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2 **Modulation of Shifting Receptive Field Activity**
3 **In Frontal Eye Field by Visual Saliency**
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47 **ABSTRACT**

48 In the monkey frontal eye field (FEF), the sensitivity of some neurons to visual
49 stimulation changes just before a saccade. Sensitivity shifts from the spatial location of its
50 current receptive field (RF) to the location of that field after the saccade is completed (the
51 future field, FF). These shifting RFs are thought to contribute to the stability of visual
52 perception across saccades, and here we investigated whether the salience of the FF
53 stimulus alters the magnitude of FF activity. We reduced the salience of the usually single
54 flashed stimulus by adding other visual stimuli. We isolated 171 neurons in the FEF of two
55 monkeys, and did experiments on 50 that had FF activity. In 30% of these that activity was
56 higher before salience was reduced by adding stimuli. The mean magnitude reduction was
57 16%. We then determined whether the shifting RFs were more frequent in the central visual
58 field, which would be expected if vision across saccades is only stabilized for the visual
59 field near the fovea. We found no evidence of any skewing of the frequency of shifting
60 receptive fields (or the effects of salience) towards the central visual field. We conclude that
61 the salience of the FF stimulus makes a substantial contribution to the magnitude of FF
62 activity in FEF. In so far as FF activity contributes to visual stability, the salience of the
63 stimulus is probably more important than the region of the visual field in which it falls for
64 determining which objects remain perceptually stable across saccades.

65

66 **INTRODUCTION**

67 Our visual perception is stable in spite of frequent and abrupt shifts of the retinal
68 image by saccades. One hypothesis is that the failure to perceive the shifts depends on
69 knowledge of the impending saccade that is provided by an internal copy of the motor
70 command, a corollary discharge or efference copy (Sperry 1950; von Holst and Mittelstaedt
71 1950). Neurons that respond to visual stimuli would anticipate the occurrence of an
72 upcoming saccade as a result of this corollary discharge input. Duhamel, Colby, and
73 Goldberg (1992) found such a potential neuronal mechanism in the parietal cortex. In
74 anticipation of an upcoming saccade, parietal neurons became sensitive to visual stimuli at
75 the spatial location that the receptive field (RF) would occupy after the saccade. They
76 proposed that this anticipatory activity at the site of the RF after each saccade indicated a
77 remapping that underlies visual stability. These shifting RFs subsequently have been
78 found in the frontal eye field (FEF, Sommer and Wurtz 2006; Umeno and Goldberg 1997)
79 and in several other cortical and subcortical areas (for summary see Sommer and Wurtz
80 2008).

81 The procedure most frequently used to identify shifting RFs is illustrated
82 schematically in Figure 1A. The RF of a neuron is first mapped while the monkey fixates
83 (red fixation cross and dotted circle in Figure 1A). Just before a saccade to a visual target,
84 a stimulus is flashed at the location the RF will occupy after the saccade, which we refer to
85 as the future field of the neuron (FF - Figure 1A blue fixation cross and blue dotted circle).
86 In a substantial fraction of neurons in FEF and LIP, there is an increase in activity following
87 the flash of the FF stimulus, which is always presented before the saccade begins.

88 From Figure 1A, it is clear that the stimuli used in most experiments to study shifting
89 receptive field activity in LIP and FEF are flashed spots of light against a uniform
90 background, which creates what must be a salient visual stimulus. The salience of the
91 stimulus is particularly relevant in light of the emerging view that both LIP and FEF can be
92 regarded as having salience maps for visual stimuli (Kusunoki et al. 2000; Thompson and
93 Bichot 2005). Such salience results from the bottom up effect of the stimulus
94 characteristics (Koch and Ullman 1985) but with modulation by top down influences (Folk et
95 al. 1992). Neurons activated by stimuli with the highest salience represent the regions of
96 the visual field that are likely to attract attention, those that are likely to be selected during

97 visual search, and those likely be selected as the target for a future saccade in FEF (Schall
98 et al. 1995; Thompson et al. 1996) and in LIP (Gottlieb et al. 1998; Kusunoki et al. 2000).
99 (Figure 1B emphasizes that top down or goal directed attention is directed toward the target
100 of the saccade being made.)

