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Suppression of frontal eye field neuronal responses with maintained fixation

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The decision of where to make an eye movement is thought to be driven primarily by responses to stimuli in neurons' receptive fields (RFs) in oculomotor areas, including the frontal eye field (FEF) of prefrontal cortex. It is also thought that a saccade may be generated when the accumulation of this activity in favor of one location or another reaches a threshold. However, in the reading and scene perception fields, it is well known that the properties of the stimulus at the fovea often affect when the eyes leave that stimulus. We propose that if FEF plays a role in generating eye movements, then the identity of the stimulus at fixation should affect the FEF responses so as to reduce the probability of making a saccade when fixating an item of interest. Using a visual foraging task in which animals could make multiple eye movements within a single trial, we found that responses were strongly modulated by the identity of the stimulus at the fovea. Specifically, responses to the stimulus in the RF were suppressed when the animal maintained fixation for longer durations on a stimulus that could be associated with a reward. We suggest that this suppression, which was predicted by models of eye movement behavior, could be a mechanism by which FEF can modulate the temporal flow of saccades based on the importance of the stimulus at the fovea.

frontal eye field | search | eye movements | oculomotor

In natural viewing, each saccade is part of a stream of consecutive eye movements and, for each, our brain has to decide the goal, rapidly and accurately. Making a decision about where to go in the context of visual search is a complex process that is thought to rely on a combination of factors, such as a representation of salience (1), the task relevance of visual objects (2), and expectations or predictions based on past experience (3). Neuronal correlates of such factors have been examined in multiple areas of the brain, including the frontal eye field (FEF) of prefrontal cortex (4), the superior colliculus (5), and the lateral intraparietal area (LIP) of parietal cortex (6). In all cases, studies have focused on the properties of the stimulus within each neuron's receptive field (RF), which is ubiquitously thought of as the main factor in the neuronal response. In natural visual foraging behavior, however, the properties of the object at the center of gaze and deciding when to leave it are of critical importance. The physical shape, complexity, or familiarity of an object (7–10) and how it is related to the task (11) significantly influence the amount of time we spend gazing at it. Indeed, a fundamental aspect of models of eye movements in visual search (12, 13), scene perception (14, 15), and reading (9, 16) is the inclusion of an inhibitory action that keeps the eye from moving if the object being foveated is important for the task.

We hypothesize that if activity in FEF plays a role in when and where a saccade is to be made, then it should incorporate the sort of suppression that these models include to accurately mimic human behavior. In particular, we predict that the response to a stimulus in the RF should be reduced when the animal is looking at an object that it should continue to fixate.

Results

To test the hypothesis that properties of the stimulus at the fovea affect the responses of neurons in FEF, we trained two monkeys (*Maccaca mulatta*) to forage for a target by freely moving their eyes among 10 objects (Fig. 1A). While the monkeys were performing the foraging task, we recorded the activity from single FEF neurons using extracellular electrodes. Five potential targets (Ts; T shape) and five distractors (+ shape) were arranged on the screen in a way that when the animal was looking at one of the objects, no more than one other object could be in the RF (large circle in Fig. 1A). One T was loaded with a reward, which the animals received if they fixated it for 500 ms. Since distractors never delivered any reward, the animals tended to forage among the Ts, fixating each for about 600 ms until they found the target and received the reward (17). Fixations of distractors were rare (less than 5% of fixations) and were significantly ($P = 8.70 \times 10^{-158}$, paired *t* test; $n = 231$) and substantially shorter [237.6 ± 50.5 ms (mean \pm SD)] than fixations of potential targets (613.7 ± 48.9 ms).

Previous studies have shown that shortly after array onset, FEF neuronal responses differentiate between a target and distractor in the RF in standard visual search tasks (18, 19). We found a similar result in our population when the array appeared: The response to a potential target in the RF (dark trace, Fig. 1B) was consistently higher than the response to a distractor in the RF (light trace, Fig. 1B). This difference began to become consistently significant ~ 180 ms after array onset (black bar on *x* axis of Fig. 1B; $P < 0.01$, paired *t* test every millisecond on the spike density function). Using trials in which the fixation point was replaced by a stimulus and another stimulus appeared in the RF, the mean response in a 150-ms window starting 150 ms after array onset was significantly greater when a T was in the RF than when a distractor was in

Significance

In natural viewing, such as reading or scene perception, fixation can be extended temporally when subjects look at a word or object that is important or requires more processing. Numerous models have suggested that this could occur by a suppressive mechanism. Here, we show that responses in the frontal eye field (FEF) are suppressed when animals maintain fixation on a stimulus that may give them a reward. This suggests that FEF may be able to modulate the temporal flow of eye movements in natural viewing using enhanced activity to generate eye movements and suppression to maintain fixation.

