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Supporting Online Material for

Selective Attention from Voluntary Control of Neurons in Prefrontal Cortex

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Materials and Methods

We trained monkeys to operantly control the activity of single or multiple frontal eye field (FEF) neurons in the absence of saccadic eye movements and visual stimulation using auditory “neurofeedback.” Two male monkeys (*Macaca mulatta*) weighing 11 kg (Monkey B) and 9 kg (Monkey C) were used as subjects in these experiments. All surgical and behavioral procedures were approved by the Stanford University Administrative Panel on Laboratory Animal Care and the consultant veterinarian, and were in accordance with National Institutes of Health and Society for Neuroscience guidelines. Each animal was surgically implanted with a head post, a scleral eye coil, and a titanium recording chamber.

Electrophysiological recording. Electrophysiological recording of FEF activity was done by lowering single tungsten electrodes (0.1–1.0 M Ω impedance measured at 1 kHz) into the recording chambers using a hydraulic microdrive. Prior to each experiment, an FEF site was localized with a separate behavioral paradigm based on the ability to evoke fixed-vector saccadic eye movements with electrical stimulation (100 ms trains of 200 Hz biphasic pulses with a 0.3 ms pulse duration) while the monkey fixated a central spot. Stimulation was delivered with a stimulator and two stimulation isolation units. The mean current threshold of all recording sites, defined as the current at which saccades were evoked on 50% of trials, was $31.8 \pm 1.6 \mu\text{A}$ (mean \pm s.e.m.). Each FEF site was then mapped using a standard visually guided delayed saccade task,

and the target location that elicited the most multiunit activity (MUA) aligned to the visual presentation or saccade was chosen as the center of that site's response field (RF). RFs were located in both the upper and lower visual hemifields of both monkeys, contralateral to the recording sites.

Multiunit activity and local field potentials (LFPs) were acquired using a Plexon Multichannel Acquisition Processor, and spike waveforms were saved for off-line sorting. Briefly, the global minima of all extracellular waveforms were first aligned, and waveforms were then sorted using their first three principal components.

Operant control task. The CORTEX system (v5.95) was used for behavioral data collection and experimental control. All visual stimuli were presented on an LCD video monitor (60 Hz) positioned 57 cm in front of the monkey. Monkeys were trained to fixate a small, central black spot on a neutral gray screen during trials lasting 3000-4000 ms. A drop of juice was given after each completed trial. Trials were aborted immediately if the monkey's gaze departed from a 2-3° diameter error window around the fixation spot. Eye position was sampled at 500 Hz using the scleral search coil method (S1,S2).

During operant control trials, the monkey received auditory feedback and juice rewards depending on the instantaneous firing rate of the recorded MUA. Calculation and production of the auditory feedback was controlled by a separate computer running Matlab. On each trial, real-time MUA was acquired using the Matlab Data Acquisition toolbox and a data acquisition card, beginning at the time the monkey acquired fixation. Auditory feedback was played through a speaker placed on the floor of the recording room, and was given in the form of discrete, pure tones lasting 300 ms each (400 ms for Monkey C), and updated every 300 ms (or 400 ms for Monkey C) throughout the operant control trial. The pitch of each tone was determined by counting the number of MUA spikes in a 500 ms window from 550 ms to 50 ms before the tone began. No feedback was given for activity prior to fixation, thus the first tone was played 550 ms

after fixation began. Feedback was stopped immediately if the monkey broke fixation during the trial. The monkey did not receive feedback between trials.

Auditory feedback followed the G major scale, with eight discrete tones from 392 to 784 Hz. Prior to the experiment, the baseline MUA level was observed and a “low threshold” and a “high threshold” were set according to the distribution of 500 ms spike counts in the absence of feedback. The low threshold was set at approximately the lowest tenth percentile of all 500 ms spike counts, and the high threshold was set at approximately the highest tenth percentile. During operant control trials, the lowest pitch (392 Hz) was played each time the spike count preceding a tone was at or below the low threshold, and the highest pitch (784 Hz) was played each time the spike count was at or above the high threshold. Intermediate spike counts were mapped linearly onto the eight note scale. For experiments with narrow or highly-skewed distributions of baseline MUA spike counts, integer threshold values would have resulted in too many threshold crossings: for example, if one-third of the MUA spike counts had 0 spikes, a low threshold of 0 would have resulted in very frequent low threshold crossings. In these experiments, a random number generator determined whether a threshold crossing would map onto the lowest pitch (and a reward) or the second-lowest pitch (and no reward), in order to keep the frequency of threshold crossings at approximately 10%.