101 One stimulus characteristic that produces salience is its abrupt onset. In our normal
102 vision, such stimulus onset plays a major role in directing attention to those stimuli.
103 Perhaps the most dramatic demonstration of this is our failure to recognize even large
104 changes made in a visual scene when the onset of the change is masked (Rensink 1997).
105 In these change blindness experiments, either a saccade or a brief blanking of the entire
106 scene sharply reduces the perception of even large changes in the visual scene. In normal
107 vision, the attention directed to a stimulus that has just appeared is referred to as
108 exogenous attention or simply stimulus onset attention (Egeth and Yantis 1997).

109 The next question is how much this onset salience contributes to the FF activity in
110 the shifting RF experiments. In LIP, the effect of stimulus salience on shifting RF activity
111 was observed as an ancillary finding in experiments that established the importance of
112 stimulus salience (Gottlieb et al. 1998). These experiments compared the response of LIP
113 neurons to a stimulus turned on in the RF to the response when the RF was brought onto
114 the stimulus by a saccade, without any abrupt onset. Gottlieb et al. (Gottlieb et al. 1998)
115 found that with the stimulus onset the visual response was substantially larger. They also
116 pointed out that for an LIP neuron illustrating this difference (their Figure 2A), the neuron's
117 activity occurred with a shorter than expected latency, which they took as an indication of
118 what we refer to as FF activity. The FF activity was larger when the visual stimulus had an
119 onset than when it did not, that is, when the stimulus had greater salience.

120 In the present experiments we test the possible contribution of visual salience to the
121 FF activity of FEF neurons. The goal was to see whether the magnitude of the FF activity
122 in previous experiments (Sommer and Wurtz 2006; Umeno and Goldberg 1997) actually
123 was enhanced by the salience resulting from stimulus onset as suggested by the
124 observation in LIP. In our experiments we first studied the FF activity as had been done
125 previously; we flashed the stimulus in the FF of the neuron just before the saccade to
126 identify the subset of neurons that showed shifting RFs. In those that did, we then added
127 the onset of other stimuli in order to see if these added stimuli reduced the FF activity. The

128 goal was to reduce the salience of the FF stimulus without changing the stimulus itself, and
129 judging from behavioral experiments, having additional stimuli in the visual field seemed a
130 reasonable way to do that. In visual search tasks, the addition of stimuli in the visual field
131 (usually referred to as non-targets or distractors) reduces the salience of a stimulus as
132 indicated by increased reaction time (Duncan and Humphreys 1989; Kim and Cave 1999).
133 In addition, the effect of stimulus onset has been shown to be reduced if distractors are
134 added to a stimulus (Wright and Richard 2003). Our goal was to place the added stimuli
135 outside of the estimated area of the RF and FF in order to minimize a direct visual effect of
136 the added stimuli. If the FF activity is ordinarily facilitated by exogenous attention, we would
137 expect to see reduced sensitivity to the FF stimulus when multiple stimuli are added, and
138 we frequently did.

139

140 **METHODS**

141 In two adult male monkeys (*Macaca mulatta*) weighing from 8 to 11 kg, we
142 implanted scleral search coils for measuring eye position, recording cylinders for
143 accessing FEF, and a post for immobilizing the head during experiments as described
144 previously (Sommer and Wurtz 2000). All procedures were approved by the Institute
145 Animal Care and Use Committee and complied with Public Health Service Policy on the
146 humane care and use of laboratory animals.

147

148 *Experimental setup*

149 The monkey sat in a primate chair with its eyes 57 cm in front of a tangent screen.
150 The chair was in the center of magnetic field coils in a dark room that was sound
151 attenuated. Computers running REX (Hays et al. 1982) and associated programs
152 controlled stimulus presentation, administration of reward, the recording of eye
153 movements and single neuron activity, and the on-line display of results. Visual stimuli
154 appeared on a gray background, back-projected by a DPI projector.

