Title: Inhibitory tagging both speeds and strengthens saccade target selection in the superior colliculus during visual search

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ABSTRACT

It has been suggested that, during difficult visual-search tasks involving time pressure and multiple saccades, inhibitory tagging helps to facilitate efficient saccade target selection by inhibiting saccades to objects in the scene once they have been searched and rejected. The superior colliculus (SC) is a midbrain structure that is involved in target selection, and recent findings suggest an influence of inhibitory tagging on activity in the SC. Precisely how, and by how much, inhibitory tagging affects target selection by SC neurons, however, is unclear. The purpose of this study, therefore, was to characterize and quantify the influence of inhibitory tagging on target selection in the SC. Rhesus monkeys performed a relatively difficult visual-search task involving time pressure and multiple saccades. During the task, target selection by SC neurons was both more rapid and more robust—as quantified via shifts in selection metrics derived from temporal receiver operating characteristic analyses—when an uninspected saccade-target object was selected from among inspected, as opposed to uninspected, objects in the display. This suggests that inhibitory tagging both speeds and strengthens saccade target selection at the level of individual SC neurons. The results provide constraints on models of target selection based on SC activity.

NEW AND NOTEWORTHY

An important aspect of efficient behavior during difficult, time-limited visual search is the efficient selection of sequential saccade targets. Recent findings suggest that inhibitory tagging may help to facilitate such efficient selection by modulating activity in the superior colliculus (SC). Here, we characterize and quantify the influence of this modulation and find that inhibitory tagging both speeds and strengthens saccade target selection at the level of individual SC neurons.

INTRODUCTION

Our daily lives are replete with examples of visual-search tasks that we need to complete efficiently. Under time pressure, we execute saccade sequences, interleaved with brief fixations, as a means to search the visual scene for a particular object of interest. In such contexts, an important aspect of efficiency is the selection of behaviorally relevant saccade targets, meaning objects in the visual scene that could plausibly be the particular object of interest. It has been suggested that inhibitory tagging may help to facilitate such efficient selection by inhibiting saccades to irrelevant objects once they have been searched and rejected (1-7).

In a recent study, we reported evidence of an influence of inhibitory tagging on the activity of individual neurons in the superior colliculus (SC) (8), a midbrain structure that is involved in saccade target selection (9-26). More specifically, we reported evidence that, during a difficult visual-search task involving time pressure and multiple saccades, the visually evoked activity of many SC neurons was lower when the objects in their response fields (RFs) had been previously fixated relative to when they had not. The largest effects of inhibitory tagging, moreover, were observed in the subset of SC neurons that had response properties consistent with a role in saccade target selection, suggesting that a modulation of the selection process at the level of individual selection-relevant neurons may provide the mechanism by which inhibitory tagging supports efficient search behavior. Precisely how, and by how much, inhibitory tagging affects target selection in the SC, however, is unclear, as we did not examine, much less quantify, the selection process in our recent study of inhibitory tagging.

The purpose of this study, therefore, was to extend our previous work and to characterize and quantify the influence of inhibitory tagging on target selection by SC neurons. As an approach, we used receiver operating characteristic (ROC) analyses based on signal detection theory (27), which have been used in numerous previous studies of visual perception, target selection, and, in particular, target selection in the SC (11-14, 18, 20, 21, 23, 26), to quantify the time course of target selection, as well as the strength of selection signals, in individual SC neurons both before and after inhibitory tagging. We reasoned that, if a modulation of the selection process at the level of individual SC neurons provides the mechanism by which inhibitory tagging supports efficient search behavior, inhibitory tagging should affect the dynamics of the selection process and/or the strength of selection signals carried by the subset of SC neurons that are involved in target selection. As will be seen, this is what we found.

METHODS

Details of the behavioral and physiological procedures can be found in our recent report (8). Briefly, we used standard methods to record the activity of individual SC neurons in two male rhesus monkeys (*Macaca mulatta*). While we recorded the activity of each neuron, the monkey performed two behavioral tasks for liquid reward: a delayed-saccade task and a visual-search task, in that order. Experimental protocols were approved by the Institutional Animal Care and Use Committee at SUNY College of Optometry and complied with the guidelines of the US Public Health Service policy on Humane Care and Use of Laboratory Animals.

At the beginning of each trial of the delayed-saccade task, a red or green disc appeared at the center of the monitor. The monkey was required to fixate this central disc for 450-650 ms, at which point a red or green target disc appeared at a peripheral location. Following the appearance of the target disc, the monkey was required to fixate the central disc for an additional 500-700 ms, at which point the central disc disappeared. The monkey was rewarded for making a saccade to the target disc within 70-400 ms. All discs subtended 0.5-2.0° of visual angle and had luminances of 12 cd/m^2. The luminance of the monitor's background was 0.3 cd/m^2. The color of the target disc always differed from that of the central disc, was randomly selected at the beginning of each recording session, and was fixed throughout each recording session. The location of the target disc was systematically varied to determine the RF of the neuron understudy. The location that yielded the highest level of visual and/or motor activity was taken as the RF center.