Auditory feedback was calculated identically on Up and Down trials, but the delivery of juice rewards was dependent on the type of trial. On Up trials, a reward was delivered simultaneously with each and every high tone, whereas on Down trials the reward was delivered with each and every low tone. Blocks of 50-150 trials of each trial type were interleaved during an experimental session (mean of 4.84 blocks, minimum of 3, maximum of 6). The monkey received no explicit cue to signal the type of block (i.e., Up or Down), but instead learned through the association of tones and rewards.

Statistical tests. When not stated in the text, the following tests were used to determine statistical significance: t-tests were used for comparisons of firing rates during upward and downward operant control, and for distributions of control indices. ANOVAs were used to identify experiments with individually significant voluntary control, as described below. Correlations were done using linear regression. Non-parametric Wilcoxon sign-rank tests were used to test for differences between paired distributions of LFP power, regression coefficients, and stimulus-driven FEF responses. Proportions of saccades were compared using chi-square tests.

Analysis of voluntary neuronal control. Multi- and single-unit activity was analyzed to determine the extent to which the monkey could voluntarily control FEF firing rates through the operant control task. Firing rate calculations excluded the last 500 ms of each trial in order to avoid any anticipatory activity related to eye movements away from fixation following the completion of each trial. In order to quantify the extent of neuronal control, we used a control index (CI) defined as the following:

$$CI = (U-D)/(U+D)$$

where U is the mean firing rate on Up trials, and D is the mean firing rate on Down trials.

To determine the statistical significance of neuronal control during a single experiment, spikes on each trial were binned into 500 ms intervals, and a two-way ANOVA was conducted over all of the bins to determine whether there was a main effect on the spike counts of (i) control direction (Up versus Down), and/or (ii) time during the trial (early in the trial versus late), or an interaction between the two. An experiment was said to show a significant effect of voluntary control on firing rate if the ANOVA yielded a significant main effect of control direction (at a significance level of $P < 0.05$), or a significant interaction term ($P < 0.05$), indicating that the control direction differentially affected how firing rates changed over the course of the trial. In determining whether the number of MUA sites (or single neurons)

significantly modulated by neuronal control was greater than that expected by chance, we used a conservative estimate of the likelihood that the ANOVA would classify the experiment as significant by chance (i.e., the Type I error). If the main effect of control direction and the interaction effect were independent, the likelihood of a false positive classification on at least one of the two tests would be

$$1 - (1 - 0.05)^2 = 0.0975$$

Because the tests are not in fact independent, the use of this value overestimates the number of significant classifications predicted by chance. Thus, our calculation indicating that the actual number of significant MUA sites and neurons is greater than that expected by chance is conservative.

Analysis of LFP power. LFPs were recorded at 89 of the 94 FEF sites by low-pass filtering the neural signal at 300 Hz. Signals were sampled and stored at 1 kHz or 5 kHz. To exclude LFP modulation associated with saccades before and after the trial, only data beginning 300 ms after fixation and ending 300 ms before the end of the trial were used for spectral analysis. For each experiment, power spectra were calculated for each trial similarly to (S3), using Welch's method with overlapping Hamming windows. Calculating the multi-taper spectrum (S4) gave similar results. The mean LFP power across trials was then calculated for four frequency bands of interest: theta (4-8 Hz), alpha (8-13 Hz), beta (13-30 Hz), and gamma (30-70 Hz).

Visual search probe trials. Approximately one-third of the operant control trials were interrupted by a visual search probe trial designed to test the perceptual and neurophysiological consequences of voluntary control. No probes occurred during the first 10 operant control trials after a block transition, and probe trials did not occur during two consecutive operant control trials. Probe trials were analyzed from 82 of the 94 total operant control experiments. In all 82 experiments, probe trial performance was greater than 67% correct. The remaining 12

experiments had no probe trials at all, lacked one or more type of probe trial, or came while the monkey was still learning the visual search probe task and had inadequate performance to allow for analysis of correct probe trials.

Probe trials began at a random time from 300-1500 ms into an operant control trial, while the monkey received feedback about the MUA at the FEF recording site. When a probe trial began, auditory feedback was immediately stopped, and the monkey no longer received juice rewards for reaching the high or low thresholds. A visual search array of three stimuli appeared on the screen, with one stimulus within the controlled neurons' RF, and the other two stimuli at equal eccentricity and evenly spaced around the screen. The exact positions of all stimuli were calculated relative to the direction of gaze at the time of the search array onset, to account for the possibility of small deviations in the gaze direction from the fixation spot.