155

156 *RF mapping*

157 The first experimental step to determine the consequences of added stimuli on the
158 magnitude of the shifting RF activity was to obtain detailed knowledge of their

159 conventional RFs. While the monkey fixated a central red cross, we determined the
160 location and extent of the RF, and the optimal stimulus size to elicit the strongest visual
161 response. This enabled us to place the added stimuli at locations that should minimally
162 invade the RF of the neuron and thus minimize visual interactions. We determined three
163 key points about the RF of each neuron.

164 RF center. We first estimated the location of the RF by creating a coarse spatial
165 map of the visual activity. While the monkey fixated a central red cross, we probed the RF
166 of the neuron by systematically presenting a visual stimulus (with a diameter of 1 - 5°
167 depending on the eccentricity) at one of nine locations on a 3x3 grid. The grid spacing
168 was adjusted to cover as much of the estimated RF as possible. The RF center was
169 taken to lie at the mean of the nine locations weighted by the magnitude of the visual
170 response at each location.

171 RF center size. On successive fixation trials, we presented filled circles of different
172 sizes (diameter between 1° and 70°) at the estimated RF center. The optimum stimulus
173 size and estimate of the RF center was taken as the point where the curve relating visual
174 response to spot size reached a peak. To determine the peak, the plot of visual response
175 to each spot size was fit to a curve using the difference of two Gaussian functions - one
176 representing a narrow excitatory center of the RF and the other the wider suppressive or
177 inhibitory surround (Rodieck, 1965). This experiment and analysis provided a two
178 dimensional model of the RF structure.

179 RF suppressive surround. Qualitative examination indicated that there was a
180 suppressive surround in all the FEF neurons studied (the area around the excitatory
181 center that when stimulated suppressed the neuron's response). We estimated the extent
182 of the suppressive surround by presenting a spot of light in the center of the RF (the size
183 and location determined from the two tasks described above) and then varying the size of
184 an annulus surrounding the spot. The annulus had a constant outer diameter of 70°, but a
185 variable inner diameter so that as we increased this inner diameter, the annulus became
186 narrower, and less light from it fell on the RF. We took the outer boundary of the
187 suppressive surround to be the smallest inner diameter at which there was no significant
188 difference from the response to a center stimulus presented alone and with the annulus.

189 In all three tests, the monkey received a liquid reward for maintaining fixation
190 (within a 1.5° square) for the duration of the trial. There were 8 presentations of a visual
191 stimulus per trial and each stimulus presentation was 50 ms in duration with an inter-
192 stimulus interval of at least 500 ms.

193

194 *Shifting RF measures*

195 Following these preliminary RF estimation experiments, we performed the main
196 experiment to test FEF neurons for a shifting RF and determine the effect of added stimuli
197 on the magnitude of this activity.

198 Shifting RF saccade task (Figure 2): The monkey was trained to make a saccade
199 to a target that appeared at the same time as the initial fixation cross was turned off. The
200 saccade target was always placed in the ipsilateral field in order to diminish the saccade
201 related responses that were stronger to the contralateral field. (For testing whether the
202 neuron was a visuomotor one, contralateral saccades were made in a separate test).
203 During this task both the RF and FF were sequentially examined. On each trial, after 500
204 ms of initial fixation of the central red cross, a visual stimulus the size of the RF excitatory
205 center (filled red circle in Figure 2A) was flashed in the center of the RF (red dashed circle
206 in Figure 2A) for 50 ms. Following a variable delay (500-700 ms), the fixation point was
207 turned off and a saccade target (blue cross) was simultaneously presented in the
208 periphery. (This delay ensured an interval of at least 500 ms between the response to the
209 RF stimulus and the FF stimulus. There was no observed interaction between the two
210 responses and the delay provided enough time to distinguish the FF activity from the
211 background activity (see Data Analysis).) Before the monkey made a saccade to the new
212 fixation point (dashed arrow), the same stimulus used to probe the RF was flashed in the
213 FF (blue dashed circle) for 50 ms. That is, the same stimulus was presented again, but at
214 a location displaced from the center of the RF by the saccade vector. For example, if the
215 center of the RF is at $x = 15^\circ, y = 10^\circ$, and the monkey is required to make a saccade from
216 the fixation point at $0^\circ, 0^\circ$ to $-30^\circ, 0^\circ$, the FF center is $-15^\circ, 10^\circ$. Importantly, the FF
217 stimulus was extinguished before the saccade was made (solid arrow). Note that on
218 every trial both the RF and the FF stimulus were presented.