At the beginning of each trial of the visual-search task, a red or green disc appeared at the center of the monitor. The monkey was required to fixate this central disc for 500 ms, at which point the search array appeared. The array consisted of multiple red and green discs positioned at the intersection points of an invisible grid centered on the central disc. One (or occasionally more than one) of the discs in the array (never the central disc) held a reward, meaning that, when fixated, a liquid reward was administered (immediately) to the monkey. The color of the reward-bearing disc(s) always differed from the color of the central disc and, within a session, was the same as the color of the target disc in the delayed-saccade task. Following the appearance of the array, the monkey had eight seconds to locate the reward-bearing disc(s). If the monkey

fixated all reward-bearing discs during this eight-second window (for trials on which there was more than one reward-bearing disc, a reward was administered only once upon fixation of each disc), the trial ended. Otherwise, the monkey did not receive a reward. For each neuron, the array was configured such that when the monkey fixated one of the discs, a nearby disc was at the center of the RF. For most neurons, this positioning scheme permitted the use of a five-by-five rectangular array, consisting of nine potentially reward-bearing and 16 not potentially reward-bearing discs. For some neurons with large RF eccentricities, the array consisted of fewer discs. For these neurons, attempts were made to maintain the same ratio of potentially reward-bearing to not-potentially reward-bearing discs. On each trial, the locations of the potentially reward-bearing and not-potentially reward-bearing discs were randomly selected. The sizes and luminances of the discs as well as the luminance of the monitor's background were the same as in the delayed-saccade task.

Data analysis

As noted in the Introduction, the purpose of this study was to examine the influence of inhibitory tagging on target selection by SC neurons. As such, we focused our analyses on neurons that exhibited significant delay-period ("prelude" or "buildup") activity in the delayed-saccade task, because SC neurons that are involved in saccade target selection tend to exhibit this type of activity (9, 10, 11-14, 20, 23, 26, 27). To determine if a particular neuron exhibited significant prelude activity in the delayed-saccade task, we compared its activity during a 100-ms window beginning 300-ms after the onset of the target (i.e., its delay-period activity) to its activity during a baseline 100-ms window beginning 100-ms before the onset of the target. Only trials on which the target was

positioned at the RF center were considered. If the delay-period activity was significantly greater than the baseline activity (Wilcoxon rank-sum test, α = 0.05), the neuron was categorized as having significant prelude activity and was included in subsequent analyses.

For the search task, a fixation was defined as the period between subsequent saccades. The activity of each neuron was analyzed separately for three categories of fixation, defined based on the fixation status of the disc at the center of the RF [previously fixated (PF) or not previously fixated (NPF) on the same trial] and whether or not it was selected as the target of the subsequent saccade: (1) fixations on which the RF disc had not been previously fixated and was selected as the target of the subsequent saccade (NPF-in-RF, saccade-towards fixations); (2) fixations on which the RF disc had not been previously fixated and was not selected as the target of the subsequent saccade (NPF-in-RF, saccade-away fixations); and (3) fixations on which the RF disc had been previously fixated and was not selected as the target of the subsequent saccade (PF-in-RF, saccade-away fixations). In addition to the requirement of significant prelude activity, a neuron was only included in further analyses if its activity was recorded on more than five fixations for each of these three categories. The initial fixation on each trial did not count towards this criterion and, moreover, this fixation was not included in any analysis. Schematic illustrations of the search task, the search array, a typical saccade sequence, and the three categories of fixation are shown in Fig. 1.