The monkey was trained to find, and direct a saccadic eye movement toward, the search target, which was a 3° by 0.2° black bar of any orientation. The other stimuli were distracters chosen randomly from a set of seven stimuli: a circle, square, ring, star, diamond, triangle, and ellipse. All distracter stimuli were black and similar in area to the search target. 75% of probe trials were *search trials*, in which the search target was present at one of the three stimulus locations. Each location was equally likely. On these trials, the monkey received two drops of juice for making a saccade to the oriented bar within 600 ms of the search array onset. The remaining 25% of probe trials were *catch trials*, in which no target appeared, and the monkey received two drops of juice for withholding a saccade and maintaining fixation for 600 ms.

Probe trial analysis. Both the monkeys' behavior and the FEF activity were analyzed to identify possible effects of neuronal control on visual search performance and on the ability of FEF neurons to discriminate targets from distracters. Saccades were identified in the eye position data by the conjunction of two different tests: whether an eye velocity threshold (10°/s) was exceeded for more than 5 ms, and whether a “moving boxcar” comparison of eye positions (50 ms boxcars

separated by 25 ms) was significant ($P < 0.01$) using a two-way Kolmogorov-Smirnov goodness-of-fit test. The use of the velocity threshold was effective at eliminating slow drift in the direction of gaze, and the moving boxcar technique avoided artifacts caused by blinking.

To determine the effects of voluntary neuronal control on FEF target discrimination, single-unit activity was analyzed on correctly completed probe trials from four different trial conditions: Up trials with a target in the RF, Down trials with a target in the RF, Up trials with a target in the opposite hemifield (and thus a distracter in the RF), and Down trials with a target opposite. Target discrimination by an FEF neuron was defined as the difference between its response to a target in its RF and its response to a distracter in the RF, when the target was opposite. To account for the possibility that differences in baseline firing rates could account for changes in the responses on probe trials, the baseline firing rate was subtracted from each response on a per-condition basis. Responses for a neuron were then normalized by the peak mean rate across all four conditions. When responses were plotted in figures, they were first smoothed with a Gaussian kernel with $\sigma = 10$ ms.

To compare the statistical significance of response differences on probe trials, a time interval of interest was first chosen according to when the population of FEF neurons significantly discriminated between “Target in RF” and “Target opposite” conditions, using a paired t-test ($P < 0.05$), and collapsing across control direction. This window of significant discrimination lasted continuously from 141-332 ms after the search array onset, so this same time window was used for all further analysis.

Testing the effects of spontaneous, pre-probe activity. Because probe trials began at random times during operant control, it was possible to ask which factor predicted visual search behavior and FEF responses more reliably: the direction of operant control at the time of the visual search array onset (either Up or Down), or the spontaneous pre-probe firing rate, which likely reflected involuntary fluctuations in firing rate as well as the voluntarily controlled activity. The

spontaneous firing rate was calculated within a 100 ms window preceding the FEF response to the probe search array, from 50 ms before probe onset until 50 ms after. We then divided all probe trials within each experiment according to the pre-probe firing rate, rather than according to Up versus Down control direction. All trials in which the pre-probe firing rate was greater than the median were labeled “High” trials, and trials in which the pre-probe firing rate was less than the median were labeled “Low.” The number of High trials was kept equal to the number of Up trials, and the number of Low trials was kept equal to the number of Down trials. When the numbers of Up and Down trials required that some trials with the same level of spontaneous activity be classified as High and others as Low, the classification of these trials was done at random for 10,000 iterations, and the mean result across all iterations was reported.

Effects of spontaneous activity on neuronal responses. To characterize the relationship between FEF spontaneous activity and FEF responses on visual search probe trials, we first asked whether the probe trial responses were correlated with the level of pre-probe activity prior to the appearance of the search array. For each of 150 neurons recorded during experiments with probe trials, we first calculated the slope of the regression line describing the relationship between normalized neuronal probe response and normalized pre-probe firing rate for all correct probe trials in which the search target appeared in the neuronal RF, and again for all correct probe trials in which a distracter appeared in the RF and the search target appeared opposite. To explore a possible effect of voluntary control direction on the neuronal responses, we further divided the probe trials into four types: Up trials with the target in the RF (“Up RF”), Down trials with the target in the RF (“Down RF”), Up trials with a distracter in the RF and the target opposite (“Up opposite”), and Down trials with a distracter in the RF and the target opposite (“Down opposite”). Due to the relatively small number of probe trials per condition per experiment, and to low baseline firing rates of certain neurons, some neurons did not have enough variability in spontaneous pre-probe rate across trials to allow for linear regression.