219 There were two conditions in this task: *with* and *without* added stimuli (bottom and
220 top rows of Figure 2A respectively). The description above is the *without added* stimuli
221 condition. During the *with* added stimuli condition, eight added visual stimuli were also
222 presented with the RF or FF stimulus in the same trial. These added stimuli were the
223 same size (determined from the RF center size task) and presented for the same duration
224 as the visual stimulus in the *without* added stimuli condition. Added stimuli were
225 positioned at locations beyond the suppressive surround, that is, where a peripheral
226 stimulus did not alter the response of a spot in the center of the RF. (This was typically 5°
227 beyond the RF extent as determined with the RF surround test). As depicted in Figure 2A,
228 we frequently placed the additional stimuli in the opposite hemifield of the RF. This had
229 two advantages: (1) there was less chance of a visual interaction because the RF field
230 rarely extended into the opposite hemifield and (2) this placement allowed us to maintain
231 all stimuli presented with the RF or FF stimulus on the screen despite the relatively large
232 saccades. Within a trial, the same configuration of the added eight stimuli was presented
233 for the RF and FF, but shifted by the saccade vector. This configuration of the added
234 stimuli was randomized from trial to trial. That is, the added stimuli were always
235 positioned outside the suppressive surround, but the exact positions varied from one trial
236 to the next. In each condition, the monkey received a liquid reward for making a saccade
237 to the new fixation cross (within a 5.0° square) within 500 ms after the appearance of the
238 saccade target.

239

240 *Control Experiments*

241 We performed several control experiments on every neuron to ensure that the
242 observed FF activity was dependent on the combination of the FF stimulus and the
243 generation of the saccade and was not solely a saccade related or a visual response. To
244 determine that the saccade alone was not producing the FF activity, the monkey made
245 saccades to the target in the Shifting RF saccade task but in the absence of the FF
246 stimulus. In this case, the saccadic eye movement was made in the absence of the FF
247 stimulus. These control trials were pseudo-randomized and embedded in the Shifting RF
248 saccade task. To ensure that the FF activity was not a visual response, we presented the
249 FF stimulus while the monkey fixated the central red cross. In this case the FF stimulus

250 was presented in the absence of the saccade. This control was done before the Shifting
251 RF saccade task to ensure that the FF was beyond the RF of the neuron.

252

253 *Neuron Recording*

254 We placed one neuron recording cylinder over the FEF approximately normal to
255 the skull. After initial estimation using MR images, we located FEF within the cylinder
256 electrophysiologically. We recorded single neuron responses and microstimulated in FEF
257 with tungsten microelectrodes advanced by a stepper microdrive. Electrodes passed
258 through guide tubes in a 1-mm-resolution grid in the recording cylinder (Crist et al. 1988).
259 Neuronal responses were discriminated from background activity using a software-based
260 waveform discriminator. We characterized visual and movement fields by monitoring
261 neuronal activity while the monkey made saccades to targets throughout the contralateral
262 visual field. We targeted neurons in the anterior bank of the arcuate sulcus, and we
263 verified that they were in FEF by using two criteria: saccade-related activity was found in
264 many neurons and saccades were evoked with currents of $\leq 50 \mu\text{A}$ (Bruce and Goldberg
265 1985). Neurons were excluded from further analysis if they did not demonstrate shifting
266 RF activity or if we were unable to acquire sufficient data.