Author contributions: K.M. and J.W.B. designed research; K.M. and Z.B. performed research; K.M. and J.W.B. analyzed data; and K.M. and J.W.B. wrote the paper.

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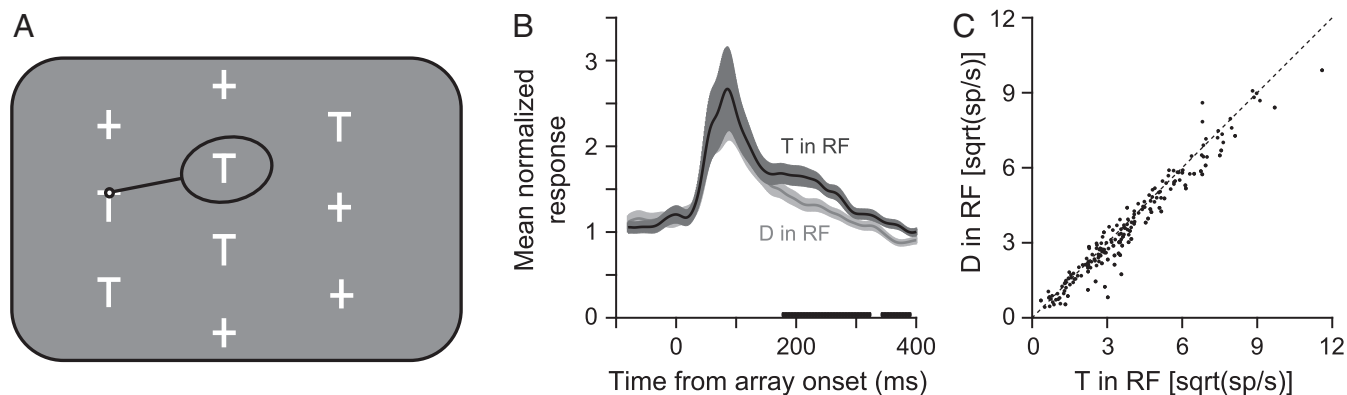


Fig. 1. Behavioral task and response of FEF neurons. (A) Example stimulus arrangement in the foraging task, in which five potential targets (T) and five distractors (+) were presented. One T had a fluid reward linked to it, such that when the monkey looked at it for 500 ms, it obtained the reward. The stimuli were arranged so that when looking at one stimulus (small circle), another stimulus was centered in the FEF neuron's RF (large circle). (B) Normalized population spike density functions in which a T (dark gray trace) or distractor (D; light gray trace) was in the neuron's RF and the animal made a saccade away from the RF. The thickness of the traces represents the SEM, with N being the number of neurons in the population. The thick black trace on the x axis represents times at which the two traces were significantly different ($P < 0.01$, paired t test every millisecond). (C) Mean responses of the 195 FEF neurons averaged during a 150-ms window starting 150 ms after array onset. Each point represents the activity of a single cell in which a T was in the RF compared with fixations in which a D was in the RF. Activity in the scatter is plotted as the square root of spike rate [$\sqrt{\text{sp/s}}$] for better visualization.

the RF [18.95 ± 1.47 spikes per second (sp/s) vs. 17.26 ± 1.35 sp/s; $P = 2.01 \times 10^{-9}$, Wilcoxon signed-rank test; $n = 195$ neurons; Fig. 1C]. At the single neuron level, 40 neurons responded significantly more to a T in the RF than to a distractor in the RF ($P < 0.05$, t test), whereas only four had a significantly greater response to the distractor, a number that is within the false-positive rate.

A similar effect was seen when we sorted data based on what was in the RF and at the fovea. Fig. 2A shows the mean normalized response of 193 FEF neurons aligned by array onset as a function of both stimulus identity in the RF and stimulus identity at the fovea for fixations that lasted at least 300 ms (vertical dashed line). Although the difference between the response to a T in the RF and the response to a distractor in the RF is visible (compare dark and light blue traces in Fig. 2A, particularly the dark and light blue traces), the more obvious result is the much higher activity when a distractor was at the fovea (blue traces) than when a T was at the fovea (green traces), which was similar to the baseline response (horizontal dashed line).