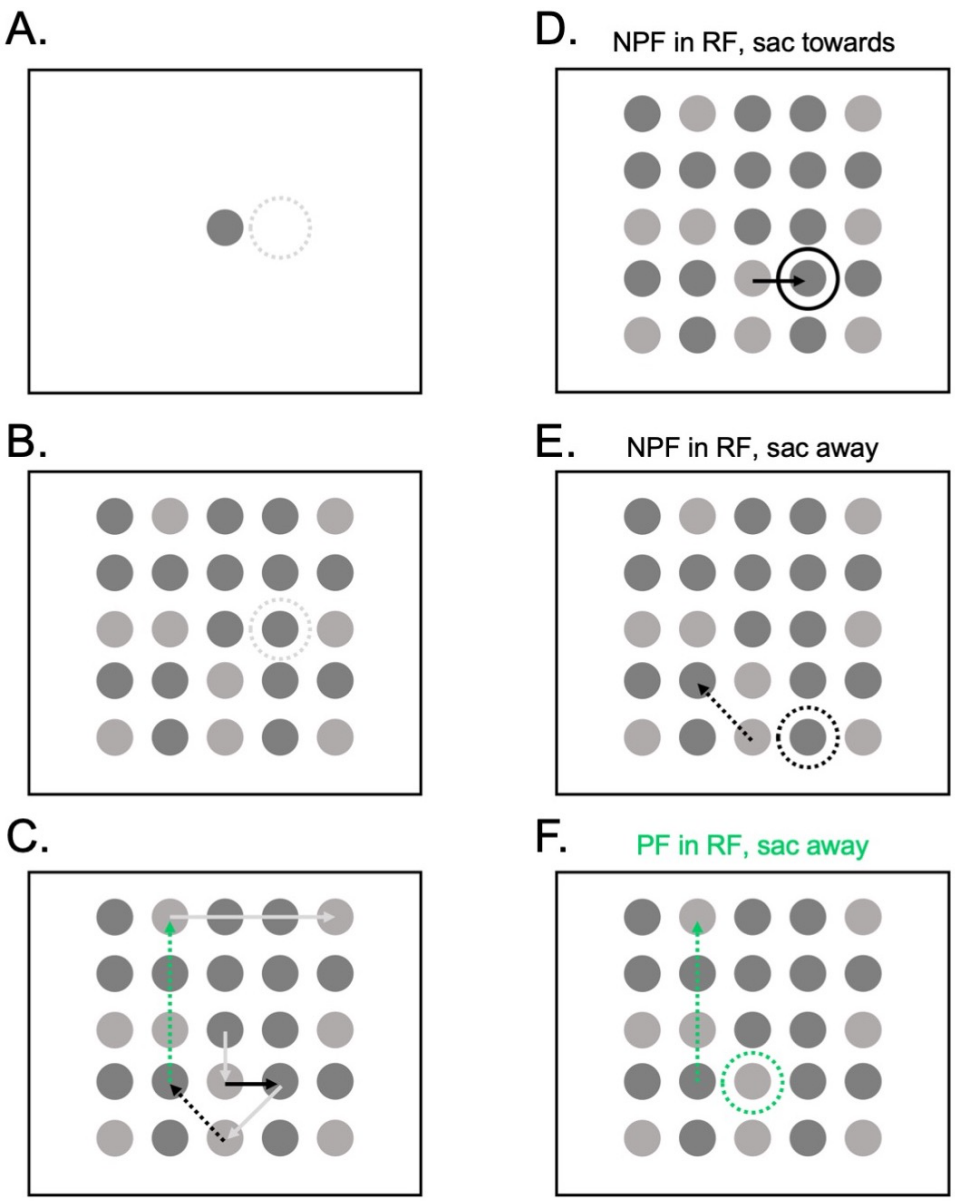


FIG. 1: Schematic illustrations of the search task, the search array, a typical saccade sequence, and the three categories of fixation. **A.** Each trial of the search task began with the appearance of a disc positioned at the center of the display, which the monkey was required to fixate for 500 ms. **B.** The search array then appeared on the screen. At fixation, the response field (RF) of the neuron under study, illustrated here and in panel A as a dotted gray circle, overlapped a nearby disc. One of the discs (and sometimes more than one of the discs) in the array held a reward. In the trial illustrated in this

figure, let us assume that the disc in the upper-right corner of the array held the reward. The monkey's task was to search the array and fixate the reward-bearing disc. **C.** Because the reward-bearing disc was only indicated by its color, which it shared with many other discs in the array, fixation of the reward-bearing disc typically entailed a sequence of multiple saccades. This panel schematizes a situation where fixation of the reward-bearing disc was preceded by six saccades. Each arrow represents a saccade vector. Our analyses focused on three categories of fixation: **D.** fixations on which the disc in the RF had not been previously fixated on the same trial [i.e., not previously fixated (NPF)] and was selected as the target of the subsequent saccade (sac) (NPF-in-RF, sac towards), **E.** fixations on which the disc in the RF had not been previously fixated on the same trial and was not selected as the target of the subsequent saccade (NPF-in-RF, sac away), and **F.** fixations on which the disc in the RF had been previously fixated (PF) on the same trial and was not selected as the target of the subsequent saccade (PF-in-RF, sac away). In **D-F**, the arrow gives the vector of the subsequent saccade, whereas the black and green circles give the RF during fixation. Note that, in the actual experiment, the discs in the array were red and green (illustrated here as different shades of gray), and the color of the central disc served to cue the monkey to the color of the reward-bearing disc.