267

268 *Data Analysis*

269 RF visual responses were measured in a time window starting 40 ms after stimulus
270 onset and ending when activity fell below 2 SD of a background activity epoch. This
271 background epoch was from 60 ms before to 40 ms after stimulus onset. Because FF
272 activity is synchronized to saccade onset (see Sommer and Wurtz 2008), neuronal
273 activity was measured in a period beginning 200 ms before to 300 ms after saccade
274 onset. Within this period, the FF activity began when neuronal activity was ≥ 2 SD of the
275 background activity epoch and ended when activity dropped below that level. This
276 background epoch was neuronal activity 300 ms to 200 ms before saccade onset.
277 Stimulus - dependent modulation of the RF response and FF activity were determined by
278 a two tailed *t*-test ($\alpha = 0.05$). In these tests, RF responses without added stimuli were
279 compared to RF responses with added stimuli, and FF activity was similarly compared
280 just to FF activity. If there was a difference in the time of the start and termination of the

281 response between the two conditions we determined the smallest window to perform the
282 statistical test. That is, the firing rates between the two conditions were compared
283 between the latest start and earliest termination time of the responses. Repeating the
284 analysis with a full window (beginning with the earliest start and ending with latest
285 termination time of the responses) yielded similar results. Saccade initiation was identified
286 as the time that eye velocity and acceleration exceeded both $100^\circ/\text{s}$ and $5,000^\circ/\text{s}^2$.

287

288 **RESULTS**

289 We recorded FEF neurons that showed shifting RFs in three hemispheres of two
290 monkeys. We studied 171 neurons of which 52 (30%) had significant FF activity. We
291 were able to assess the saccade related activity in addition to the visual response in 47 of
292 these 52 neurons, and found that 41 of the 47 were visuomotor neurons. We were able to
293 compare the magnitude of the RF response and FF visual activity with and without added
294 stimuli in 50 neurons (24 from monkey Ar and 26 from FI). We saw no significant
295 difference between the monkeys and have combined their results.

296

297 **Effect of Added Stimuli on RF and FF Activity**

298 We compared the response to the RF and FF stimulus presented alone to that with
299 added stimuli. Figure 3 illustrates the results for an example neuron with the test of the
300 RF response in the left column and that for the FF activity in the right column. First, a
301 stimulus of the optimal size (in this case 6°) was flashed in the RF (red dashed circle)
302 long before the saccade to the target to serve as a baseline for the magnitude of the
303 visual response (Figure 3A). Then the same stimulus was flashed in the FF (blue dashed
304 circle) just before the saccade to see if there was FF activity and to determine its
305 magnitude (Figure 3B). In the next series of trials, we then interleaved these trials with RF
306 and FF stimuli alone with trials with eight added stimuli flashed at the same time and for
307 the same duration as the RF and FF stimuli (Figure 3C and D). Figure 3E and F show the
308 effect of these added stimuli on the RF response and the FF activity. Note that the RF
309 response has a sharp onset typical of a visual response while the FF is best described as
310 “activity” because of its synchrony with the saccade rather than the FF stimulus (see
311 Sommer and Wurtz 2008; Umeno and Goldberg 1997). For this example neuron, there

312 was little effect of these added stimuli on the RF response (Figure 3E). The average
313 firing rate was statistically indistinguishable with and without the added stimuli ($P=0.93$,
314 two-tailed t -test). In contrast, the FF activity showed a 44% decrease in the response with
315 the added stimuli (Figure 3F, $P < 0.001$, two-tailed t -test). The latency of the activity was
316 not affected, a finding that was consistent across our sample (two-tailed t -test, $P=0.83$).

317 We attempted to keep the added stimuli out of the RF (and by inference out of the
318 FF) of the neuron by placing them at least 5 degrees outside of the RF, including both the
319 excitatory central area and the suppressive area (see Methods). For the example neuron
320 in Figure 3, the lateral extent of the RF was 25 degrees from the RF center and the added
321 stimuli were placed at locations outside a 30 degree radius from the RF center. The lack
322 of any significant difference in the visual activity with and without the added stimuli (Figure
323 3E) is consistent with their placement outside the RF.

324 Figure 4 shows the effect of the added stimuli for the 50 FEF neurons studied. The
325 RF response and FF activity are again in the left and right columns respectively. In Figure
326 4A and B the responses with added stimuli are plotted against the responses without
327 them. The circles represent neurons that had a significant change in activity with added
328 stimuli (two-tailed t -test, $P < 0.05$) and the filled circles indicate where the change was a
329 decrease. There was a significant decrease in the RF response in 14 (28%) of the 50
330 neurons and a significant increase in the response in 3 (6%). There was a significant
331 decrease in the FF activity in 15 (30%) of the 50 neurons and a significant increase in the
332 activity in 2 (4%).