Therefore, the numbers of neurons included for this analysis in each population are as follows: n = 131 (Up RF), n = 128 (Down RF), n = 130 (Up opposite), n = 132 (Down opposite).

Supporting Text

Variability of neuronal control. The magnitude of control varied considerably throughout the course of each experiment. Control indices calculated by comparing the FRs across each block transition (Up→Down or Down→Up) differed significantly across the experimental session ($P = 0.0045$, ANOVA; Fig. S1). At the peak block transition, the mean CI was 0.050, corresponding to a 10.5% difference in FR. The magnitude of control during each experiment did not correlate with the baseline FR (Fig. S2; $R^2 = 0.0084$, $P = 0.3791$).

Positive and negative control of FEF activity. The majority of recording sites had individually significant effects of voluntary control on the FEF MUA (55 of 94 sites). Most of these had positive effects of control (38 sites), but we also found sites with significant negative effects (17 sites). The number of experiments with significantly positive and negative control were both greater than that expected by chance ($P < 10^{-14}$, positive; $P = 0.009$, negative). Our observation of negative neuronal control may be explained by recordings from inhibitory neurons, or neurons that received connections from inhibitory neurons. We did not see a tendency for the negative-CI sites to be clustered in the FEF.

Voluntary control of single FEF neurons. We examined the FRs of 174 neurons (Monkey B: 74, Monkey C: 100) sorted off-line from the multiunit recordings. Eighty-six neurons (49%) had a significant main effect of control direction on FR, or an interaction between control direction and time during trial, or both. Of these, 57 (66%) had positive CIs (mean = 0.111, $P < 10^{-4}$), and 29 (34%) had negative CIs (mean = -0.074, $P < 10^{-4}$). As with the MUA data, the numbers of

sites with significantly positive and negative neuronal control both exceeded those expected by chance ($P < 10^{-6}$, positive; $P = 0.003$, negative).

Voluntary control of visual- and movement-related neurons. Before each experiment, we classified the neurons according to their responses during a visually guided delayed saccade task. A neuron's "visual index" was defined as

$$(V-B)/(V+B)$$

where V is the mean firing rate in the interval 60-120 ms after the presentation of a visual stimulus (a 1° diameter white circle) within its RF, and B is the mean baseline firing rate during the 200 ms prior to stimulus presentation. Similarly, a neuron's "saccadic index" was defined as

$$(S-D)/(S+D)$$

where S is the mean firing rate in the interval from 50 ms before the saccade until 25 ms after, and D is the mean delay period activity, calculated from 400 to 200 ms before the saccade. Positive values for the visual and saccadic indices indicate that a neuron responded with an increase in firing rate to the onset of the visual target or to the execution of the saccade, respectively. Conversely, negative values for the indices mean that the activity of the neuron was suppressed. In the population of single neurons, we observed a range of visual and saccadic indices (Fig. S3), with a mean (\pm s.d.) visual index of 0.34 ± 0.47 , and a mean saccadic index of 0.19 ± 0.32 . The magnitudes of the two indices should not be compared directly, as the visual index is computed relative to the baseline activity, and the saccadic index is computed relative to delay activity.

Possible control strategies. Recent studies have revealed a contribution of the FEF to the head component of gaze shifts, as well as the eye component (S5). Thus, one possibility is that changes in neck muscle tension might be sufficient to achieve the modest changes in neuronal activity between Up and Down blocks.

We also considered that modulation of FEF neuronal activity might be achieved via differences in fixational eye movements (e.g. microsaccades) between Up and Down blocks, given that the operant control task did not eliminate such movements within the fixation window (Fig. S4A). It has previously been shown that the activity of neurons in visual cortex (S6) and the superior colliculus (S7) is modulated around the time of microsaccades. Because FEF neurons are typically responsive during saccades into the visual hemifield contraversive to the recording site (and thus toward the neuronal RF), we hypothesized that FEF firing rates might increase around the time of contraversive microsaccades as well, and that the monkey might make more contraversive microsaccades on Up trials than on Down trials in order to achieve higher firing rates.