We recorded the activity of 113 neurons across the two monkeys. Of these, 65 met our inclusion criteria. For each neuron, spike-density functions were created by convolving individual spikes with a Gaussian kernel (σ = 10 ms) and two ROC analyses

were performed. The first compared the activity on NPF-in-RF, saccade-towards fixations to the activity on NPF-in-RF, saccade-away fixations. We refer to this as the NPF-re-NPF analysis. The other compared the activity on NPF-in-RF, saccade-towards fixations to the activity on PF-in-RF, saccade-away fixations. We refer to this as the NPF-re-PF analysis. Note that the only difference between the two analyses was the fixation status of the RF disc on saccade-away fixations and so any differences in the results can be attributed to inhibitory tagging. For both analyses, activity was aligned on both fixation onset and offset. An ROC curve was then computed at each ms by comparing the distribution of activity (across fixations) on NPF-in-RF, saccade-towards fixations to the distribution of activity on saccade-away fixations (NPF-in-RF or PF-in-RF, depending on the analysis). An ROC area was computed at each ms by integrating the area under the ROC curve. ROC areas were bounded between 0.0 and 1.0 and provided an estimate of the degree to which the two distributions overlapped. An ROC area of 0.5 indicated complete overlap, areas closer to 1.0 indicated greater levels of activity on saccade-towards fixations, and areas closer to 0.0 indicated greater levels of activity on saccade-away fixations. Thus, areas greater than 0.5 were suggestive of saccade target selection, whereas those equal to or less than 0.5 were not.

For both ROC analyses and alignments, we obtained two selection metrics: discrimination time and magnitude. Discrimination time was defined as the earliest time at which saccade-towards activity was significantly greater than saccade-away activity and stayed that way for a particular duration. Significance was determined by performing a permutation test (2,000 iterations) on the ROC curve (11, 12, 18, 23, 29) and was assessed at each ms beginning 50 ms before and ending 150 ms after fixation

onset for the fixation-onset alignment or beginning 150 ms before and ending with fixation offset for the fixation-offset alignment. For the fixation-onset alignment, discrimination time was taken as the first time point within the analysis window at which the permutation test indicated that the ROC area was significantly different from 0.5 ($P < .05$), the mean saccade-towards activity was greater than the mean saccade-away activity, and both of these conditions were met for at least 20 consecutive ms. For the fixation-offset alignment, discrimination time was taken as the first time point within the analysis window at which the permutation test indicated that the ROC area was significantly different from 0.5 and the mean saccade-towards activity was greater than the mean saccade-away activity for all remaining time points until the onset of the saccade. For each analysis and alignment, discrimination magnitude was taken simply as the maximum (max) ROC area within the analysis window. Statistical comparisons of discrimination times and magnitudes were accomplished using Wilcoxon signed-rank tests ($\alpha = 0.05$).

RESULTS

The results for an example neuron are shown in Fig. 2. Focusing first on the activity associated with RF objects that had not yet been searched nor rejected, it can be seen that, for the example neuron, activity was higher on fixations on which the object at the center of the RF was (Fig. 2A, solid-black trace), versus was not (Fig. 2A, dotted-black trace), selected as the target of the subsequent saccade. The difference emerged shortly following fixation onset (the fixation-onset-aligned discrimination time for the NPF-re-NPF analysis was 53 ms relative to fixation onset; Fig. 2B, left column, vertical

dotted black line), well before fixation offset (the fixation-offset-aligned discrimination time for the NPF-re-NPF analysis was -112 ms relative to fixation offset; Fig. 2B, right column, vertical dotted black line), and persisted throughout the full fixation duration. The discrimination magnitude was large as well (the fixation-onset- and -offset-aligned max-ROC areas for the NPF-re-NPF analysis were 0.76 and 0.83, respectively; Fig. 2B, solid-black traces). Thus, the pattern of activity exhibited by the example neuron was consistent with the notion that this neuron played a role in saccade target selection, at least when both the target and nontarget objects had not yet been searched nor rejected.