333 The histograms in Figures 4C and D show the percent change in the magnitude of
334 activity with added stimuli for the RF response and FF activity. The black triangles mark
335 the average percent change for the 50 neurons, and the red and blue markers are the
336 percent change values for RF and FF of the example neuron in Figure 3. On average, the
337 added stimuli led to a small (4%) but significant decrease in the RF response ($P=0.03$,
338 significantly different from 0, two-tailed t -test). Added stimuli had a greater influence on
339 FF activity, causing an average 16% decrease that was also significantly different from 0
340 ($P < 0.001$). The magnitude of the change in the RF response and the FF activity for
341 individual neurons was not correlated ($R=0.087$, $P=0.548$).

342 The slight decrease in the RF response in some neurons could be the result of
343 either the effect of added stimuli on salience or an indication that they invaded the
344 suppressive surround of the neuron. If we make the worst case assumption on the
345 placement of the added stimuli, and assume they invade the RF of these neurons, they
346 likely act on FF as well (making the additional assumption the RF and FF are similar).
347 Therefore, the most conservative estimate of the effect of the added stimuli on the FF
348 activity would be the difference in the average percent change of the RF response and FF
349 activity. This difference of the percent change with added stimuli (a reduction in the RF
350 response by 4% and FF activity by 16%) is 12% for the sample of neurons. The average
351 percent reduction of the FF activity with added stimuli is significantly greater than the
352 average percent reduction of the RF activity (two-tailed *t*-test, $P=0.003$). This indicates
353 that the decrease in the FF activity was greater than the amount that could be attributed
354 to any visual interaction.

355 The histograms in Figures 4E and F are for the subset of 17 neurons that
356 demonstrated a significant change (decrease or increase, two-tailed *t*-test, $P<0.05$) in the
357 FF activity with added stimuli. The RF response for this subset decreased by an average
358 of 6% and the FF activity decreased by 34%. The average decrease in the RF response
359 was not significantly different from 0 (two-tailed *t*-test, $P=0.08$). Similar to results for the
360 entire sample, the average decrease in FF activity was significantly different from 0 (two-
361 tailed *t*-test, $P<0.001$). Additionally, the average reduction in the FF activity was
362 significantly greater than that in RF (two-tailed *t*-test, $P<0.001$).

363 In summary, we saw a clear reduction of the FF activity with the addition of stimuli
364 in 30% of the FEF neurons that have FF activity. Across the population and for the
365 subset of cells that demonstrated a significant change, the average FF activity reduction
366 with the additional stimuli was significantly greater than the average reduction in the RF
367 responses.

368

369 **Distribution of Shifting RFs in the Visual Field**

370 If the shifting RFs are related to stable visual perception during saccades, one
371 possibility is that these shifts are concentrated in the fovea or the central visual field
372 rather than distributed equally throughout the visual field. If that were the case, we might

373 expect that the frequency of shifting receptive fields and the magnitude of the shift activity
374 would be higher in the central visual field. We therefore attempted to study FEF neurons
375 with RFs over a range of eccentricities.