When we compared the responses based on what was at the fovea, 107 of 204 neurons showed significantly higher responses when a distractor was at the fovea than when a T was at the fovea ($P < 0.05$, t tests; blue points, Fig. 2B), whereas only 24 responded more when a target was at the fovea (green points, Fig. 2B). Across the population of 204 neurons, the mean response when a distractor was at the fovea (22.13 ± 1.76 sp/s; 150-ms window starting 150 ms after array onset) was significantly greater than when a T was at the fovea (15.30 ± 1.21 sp/s; $P = 1.64 \times 10^{-15}$, Wilcoxon signed-rank test; Fig. 2B) and the response when a T was at the fovea was not significantly different from the baseline activity seen in the 100 ms before array onset (14.25 ± 1.11 sp/s; $P = 0.269$). The effect of stimulus identity at the fovea was significant both when a T was in the RF ($P = 8.18 \times 10^{-15}$; Fig. 2C) and when a distractor was in the RF ($P = 1.41 \times 10^{-9}$; Fig. 2D). It is worth noting that both the response difference and the number of neurons showing a significant difference were substantially greater when comparing the identity of the stimulus at the fovea (Fig. 2B) than when comparing the identity of the stimulus in the RF (Fig. 1C). Thus, the effect of the identity of the stimulus at the fovea is far greater than the effect of the identity of the stimulus in the RF.

The strong modulation of the neuronal response by the identity of the object at the fovea was also observed during

ongoing visual search. Fig. 3A shows the mean normalized response to the population of all 231 neurons during ongoing search from fixations of at least 150 ms (vertical dashed line) and

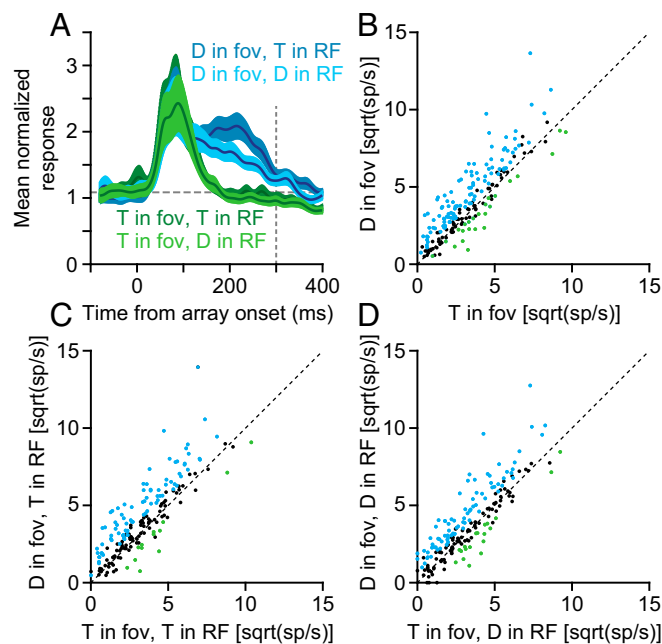


Fig. 2. (A) Mean normalized responses of 193 FEF neurons aligned by array onset as a function of both stimulus identity in the RF and stimulus identity at the fovea (fov) for fixations that lasted at least 300 ms (vertical dashed line) and for which the following saccade was made away from the RF. Blue traces represent a distractor (D) at the fov, green traces represent a T at the fov, dark traces represent a T in the RF, and light traces represent a D in the RF. The horizontal dashed line indicates the mean response before array onset, and the thickness of the traces represents the SEM, with N being the number of neurons in the population. (B–D) Mean responses of FEF neurons during a 150-ms window starting 150 ms after array onset. Each point represents the activity of a single cell when a D was at the fov plotted against the activity when a T was at the fov under conditions in which any stimulus was in the RF (B), a T was in the RF (C), and a D was in the RF (D). Blue points indicate neurons that had a significantly higher response when a D was at the fov, and green points indicate neurons that had a significantly higher response when a T was at the fov ($P < 0.05$, t tests). $\sqrt{\text{sp/s}}$, square root of spike rate.