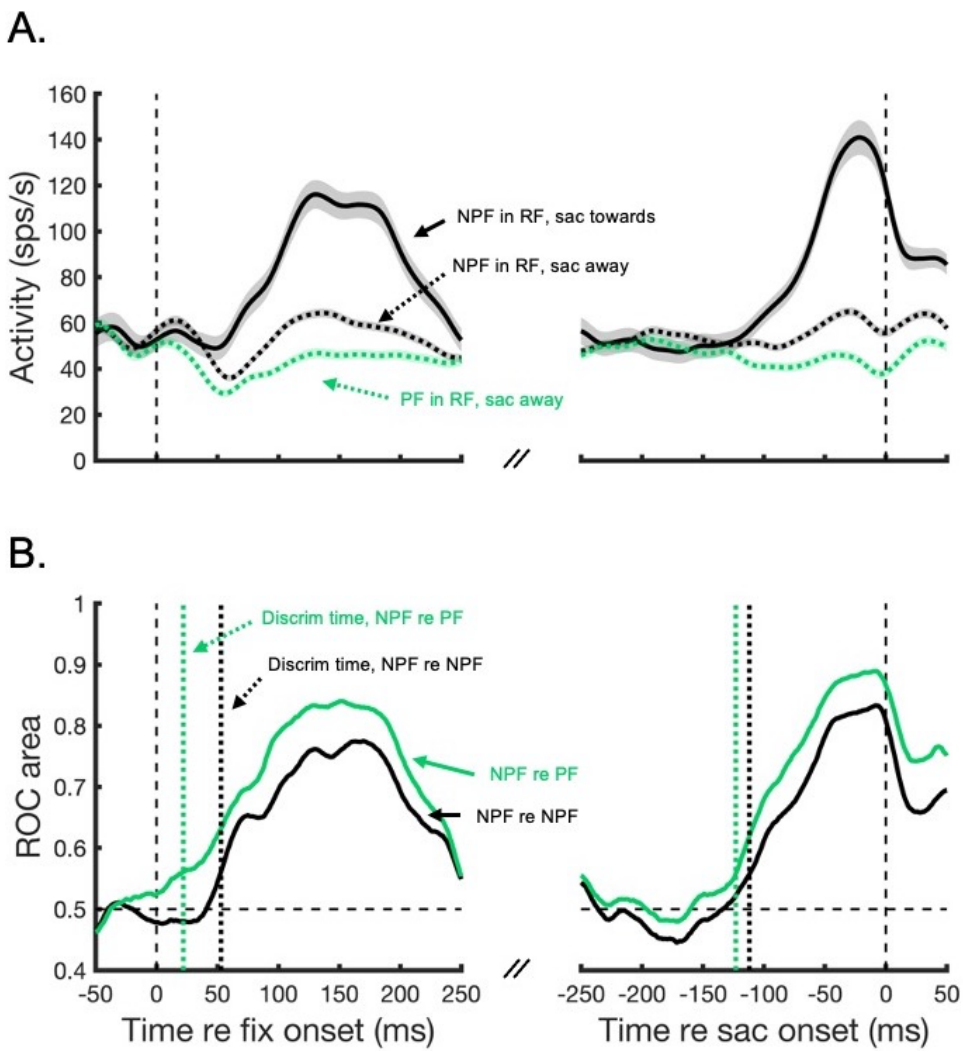


FIG. 2: Activity and ROC area functions for an example SC neuron. **A.** Mean fixation-onset- (left panel) and -offset- (right panel) -aligned spike-density functions. Different traces show activity for different categories of fixation: the solid black trace shows the activity on NPF-in-RF saccade-towards fixations, the dotted black trace shows the activity on NPF-in-RF saccade-away fixations, and the dotted green trace shows the activity on PF-in-RF saccade-away fixations. Each trace represents the mean activity across all fixations in the relevant category, and the shaded region represents +/-1 standard error of the mean across fixations. **B.** Fixation-onset- (left panel) and -offset- (right panel) -aligned ROC area functions for the same neuron. The black trace shows

the results of the NPF-re-NPF analysis, whereas the green trace shows the results of the NPF-re-PF analysis. The vertical dotted black and green lines show the discrimination (discrim) times for the NPF-re-NPF and NPF-re-PF ROC analyses, respectively.

Moreover, the visually evoked activity of the example neuron was affected by the placement of inhibitory tags (i.e., this neuron exhibited lower levels of activity on saccade-away fixations on which there was a previously fixated, rather than not previously fixated, object in its RF; Fig. 2A dotted green versus dotted-black traces; cf. Conroy et al., 2023), and this influence, in turn, affected the dynamics and strength of saccade target selection. That is, for the example neuron, target selection was both more rapid and more robust (i.e., discrimination times were shorter and discrimination magnitudes were larger) when an uninspected saccade-target object (i.e., a not previously fixated object) was selected from among inspected (i.e., searched and rejected) as opposed to uninspected objects in the display. As noted above, for the fixation-onset-aligned NPF-re-NPF analysis, the discrimination time was 53 ms relative to fixation onset, and the discrimination magnitude was 0.76. For the same alignment, the discrimination time decreased to 22 ms and the discrimination magnitude increased to 0.84 for the NPF-re-PF analysis. A decrease in discrimination time (from -112 ms to -123 ms for the NPF-re-NPF to NF-re-PF analysis) and increase in discrimination magnitude (from 0.83 to 0.89 for the NPF-re-NPF to NF-re-PF analysis) occurred for the fixation-offset-aligned analysis as well.