Contrary to our expectations, but consistent with the observations of Kobayashi and colleagues (S8), there were slightly but significantly fewer contraversive microsaccades on Up trials than on Down trials (Fig. S4B; Up = 1.31 s^{-1} , Down = 1.33 s^{-1} , $P = 0.0018$, paired t-test). Similarly, there were significantly fewer ipsiversive microsaccades (Fig. S4C; Up = 1.17 s^{-1} , Down = 1.19 s^{-1} , $P = 0.0014$). FEF activity was indeed modulated around the time of microsaccades, with greatest modulation following contraversive microsaccades (Fig. S5). However, the moderate size of the difference in neuronal activity and the small absolute difference in overall microsaccade rate (0.04 microsaccades/s greater on Down trials) were insufficient to explain the observed magnitude of voluntary neuronal control. Moreover, the CIs for the experiments did not correlate with differences in microsaccade frequency (Fig. S6; CI versus contraversive rate: $P = 0.567$, linear regression; CI versus ipsiversive rate: $P = 0.858$).

Effects of neuronal control on saccade metrics. To determine whether voluntary control of FEF activity affected the metrics of saccades during visual search, we calculated the latencies, peak velocities, and amplitudes of saccades on correct probe trials. Because target eccentricities varied across experiments, and because monkeys may have spatial biases that affect their

latencies to different locations, we used z-score normalized latencies on a per-session, per-location basis and made comparisons between probe trials during upward versus downward control. We found no effect of voluntary control on the latencies of saccades directed to search targets inside the FEF RF (Fig. S7; normalized latency for Up = -0.001 ± 0.033 , Down = 0.001 ± 0.032 , $P = 0.967$). However, on trials in which the target was opposite the RF, latencies were shorter on Up than on Down trials (Up = -0.054 ± 0.029 , Down = 0.055 ± 0.032 , $P = 0.0118$).

We also used an ANCOVA to determine whether the direction of voluntary control affected the saccadic “main sequence,” i.e. the well-described relationship between the saccadic peak velocity and amplitude (Fig. S8) (S9). For this analysis both the log of the peak velocity and the log of the amplitude were used, because these values are known to covary linearly. For both monkeys there was no interaction between control direction and amplitude on the peak velocity (Monkey B: $P = 0.7154$, Monkey C: $P = 0.7473$), indicating that the relationship between peak velocity and amplitude was not influenced by voluntary control.

Spatial extent of the perceptual effects of voluntary control. The direction of voluntary control of FEF activity influenced the monkeys’ performance on visual search probe trials. Specifically, both monkeys were more likely to miss a search target within the controlled neurons’ RF and incorrectly withhold a saccade when the search array appeared during Down trials, compared to Up trials. We wanted to quantify the spatial extent of this performance effect in order to infer the size of the population of neurons that the monkeys were likely controlling. A global effect would indicate that the monkeys’ strategy was to non-selectively modulate the firing rate of a large number of neurons, while a localized effect would support the notion that the monkeys’ strategy was to selectively control a smaller population of neurons.

Figure S9A shows the locations of all search targets during the visual search probe trials. For each experiment, we calculated the difference in target miss percentage during Down and Up trials at each target location separately. Greater differences between Down and Up miss

percentages indicate a stronger influence of voluntary control on search performance. We then plotted the difference in miss percentage as a function of the distance of the target from the center of the controlled neurons' RF (Fig. S9B). An exponential fit of the data ($n = 246$ data points, i.e. three targets' points from each of 82 experiments; fit of the form $y = y_0 e^{-\lambda x}$) yielded a decay constant (λ) of 0.128, which corresponds to a distance of 5.4° from the center of the RF at which the performance effect reached half its maximum value. Thus, voluntary control had a localized effect on visual search performance, rather than a global one.

Effect of spontaneous FEF activity on visual search behavior. To determine the extent to which visual search performance correlated with the direction of voluntary control *per se*, we divided the population of trials into two groups with greater than, and less than, the median rate of pre-probe activity ("High" and "Low," respectively; Fig. S10A). When trials were divided in this way, the overall fraction of probe trials in which the monkey made a saccade to the RF was still the same for High versus Low trials, as with Up versus Down (Fig. S10B; High = 22.4% of 4441, Low = 23.2% of 4346, $P = 0.36$; Monkey B: $P = 0.18$; Monkey C: $P = 0.85$). However, unlike the Up versus Down effect, there was no effect of pre-probe activity on the probability of target misses in the RF (Fig. S10C; High = 7.1% of 1105, Low = 8.0% of 1117, $P = 0.42$; Monkey B: $P = 0.97$; Monkey C: $P = 0.25$). Similarly, there was also no effect of pre-probe activity on opposite misses (Fig. S10D; High = 3.0% of 1139, Low = 3.1% of 1095, $P = 0.87$; Monkey B: $P = 0.36$; Monkey C: $P = 0.17$). Thus, the performance effects observed were only correlated with the direction of operant control, and not with spontaneous fluctuations in FR.

