement related responses [41].

Visual Search Task

In the visual search task, monkeys searched for a light gray target (T or L in one of four orientations) among a homogeneous array of non-target items (L or T in one of four orientations) presented against a black background (Figure 1A). Critically, a salient, task-irrelevant color singleton distractor appeared randomly on half of trials. This task is identical to that typically used to study distraction control in human electrophysiological and behavioral studies [16, 42]. Importantly, in this task the distractor and target items can either appear at lateral positions or along the vertical midline, allowing us to isolate lateralized neural responses to the target and salient distractor items in both single units and EEG.

To initiate each trial, monkeys fixated a small square at the center of the screen for a variable delay of 500–1000 ms. Following this delay, a visual search array containing eight items was presented around fixation with each item appearing at isoeccentric locations. Monkeys were required to make a single saccade to the target for a small liquid reward, allowing us to track the covert deployment of attention to the target item leading up to the motor response. Accurate saccades were defined as having endpoints falling within a $2.5 \times 2.5^\circ$ window centered on the target item, and held for a duration of 500 ms. Monkeys were not rewarded for making saccades to non-target items, including salient distractors, allowing us to track covert processing of salient but overtly ignored distractor items.

Monkeys trained on the visual search task until they reached a criterion level of accuracy (80%), at which point we began to include a salient distractor item unpredictably in 50% of trials. Initially, for monkeys Ga and He the salient distractor item caused large distractor effects that were most prominent in saccadic accuracy, with monkeys tending to make a large proportion (~50%) erroneous saccades to the salient distractor item. Given that the debate over distraction control has played out in the context of tasks where little behavioral effect of salient, task-irrelevant information is observed (i.e., cases where control over distraction is effective [3, 4, 6]), we had monkeys train on the task until they no longer showed a reliable effect of the salient distractor item on either saccadic reaction times or accuracy (Figure 2A). This occurred relatively rapidly over the course of ~20 sessions, mirroring the learned control over distraction typically observed in humans albeit over a longer timescale [20, 21]. At this point we began to perform neurophysiological recordings in Ga and He to examine the cascade of events that ultimately led to this effective control over distraction. In monkey Da, neural recordings were performed from the time that the salient distractor was initially introduced, allowing us to examine neural responses to salient distractors under conditions of behavioral distraction. In monkey Da, the impact of the salient distractor on saccadic accuracy diminished over time but was still present even after months of training (Figure 2A).

Neural and eye movement recording

Monkeys sat in a primate chair with a head-post restraint facing a CRT monitor, and eye movement responses were collected using an EyeLink 1000 infrared eye tracking system (SR Research Kanata, Ontario, Canada). During task performance, we recorded spikes from FEF neurons in the right hemisphere of two monkeys (*Macaca radiata*) while simultaneously recording from EEG electrodes implanted on the surface of the skull in locations scaled to match a subset of the human 10–20 system. Analyses focused on EEG signals recorded from approximate electrode position OR over right extrastriate cortex, where signals related to target selection and distractor suppression are maximal [33, 34]. In order to verify chamber and recording locations in FEF we used structural MRI scans co-registered with penetration maps. These data were complemented by microstimulation at a subset of the recording sites to verify that saccades could be evoked at low thresholds ($< 50 \mu\text{V}$ [43]).

Surface EEG signals were sampled at 1 kHz, filtered between 0.7 and 300 Hz, and referenced online to the right earlobe then re-referenced offline to the average of the right and left earlobes. All waveforms were aligned relative to the onset of the search array, and baseline corrected by subtracting the mean voltage during the 100ms prior to search onset. Spiking data were acquired using multicontact arrays (NeuroNexus Vector Array; Plexon U-Probe) sampled at 40 kHz. All single unit waveforms were isolated online and resorted offline. For the dataset described here, we only included well-isolated single unit responses leading to 80 neurons from monkey G, 71 from monkey H, and 62 from monkey D.

QUANTIFICATION AND STATISTICAL ANALYSIS

All analyses were performed using MATLAB (MathWorks, Natick, MA). Single unit firing data were characterized using a spike density function in which we convolved each spike with a post-synaptic potential function (Figures 2 and 3). These change only absolute, not relative values. For population analyses, SDFs were normalized by dividing each mean SDF by its standard deviation across time and subtracting the mean baseline activity in the 200 ms before stimulus onset (Figures 2 and 3). Task-relevant visual neurons were identified by comparing responses in the 50–150ms following onset of the search array to responses in the 50ms prior to the onset of the search array using Wilcoxon rank sum tests. We focused on visually responsive neurons in our analyses because these neurons are more likely to project to extrastriate cortex and directly participate in the modulatory functions of interest in the current work. Visually responsive FEF neurons have also been proposed as putative generators of scalp-recorded EEG signals related to target selection processes [34, 35].

Only neurons showing nonzero target selection or distractor suppression (i.e., those that participate in attentional control), determined using distributions of response ratios, were included in our analyses. Given the right hemisphere positioning of recording chambers in monkeys Ga and He and left hemisphere positioning in monkey Da, only neurons with receptive fields in the contralateral visual hemifield were included in our analysis. Likewise, in monkeys Ga and He the *N2pc* and *Pd* components were only calculated at extrastriate electrode site OR in the right hemisphere, which responds to stimuli in the left visual hemifield, and in monkey Da at electrode site OL, which responds to stimuli in the right visual field. This allowed direct comparison across recording modalities, and the same trials used to calculate single unit selection and suppression were used to calculate ERP measures of these two processes.

To measure the latency of target selection and distractor suppression by FEF neurons in our task, we used millisecond-by-millisecond Wilcoxon rank-sum tests to determine the time at which responses to a search target within a given FEF neuron's receptive field were significantly greater than responses of the same neuron when either the non-salient or salient distractor item fell within its receptive field for 10 consecutive milliseconds with $p < 0.01$ (a neuron-antineuron approach [34]). To determine the latency of distractor suppression, we employed an analogous approach, but instead measured the point in time at which neuronal responses to a salient distractor became significantly *weaker* than responses to a nonsalient distractor. We applied an identical method to determine the timing of target selection and distractor suppression in the extrastriate EEG signal across sessions.

DATA AND SOFTWARE AVAILABILITY

All datasets and custom analysis programs will be made available upon request to the Lead Contact, Joshua Cosman (jdcosm@gmail.com).