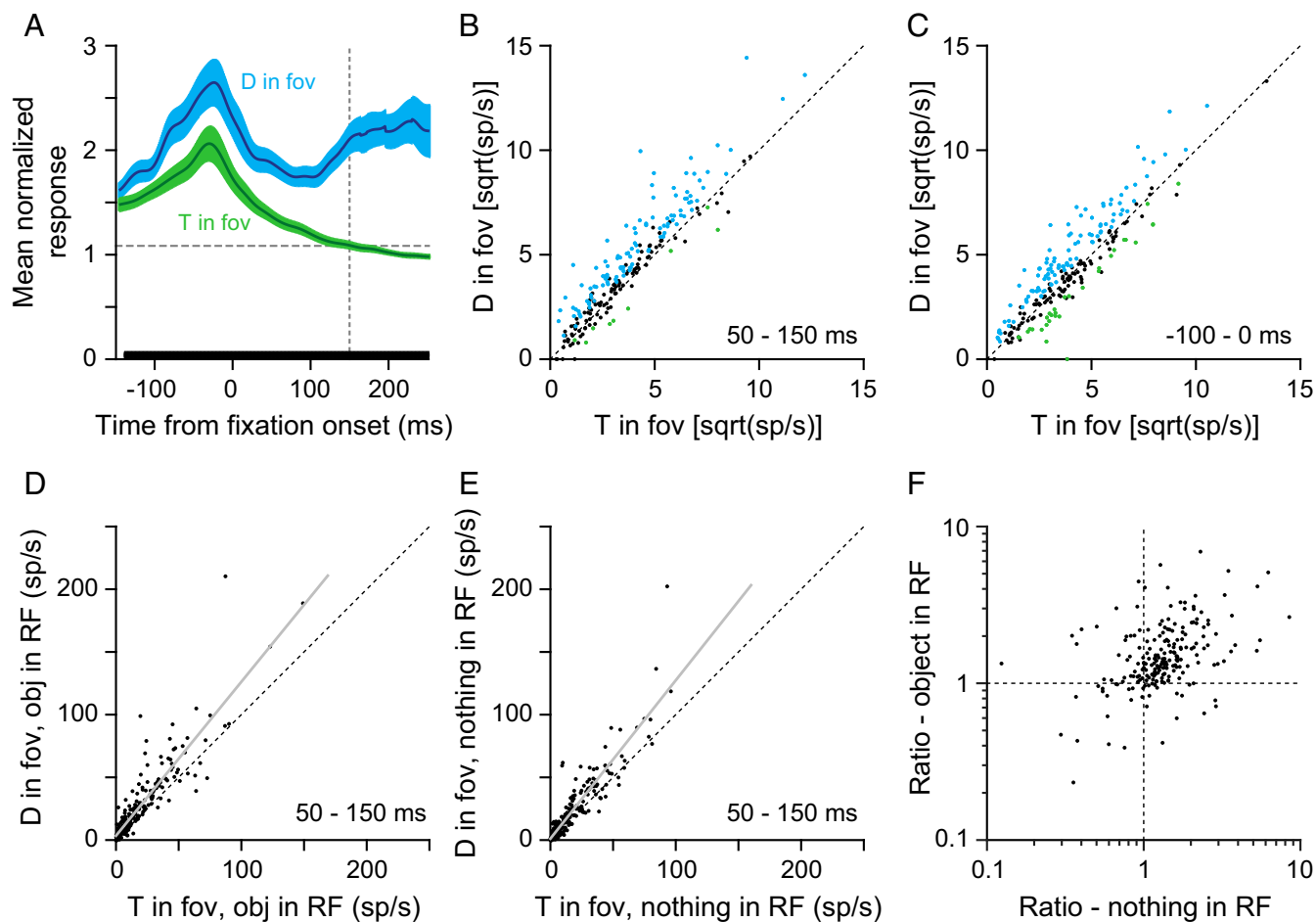


Fig. 3. (A) Mean normalized responses of 231 neurons during ongoing search from fixations of at least 150 ms (vertical dashed line) when a distractor (D; blue) or a potential T (green) was at the fovea and in which the following saccade would go away from the RF. The horizontal dashed line indicates the mean response before array onset, and the thickness of the traces represents the SEM, with N being the number of neurons in the population. The thick black trace on the x axis represents times at which the two traces were significantly different ($P < 0.01$, paired t test every millisecond). The raw population response is illustrated in Fig. S1. Mean responses of single FEF neurons to a D at the fovea (fov) compared with a T at the fov are shown during a 100-ms window starting 50 ms after fixation onset (B) or 100 ms before fixation onset (C). Blue points indicate neurons that had a significantly higher response when a D was at the fov, and green points indicate neurons that had a significantly higher response when a T was at the fov ($P < 0.05$, t tests). $\sqrt{\text{sp/s}}$, square root of spike rate. Data are plotted separately by neuronal class in Fig. S2. Mean activity of single FEF neurons to a D at the fov compared with a T at the fov are shown during a 100-ms window starting 50 ms after fixation onset with an object in the RF (D) or with nothing in the RF (E). Data are plotted as $\sqrt{\text{sp/s}}$ units in Fig. S3. (F) Ratio of the activity with a D at the fov divided by the response with a T at the fovea for conditions in which an object was in the RF or nothing was in the RF.