A decrease in discrimination times and increase in discrimination magnitudes after inhibitory tagging was evident for many of the neurons in our sample. Figure 3 shows the fixation-onset-aligned target-selection metrics for the 51 (of 65) neurons that selected the saccade target during the fixation-onset-aligned analysis window (i.e., that yielded a fixation-onset-aligned discrimination time for both the NPF-re-NPF and NPF-re-PF analyses). For these neurons and alignment, the median discrimination time was significantly shorter for the NPF-re-PF than NPF-re-NPF analysis (33 versus 49 ms relative to fixation onset; $Z = -3.953$; $P < .001$; Fig. 3A-B). Indeed, for the NPF-re-PF analysis, many neurons exhibited very early discrimination times, with a substantial number selecting the saccade target even before fixation onset and/or the visual-afferent delay. Such predictive saccade target selection has been reported previously by SC neurons (27) and, in the case of the NPF-re-PF analysis, is consistent with a remapping of inhibitory-tagging across saccades (cf. Refs 8, 30, 31). Note that, in our analysis, the earliest-possible discrimination time was -50 ms relative to fixation onset because that was the earliest time point at which an ROC curve was computed. As such, inhibitory tagging may have an even greater influence on the dynamics of target selection than is evident from Fig. 3.

For the same subset of 51 neurons, the median discrimination magnitude for the fixation-onset alignment was higher for the NPF-re-PF than NPF-re-NPF analysis (0.79 versus 0.73; $Z = 5.521$; $P < .001$; Fig. 3C-D), and, for the 48 neurons that selected the saccade target during the fixation-offset-aligned analysis window, we observed the same basic effect of inhibitory tagging on the dynamics and strength of saccade target selection: the median discrimination time was shorter (-113 versus -97 ms relative to

fixation offset; Z = -2.962; P = .003; Fig. 4A-B) and the median discrimination magnitude was larger (0.83 versus 0.79; Z = 4.636 P < .001; Fig. 4C-D) for the NPF-re-PF than NPF-re-NPF analysis. Moreover, the color of the RF disc—meaning, its color in the context of the task: potentially reward bearing or not—did not influence this general pattern of results. To confirm this, we performed the same ROC analyses on a restricted dataset including only fixations on which the RF object was potentially reward bearing on that trial [i.e., had the same color as the reward-bearing disc(s)] and found that, after inhibitory tagging, there was a decrease in discrimination times and increase in discrimination magnitudes for both the fixation-onset and -offset alignments. For the 45 neurons from this restricted dataset that selected the saccade target during the fixation-onset-aligned analysis window discrimination times decreased from 62 ms to 27 ms relative to fixation onset (Z = -4.632; P < .001) and discrimination magnitudes increased from 0.74 to 0.80 (Z = 4.984; P < .001) for the NPF-re-NPF to NPF-re-PF analysis. For the 41 neurons that selected the saccade target during the fixation-offset-aligned analysis window, discrimination times decreased from -70 ms to -97 ms relative to fixation offset (Z = -3.630; P < .001) and discrimination magnitudes increased from 0.81 to 0.84 (Z = 4.970; P < .001). We also performed the ROC analyses on a restricted dataset including only fixations on which the RF object was not potentially reward bearing and found a significant decrease in discrimination times (from 59 to 45 ms relative to fixation onset for the NPF-re-NPF relative to the NPF-re-PF analysis; Z = -2.245; P = .025) and increase in discrimination magnitudes (from 0.75 to 0.81 for the NPF-re-NPF relative to the NPF-re-PF analysis; Z = 4.128; P < .001) for the 35 neurons that selected the saccade target during the fixation-onset-aligned analysis window, a

significant increase in discrimination magnitudes (from 0.80 to 0.85 for the NPF-re-NPF to NPF-re-PF analysis; $Z = 3.259$; $P = .001$) for the 35 neurons that selected the saccade target during the fixation-offset-aligned analysis window, and clear trend towards a decrease in discrimination times (from -74 to -91 relative to fixation offset for the NPF-re-NPF relative to NPF-re-PF analysis; $Z = -1.936$; $P = .053$) for the same 35 neurons. Thus, taken together, the results suggest that inhibitory tagging both speeds and strengthens saccade target selection at the level of individual SC neurons.