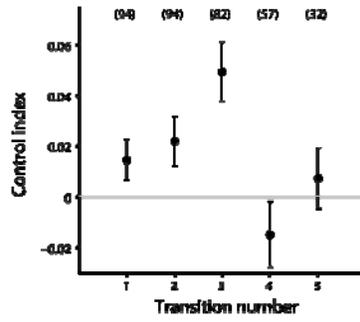


Fig. S1. Voluntary control over the course of an experiment. The control index was calculated at each of 359 block transitions across 94 experiments, and the mean control index is shown for each block transition. “Transition number 1” refers to the transition between the first two blocks of trials in an experiment, “Transition number 2” refers to the transition between the second and third blocks of trials, etc. Numbers in parentheses above each data point indicate the number of experiments during which each transition occurred. Error bars are s.e.m.

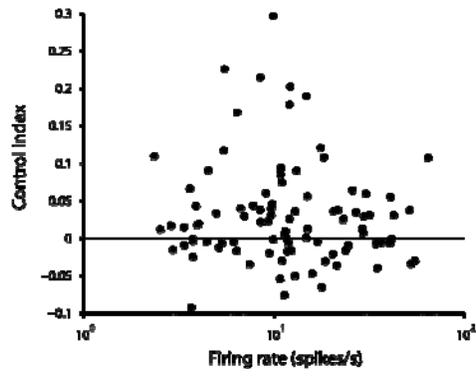


Fig. S2. Control index as a function of baseline MUA firing rate.

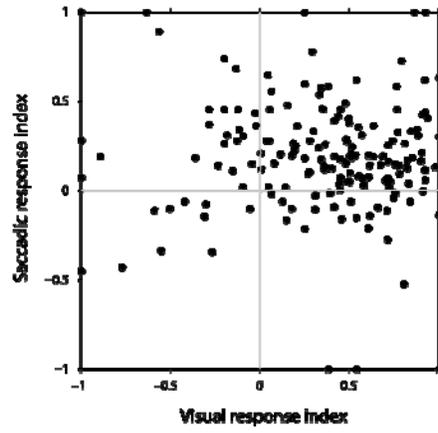


Fig. S3. Saccadic and visual response indices for the population of 174 FEF neurons.

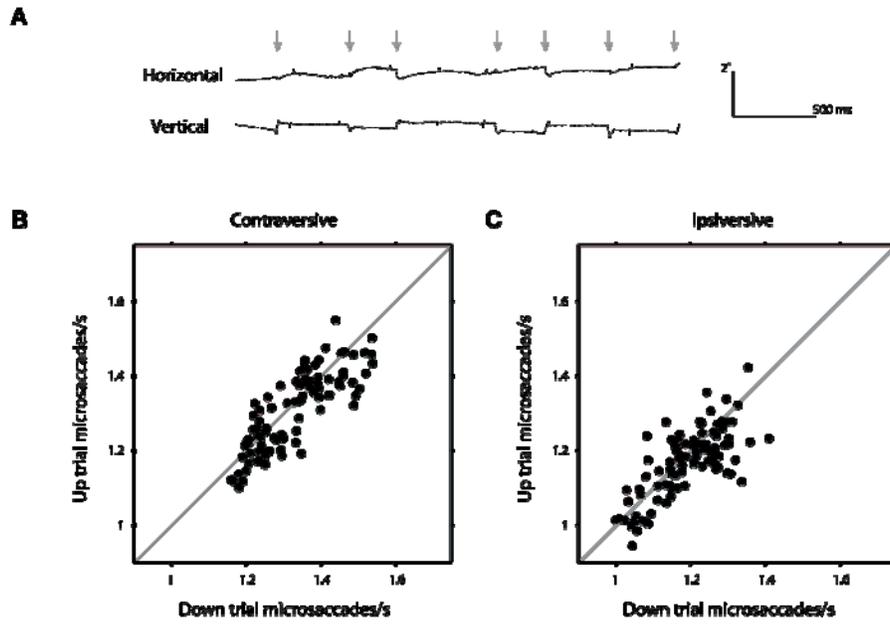


Fig. S4. Microsaccadic eye movements during voluntary neuronal control. **(A)** Horizontal and vertical eye position traces during an example operant control trial. Gray arrows indicate the times of microsaccades. **(B and C)** Rates of microsaccades during voluntary control. The microsaccade rate on Up trials is plotted against the rate on Down trials for microsaccades contraversive **(B)** and ipsiversive **(C)** to the recording site. Each black circle represents the average across all operant control trials from a single experiment. Circles located in red regions indicate that the rate of microsaccades was greater on Up than on Down trials for that experiment, those in blue regions indicate the opposite.