in which there was a stimulus at the fovea and a stimulus in the RF. For this and the following analyses, we have pooled the responses to Ts and distractors in the RF, but the results are qualitatively similar if we restrict the analyses to only one of the two stimulus categories, as illustrated in Fig. 2 B–D. The response when a distractor was at the fovea (blue trace, Fig. 3A) was substantially and significantly ($P = 2.34 \times 10^{-21}$, Wilcoxon signed-rank test; $n = 231$ neurons; Fig. 3B) higher than when a T was at the fovea (green trace, Fig. 3A). Interestingly, this difference started ~ 140 ms before the fixation onset (black bar on x axis of Fig. 3A; $P < 0.01$, paired t test at each millisecond) and was significant in 100 of 231 neurons ($P < 0.05$, t tests) and in the population as a whole ($P = 8.17 \times 10^{-7}$, Wilcoxon signed-rank test; Fig. 3C) in the 100-ms window before the fixation onset. This is a greater proportion of neurons than the proportion showing traditional RF remapping in FEF (20), and it suggests that knowledge about the identity of the stimulus that is about to be fixated affects a large proportion of the neurons in FEF and may be independent of previously documented RF remapping.

The modulation of the neuronal response by the stimulus at the fovea was seen in all classes of neurons as categorized in the

memory-guided saccade (class definitions are provided in *SI Methods*). Fig. S2 plots the data from Fig. 3B for the 157 neurons that had sufficient memory-guided saccade mapping data to characterize the neurons as visual (Fig. S2A), visuomovement (Fig. S2B), or movement (Fig. S2C) neurons. For each class of neuron, we found that the response to a stimulus in the RF was significantly greater when a distractor was at the fovea than when a T was at the fovea (all $P < 6 \times 10^{-4}$, Wilcoxon signed-rank tests). In addition, the percentage of neurons that responded significantly more when a distractor was at the fovea than when a target was at the fovea was not statistically different across each population [17 of 37 neurons (45.9%), 54 of 91 neurons (59.3%), and 14 of 29 neurons (48.3%) for visual, visuomovement, and movement, respectively; all $P > 0.170$, χ^2 tests].

To quantify the magnitude of the effect of each factor on the response of all 231 neurons, we ran an ANOVA model on the neuronal responses from a 150-ms window starting at fixation onset using the identity of the object at the fovea and the identity of the object in the RF as fixed variables and neuron identity as a random variable. Neuron identity is an identifier associated with each neuron. We included this as a random variable to take into

account the overall responsiveness of the neuron; in this way, the ANOVA can deal with nonnormalized responses across neurons with different response gains and variations. The only significant fixed factor was the identity of the object at the fovea ($P = 0.00054$). The magnitude of this factor was about 30-fold stronger than the factor representing the identity of the object in the RF (3.413 compared with 0.113) and there was no significant linear interaction between the fixed factors ($P = 0.97$). Note that the effect of the stimulus identity in the RF is considerably weaker in ongoing visual search compared with array onset. This is due to some heterogeneity in the responses to the stimulus in the RF in ongoing search. At the single-neuron level, 110 (51%) neurons showed a significant effect of object identity at the fovea, compared with only 38 (18%) of neurons with RF effect. Only a few neurons [25 (12%)] showed any interaction between the fixed variables (average absolute value of the ANOVA coefficients for all neurons = 1.339).