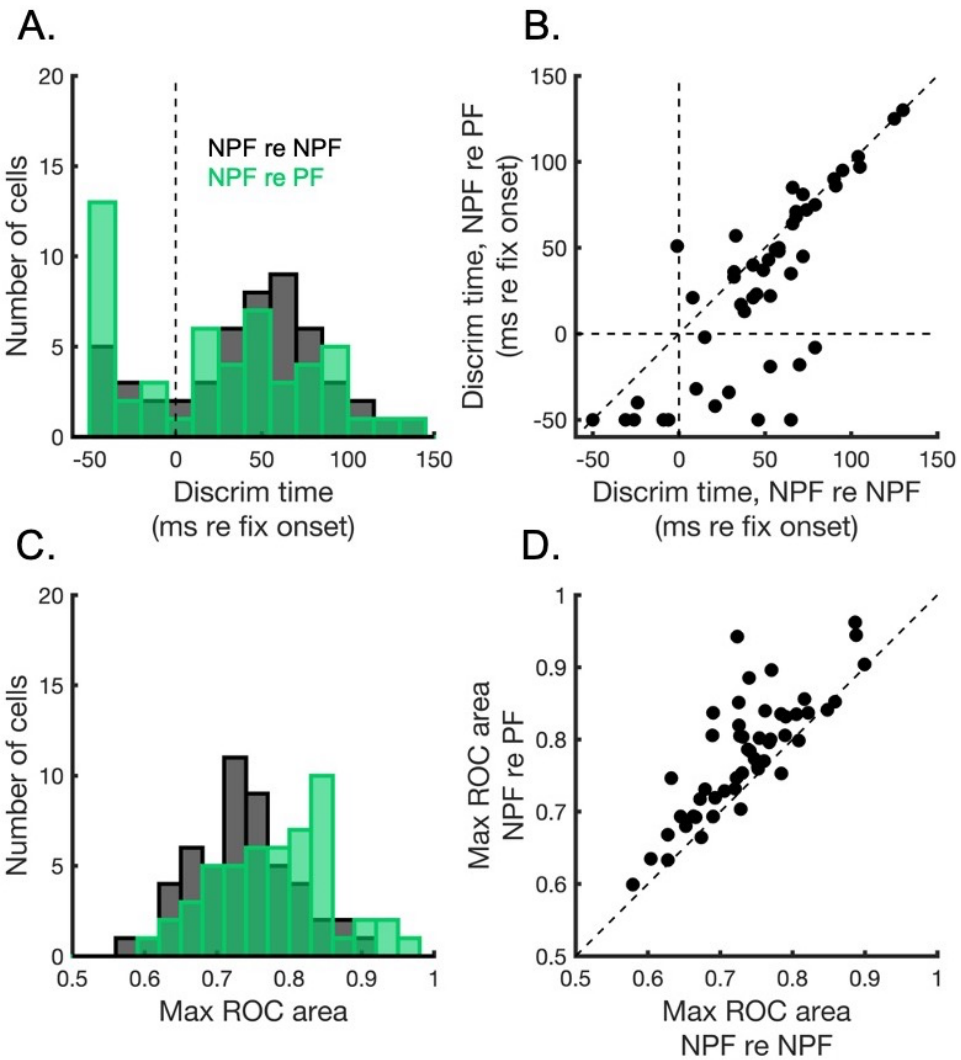
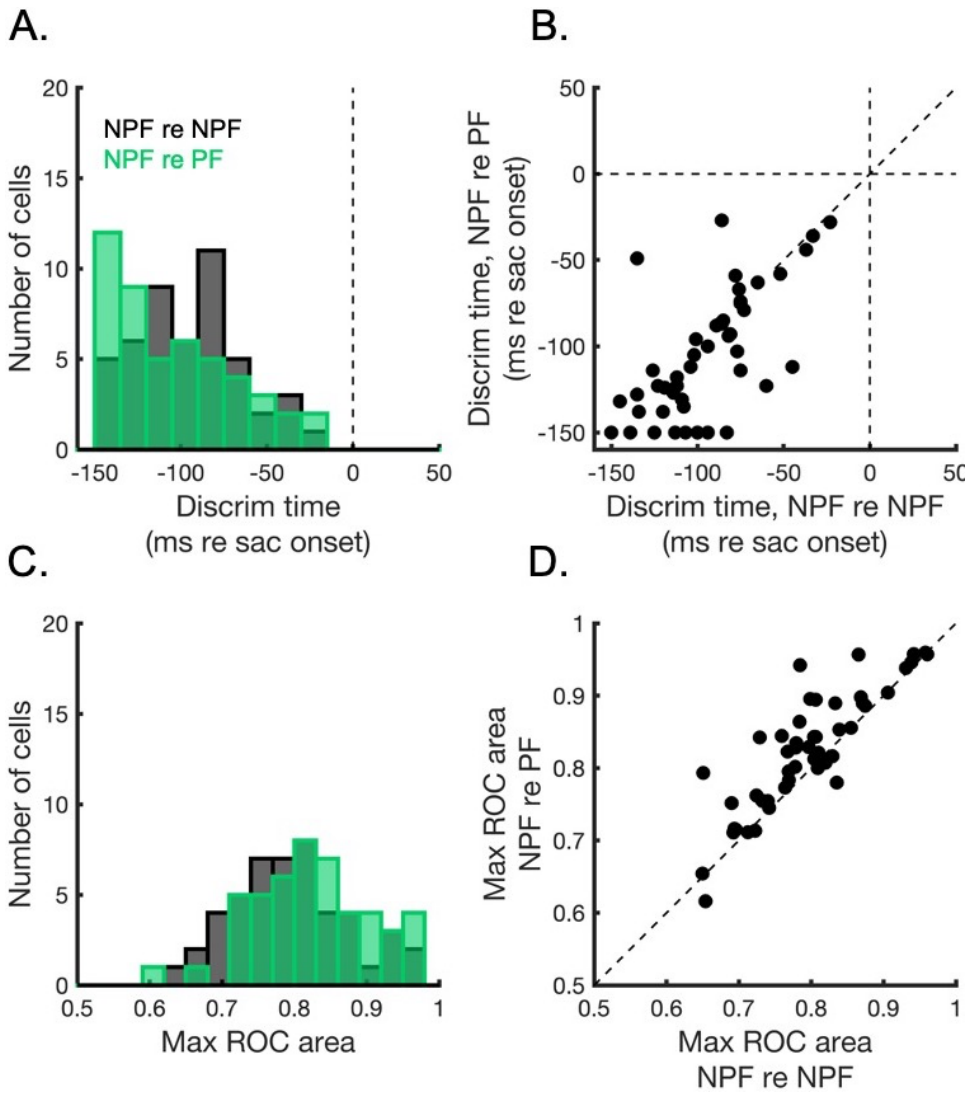