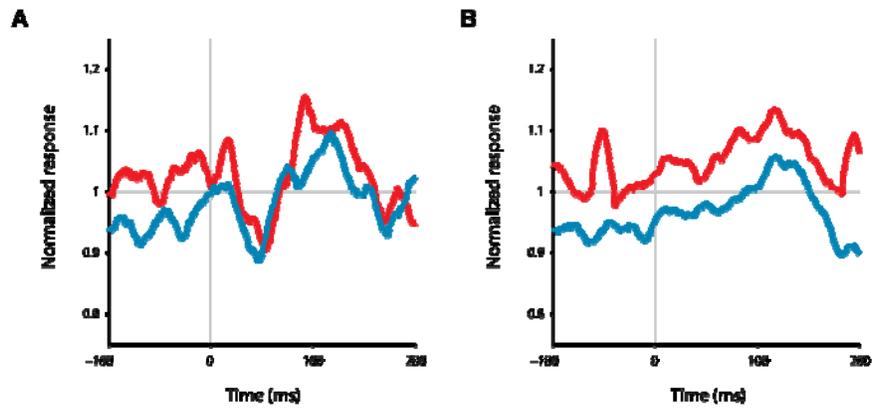


Fig. S5. Microsaccade-related FEF activity. Microsaccade triggered average normalized firing rate of 174 FEF neurons for microsaccades contraversive (**A**) and ipsiversive (**B**) to the recording site. Red and blue lines are for Up and Down trials, respectively.

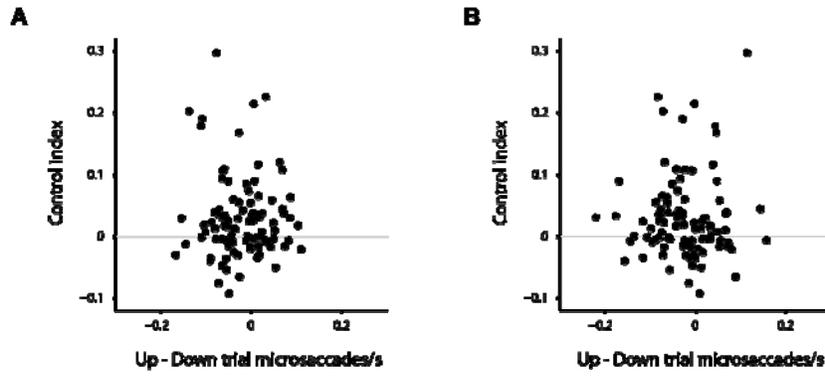


Fig. S6. Relationship between microsaccade rate and voluntary control. The control index is plotted against the difference between Up and Down microsaccade rates for microsaccades contraversive (**A**) and ipsiversive (**B**) to the recording site.

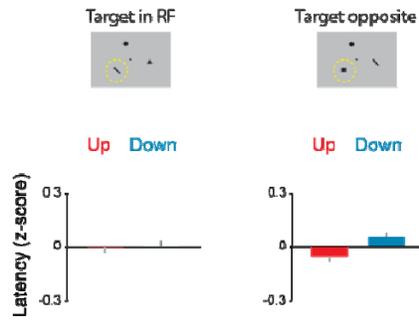


Fig. S7. Effect of voluntary control of FEF neurons on saccade latency. Means of z-score normalized saccade latencies are shown for correct visual search probe trials that appeared during Up (red) and Down (blue) operant control trials. Saccades to targets within the controlled neurons' RF are shown on the left; saccades to targets opposite the RF are on the right. Error bars show s.e.m.