To test whether the large effect of object identity at the fovea may represent a change in response gain, we looked at two pairs of conditions in which we compared the response to an object in the RF (Fig. 3D) or the activity when nothing was in the RF (Fig. 3E) as a function of the identity of the object at the fovea. If the increase in activity is due to a consistent gain increase, then the activity should be correlated, with a slope that is significantly different from 1 and with slopes that are the same whether a stimulus was in the RF or not. We found that whether a stimulus was in the RF or not, the activity when a distractor was at the fovea was a little more than 1.2-fold greater than when a T was at the fovea, with best-fit slopes of 1.23 ± 0.079 ($P = 8.1 \times 10^{-82}$, $R^2 = 0.81$) with an object in the RF (Fig. 3D) and 1.26 ± 0.081 ($P = 4.9 \times 10^{-90}$, $R^2 = 0.84$) with nothing in the RF (Fig. 3E). Intercepts of the fits were close to the origin (3.57 ± 2.26 sp/s with an object in the RF and 1.17 ± 1.88 sp/s with nothing in the RF), showing that the difference in activity could easily be due to a gain change. To confirm that this was not due entirely to the overall responsiveness of individual neurons, we plotted the ratio of the activity with a distractor at the fovea divided by the activity with a T at the fovea for conditions in which an object was in the RF or nothing was in the RF (Fig. 3F). The ratios in the two conditions were correlated ($P = 0.0081$), but, more importantly, the majority of the cells [145 of 219 (66.2%)] lie in a cluster in the top right quadrant (Fig. 3F), meaning they have a positive gain in both conditions. If we only look at neurons that showed a significant effect of object identity at the fovea from the ANOVA analysis described in the previous paragraph, then 75.2% (82 of 109) lie in the top right quadrant (Fig. 3F) and the correlation is much stronger ($P = 2.35 \times 10^{-6}$, $R^2 = 0.189$), with a slope of 1.03 ± 0.41 and an intercept of 0.73 ± 0.81 . Thus, the data are consistent with the hypothesis that the identity of the stimulus at the fovea changes the gain of the neuronal response and that this gain change is relatively consistent across neurons and sessions and is independent of the overall responsiveness of each neuron.

We propose that the reduced response seen when a T is at the fovea is due to a mechanism that suppresses responses throughout the peripheral representation in FEF, thereby minimizing the chance that a saccade will be generated when fixation should be maintained. We have previously shown that animals rarely fixate previously examined Ts (less than 5% of fixations), which will not give them a reward (17). Because fixation durations of previously fixated Ts are bimodal (Fig. 4A), we can test our hypothesis by examining the responses during the two types of fixation. If the reduced response seen when the animal fixates a T is due to a suppressive input aimed at keeping the animal from moving on, then we should see suppression when the animal fixates a previously fixated T for a long duration (>350 ms; vertical dashed line in Fig. 4A), even though it should know that it will not get a reward from the stimulus. Likewise, we should

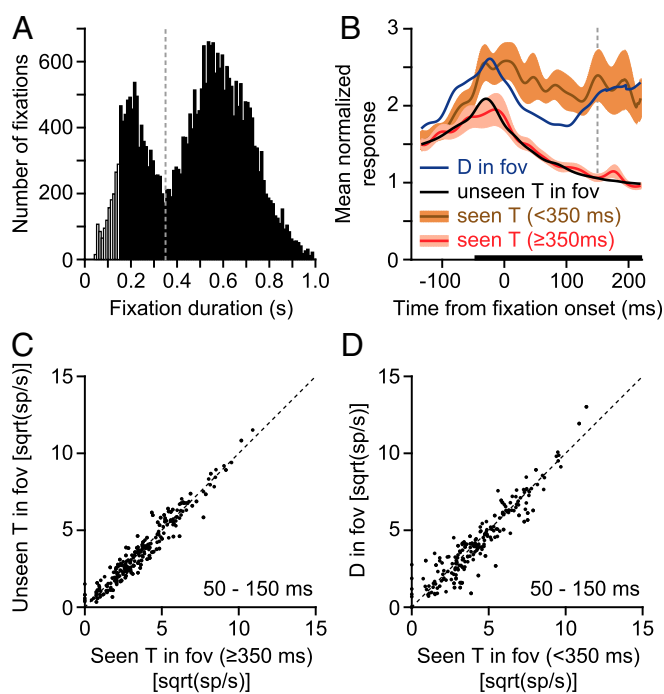


Fig. 4. (A) Distribution of fixation durations when a previously fixated T (seen T) was at the fovea. (B) Mean normalized responses of 224 neurons during ongoing search from fixations of at least 150 ms (vertical dashed line) when a previously fixated T was at the fovea (fov) for <350 ms or ≥ 350 ms or an unfixated target or a distractor was at the fov. The thickness of the traces represents the SEM, with N being the number of neurons in the population. The thick black trace on the x axis represents times at which the two seen T traces were significantly different ($P < 0.01$, paired t test every millisecond). D, distractor. (C) Mean responses of single FEF neurons to a D at the fov compared with a previously fixated T (fixation ≥ 350 ms) during a 100-ms window starting 50 ms after fixation onset with an object in the RF. (D) Mean responses of single FEF neurons to an unseen T at the fov compared with a previously fixated T (fixation < 350 ms) during a 100-ms window starting 50 ms after fixation onset with an object in the RF. $\sqrt{\text{sp/s}}$, square root of spike rate.