FIG. 3: Summary of the fixation-onset-aligned target-selection metrics (discrimination times and magnitudes) for the 51 of 65 neurons in our sample that selected the saccade target within the fixation-onset-aligned analysis window (-50-150 ms relative to fixation onset) for both the NPF-re-NPF and NPF-re-PF analyses. **A.** Distributions of discrimination times for the two ROC analyses. The black and green bars give the distributions for the NPF-re-NPF and NPF-re-PF analyses, respectively. Note that -50 ms relative to fixation onset was the earliest possible discrimination time given the analysis window. **B.** Relationship between NPF-re-PF and NPF-re-NPF discrimination times for individual neurons (individual symbols). **C.** Distributions of discrimination magnitudes for the NPF-re-NPF (black bars) and NPF-re-PF (green bars) analyses. **D.** Relationship between NPF-re-PF and NPF-re-NPF discrimination magnitudes for individual neurons (individual symbols).



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347 **FIG. 4:** Summary of the fixation-offset-aligned target-selection metrics for the 48 of 65
348 neurons in our sample that discriminated the saccade target within the fixation-offset-
349 aligned analysis window (-150-0 ms relative to fixation offset) for both the NPF-re-NPF
350 and NPF-re-PF analyses. Otherwise, what is shown in each panel corresponds to what
351 is shown in Fig. 3 and the plotting conventions are the same. Note that, for the fixation-
352 offset-aligned discrimination times, however, the earliest possible discrimination time
353 was -150 ms.

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DISCUSSION

Saccade target selection involves a competition between representations of potential saccade plans on the SC visuomotor map. An inhibitory-tagging mechanism that seeks to facilitate efficient selection would be expected to affect this competitive process by reducing the activity associated with particular saccade plans—specifically, those that would move the eyes towards objects in the scene that have already been searched and rejected—and increasing the relative level of activity associated with others—specifically, those that would move the eyes towards objects in the scene that have not yet been searched nor rejected. Previously, we showed this basic pattern of modulations after inhibitory tagging in the SC (8), and, here, we characterized and quantified the influence of these modulations on target selection by SC neurons. Using ROC analyses, We found that inhibitory tagging both speeds and strengthens saccade target selection at the level of individual SC neurons, yielding significantly shorter target-nontarget discrimination times and significantly larger target-nontarget discrimination magnitudes in the subset of SC neurons that were likely involved in saccade target selection. Thus, we conclude that modulations of the selection process at the level of individual SC neurons may provide the mechanism by which inhibitory tagging supports efficient search behavior. Models of target selection based on SC (or, more generally, neural-priority-map) activity (e.g., Ref 32) may wish to take these modulations into account to more accurately capture the dynamics of the selection process during difficult, time-limited search.

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