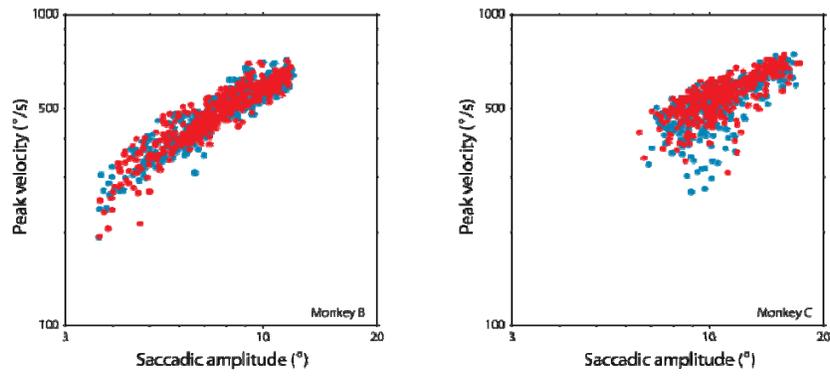


Fig. S8. Saccadic main sequence. The relationship between saccadic peak velocity and amplitude is shown for Monkey B (left) and Monkey C (right). Each point represents a single correct saccade to a target within the voluntarily controlled FEF neurons' RF during a visual search probe trial. Red points are saccades that occurred during Up trials, blue points are from saccades during Down trials.

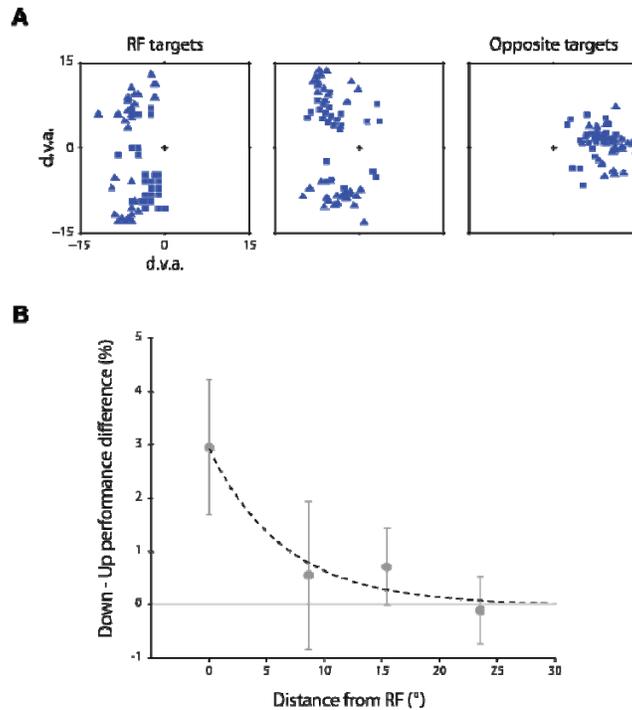


Fig. S9. Spatial specificity of the visual search performance effect. **(A)** Locations of visual search targets on probe trials, in degrees of visual angle from the fixation spot. Each point shows the RF target (left panel), opposite target (right panel), and intermediate target (middle panel) of the search array from a single experiment. Squares: Monkey B, triangles: Monkey C. **(B)** The difference in proportion of search target misses, i.e., the percentage of visual search probe trials in which the search target was not detected and the monkey erroneously maintained fixation, during downward, minus upward, voluntary control. The four data points are the means for all trials in which the search target was, respectively, at the center of the RF, less than 10 degrees of visual angle from the RF center, 10-20° from the RF center, and greater than 20° from the center of the RF. Error bars are s.e.m.; horizontal error bars are present, but are shorter than the widths of the data points. Dotted line shows an exponential fit of all data points.

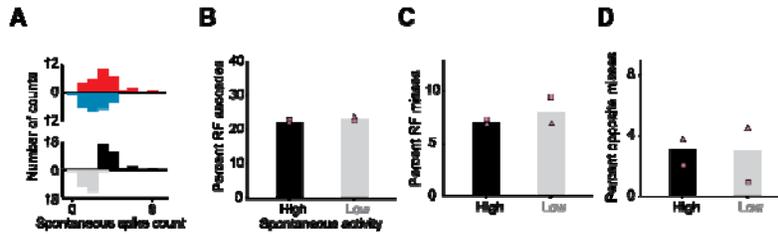


Fig. S10. Effects of spontaneous FEF activity on behavior and physiology. **(A)** Instead of dividing probe trials based on Up or Down control (top, red and blue histograms), the same trials could be split according to the actual level of spontaneous activity prior to the appearance of the visual array (bottom, black and gray histograms). **(B-D)** show the same behavioral data as in Fig. 3B-D. Trials with high spontaneous activity are shown in black, and trials with low activity are in gray. **(B)** Percentage of probe trials in which a saccade was directed into the RF, correctly or incorrectly. Purple triangles: Monkey B; purple squares: Monkey C. **(C)** Misses of the target in the RF. **(D)** Misses of the target opposite the RF.

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