see a strong response, similar to that when the distractor is at the fovea, if the animal only fixates the previously fixated T for a short duration (<350 ms). Alternatively, if the response modulation is purely due to the identity of the stimulus at the fovea, then we would predict that fixation duration should not affect the response when a previously seen T is being fixated.

Fig. 4B shows the response of the neurons to a previously fixated T at the fovea for long- and short-fixation durations, as well as the mean response to a distractor and unseen T at the fovea (lines without error bars). All data are from trials with fixations that lasted for more than 150 ms (vertical dashed line in Fig. 4B). In fixations in which the animals fixated the previously fixated T for more than 350 ms, the response was suppressed to a level that was not significantly different from the response when an unseen T was at the fovea ($P = 0.406$, Wilcoxon signed-rank test; $n = 207$; 100-ms window starting 50 ms after fixation onset; Fig. 4C). For short-duration fixations, the response was significantly higher than for longer durations ($P = 8.32 \times 10^{-19}$) and was statistically indistinguishable from the response when a distractor was at the fovea ($P = 0.165$, Wilcoxon signed-rank test; Fig. 4D). This is consistent with our hypothesis that responses in FEF are suppressed when the animal maintains fixation for longer durations.

All of the analyses presented so far utilized the responses aligned by the start of fixation when the animals made a saccade away from the RF of the neuron. Consistent with previous

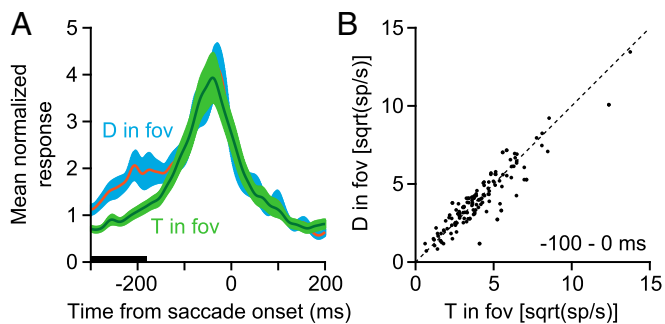


Fig. 5. (A) Mean normalized responses of 221 neurons during ongoing search aligned by saccade onset when the animal made a saccade toward the RF. The thickness of the traces represents the SEM, with N being the number of neurons in the population. The thick black trace on the x axis represents times at which the two traces were significantly different ($P < 0.01$, paired t test every millisecond). D, distractor. (B) Mean responses of single FEF neurons to a D at the fovea (fov) compared with a T at the fov during a 100-ms window starting 100 ms before saccade onset. sqrt(sp/s), square root of spike rate.

studies, when the animals made a saccade to the RF, the response of the population ramped up to the highest levels we measured (Fig. 5A). Notably, starting ~ 180 ms before the saccade was made, this movement-related activity was not affected by the identity of the stimulus at the fovea (thick black line on x axis, Fig. 5A; $P < 0.01$, paired t tests each millisecond). Looking at the activity in the 100-ms window leading up to the saccade, there was no significant difference in response as a function of what was currently at the fovea ($P = 0.978$, Wilcoxon signed-rank test; $n = 138$; Fig. 5B), and this was true even in the subset of neurons that showed a significant effect of object identity at the fovea in the ANOVA analysis described above ($P = 0.801$; $n = 71$). In addition, the saccade metrics were similar in both cases (details are provided in *SI Results*). Thus, in the time leading up to the saccade, the identity of the stimulus at the fovea no longer affects the movement-related activity or the movement itself, and the identity of the stimulus that will end up at the fovea starts to have an effect on responses in other locations away from the saccade goal (as shown in Fig. 3A).

Discussion

Here, we showed that the response to a stimulus in the RF was greatly affected by the properties of the stimulus at the fovea: When the animal maintained fixation on a stimulus that could be related to a reward for at least 350 ms, the response was strongly suppressed. This surprisingly strong effect appeared to be implemented by a gain control mechanism. This resulted in a robust response to a stimulus in the RF, but only when the animal was fixating a stimulus it would quickly move away from. These results fit with the idea of FEF as an oculomotor area that not only identifies where the next saccade should go but can also affect the flow of saccadic behavior.

Within the eye movement literature, the mechanisms thought to be important in driving the temporal flow of saccades are quite different depending upon the field of research. Within the field of reaction time analyses, particularly in decision making and visual search, and within the neurophysiology community, studies have primarily focused on models in which evidence is accumulated before an eye movement is triggered (21–23), including recent work in FEF (24, 25). However, these studies almost all involve eye movements that are punished or rewarded based on whether the eyes go to the correct stimulus. Given that this does not generally occur in natural behavior, it is unclear whether such mechanisms are involved in generating eye movements in unrestrained conditions; indeed, when animals were

allowed to move their eyes freely, we previously found that a saccade was generated ~ 50 ms after a peak of activity emerged in LIP (26) rather than when the activity reached a threshold response (27).

On the other hand, within the reading (9, 16) and scene perception (14, 28) communities, it has long been thought that at least part of the intersaccadic interval is due to a suppressive mechanism that keeps the eyes from moving away from items of interest. Models of these eye movements usually include a mechanism in addition to the suppressive mechanism to affect fixation duration, which can include an adaptive timer (13) or an accumulator mechanism (15). Our data bridge the divide between these two communities of oculomotor research by clearly showing that activity in FEF can be suppressed in a way consistent with these models and indicate that this mechanism, which is necessary to describe fixation durations in natural behavior, is present in the brain. In doing so, we validate these models at the neural level, while showing the neurophysiological field that understanding when a saccade will occur depends on more than accumulators alone. Indeed, whether the suppression mechanism in natural viewing works in concert with accumulator mechanisms, as suggested by Tatler et al. (15), or whether there is an alternative mechanism that allows saccades to go to locations of high priority after a timer expires (13) or a peak emerges (26) is yet to be determined.

Although it is not possible to pinpoint the exact origins of this modulatory signal in such a free parameter task, the phenomenological value of this observation is not changed. Considering that most of the neurons showed no interaction between the modulation of the RF and fovea, this gain-based mechanism can easily represent both inside and outside RF parameters, such as salience (29) or task relevance (30), although it is unlikely that reward modulation itself causes this effect, since reward modulation in FEF has been reported to be spatially selective and nonsignificant outside the RF (31, 32). The fact that both signals are evident in the response suggests that the activity represents the integration of eye movement priority signals, such as shown in LIP (17, 33), with ongoing cognitive control to fine-tune the flow of eye movements.

It may be noted that the difference in response between a T and a distractor in the RF (Fig. 1B) occurs later and is not quite as strong as shown in some previous studies (18, 34, 35). This is due to our choice of comparing the responses on trials in which a saccade was not made to the T in the RF. A similarly small difference can be seen when comparing across conditions in FEF (4) and has been shown in LIP when comparing the responses of targets and distractors when a saccade is made outside of the RF (36) compared with when it is made toward the RF (26).

Our results can also be seen as a multiplexing scheme that integrates multiple factors into a neural code that controls eye movement patterns. In this scheme, the priority of the motor movement is defined by the final readout, but the parameters of the decision are also decodable. Although the task we presented here was relatively simple, with two categories of objects and one level of reward, we hypothesize that the results may be extended to more complex situations. Therefore, a contingency of multiple layers of stimulus identity and reward value related to eye movements could be multiplexed with a gain change mechanism as suggested in other brain areas (37). This kind of coding scheme would not only make the cortical representations more efficient and condensed but could also be beneficial in solving the dynamic relationship between the current task state in general and a focal object as the goal of the eye movement during strategic planning. In addition, having different levels of gain can be used as the source of diverse top-down modulations on other cortical areas independent of eye movement execution.

Methods

Details can be found in the *SI Methods*. All experiments were approved by the Chancellor's Animal Research Committee at University of California, Los Angeles as complying with the guidelines established in the Public Health Service *Guide for the Care and Use of Laboratory Animals* (38). Electrophysiological recordings were made from two rhesus monkeys, which were trained on a standard memory-guided saccade task and the visual foraging

search task (Fig. 1A). Single-unit activity was analyzed during fixations in which there was a single object inside the RF and the animal was foveating an object.

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