376 Figure 5 shows the frequency of the RF shifts from both monkeys expressed as a
377 function of RF eccentricity. The graph shows cumulative plots in which each point on the
378 cumulative curve represents the *percentage* of the total number of neurons reached at the
379 eccentricity shown on the horizontal axis. The black cumulative curve shows the
380 proportion of FEF neurons at each eccentricity whose RFs were determined ($n = 171$).
381 This curve shows a reasonably linear progression out to the maximum eccentricity
382 studied (39°) indicating that our sampling was reasonably distributed across the visual
383 field. The blue cumulative curve plots the sub-sample of these cells with shifting RFs
384 ($n=52$), about 30% of the total sample. The cumulative curve for neurons with shifting
385 receptive fields shows a similar linearity except for the anomaly between 20° and 30°
386 where no neurons with shifting RFs were sampled and the subsequent series of points
387 appear piled up at 30° . This implies that the number of neurons with shifting RFs occurs
388 with equal frequency across the visual field; there was no significant difference between
389 the two distributions (two-sample Kolmogorov-Smirnov test, $P=0.37$). In addition, there is
390 no evidence that the shifts are particularly related to neurons with RFs near the center of
391 the visual field. We also examined the magnitude of FF activity across receptive field
392 eccentricity. Figure 6A displays the distribution (bin width 5°) of the magnitude of the FF
393 activity as a function of RF eccentricity ($n=52$). There was no significant difference in the
394 mean magnitude of the FF activity across eccentricity (one-factor ANOVA, $P=0.73$). Thus
395 both the frequency and the magnitude of the shift activity in FEF neurons remained
396 roughly constant across the central 30° of the visual field.

397 Another factor that might vary with eccentricity is the frequency with which added
398 stimuli reduced the FF response. In Figure 5, the orange points on the graph show the
399 fraction of shifting RF neurons whose FF activity was significantly reduced by added
400 stimuli ($n=15$, 30% of the sub-sample). We found no such neurons within the central 10° ,
401 and there was a significant difference between this distribution and the cumulative curve
402 for neurons with shifting receptive fields (two-sample Kolmogorov-Smirnov test, $P=0.002$).
403 Within our small sample, neurons showing decreased responses with added stimuli may

404 be more frequent in the peripheral visual field. Figure 6B displays the distribution (bin
405 width 5°) of the mean magnitude of FF activity with (orange bins) and without added
406 stimuli (blue bins) as a function of RF eccentricity. Only cells that demonstrated a
407 significant decrease in the FF activity with added stimuli are shown (n=15). There were
408 variations in the magnitude of FF activity with and without added stimuli at different
409 eccentricities, but the difference between them (black triangles) did not systematically
410 vary with eccentricity (one-factor ANOVA, $P=0.24$). (The gaps at three eccentricity ranges
411 are due to a lack of cells that demonstrated a significant decrease in the FF activity with
412 added stimuli.)

413 In summary, we find that both the frequency of neurons with shifting receptive
414 fields and the magnitude of any shift activity was relatively constant within the central
415 35° of the visual field, with no special emphasis on the central visual field.

416

417 **Tests for Extraneous Visual and Saccadic Factors**

418 The goal of our experiments was to test the effect of reducing stimulus salience
419 due to stimulus onset on the shifting RF activity by using the added stimuli. Since we had
420 both the RF and the FF stimulus flashed on each trial and had the additional stimuli on
421 many trials, we included several control experiments and analyses to address the
422 following questions.

423

424 *Are there visual interactions between RF, FF, and added stimuli?*

425 From the information we had about the RF size of the neurons studied, we placed
426 our FF stimulus and added stimuli outside the measured RF. This was, however, only a
427 best estimate and we therefore adopted an empirical approach to test whether the FF
428 stimulus and the added stimuli invaded the RF by examining the timing of the FF visual
429 activity. If the activity after the FF stimulus and FF added stimuli were the result of a
430 shifting RF, the latency of that activity would be related to the onset of the saccade.
431 However, if the activity was a visual response because the FF stimulus, added stimuli or
432 both impinged on the RF of the neuron, the latency would be fixed to the onset of the FF
433 and added stimuli.

434 Figure 7 shows that for the same example neuron presented in Figure 3 the
435 increased neuronal activity occurred long after the visual latency of the neuron and was
436 not aligned to the stimulus onset but was aligned on the saccade onset as expected for
437 shifting RF activity. Figure 7A shows neuronal activity for the example neuron aligned
438 with onset of the FF stimulus and added stimuli (green vertical line). Each row of dots
439 represents spikes on one trial with the trials plotted in ascending order of saccade latency
440 – shortest latency at the bottom. The dashed red line parallel to the green FF stimulus
441 line indicates the time at which the activity should increase if it were a visual response.
442 The activity increases much later than the 47 ms visual latency of this neuron.
443 Furthermore, the increase in neuronal activity is not parallel to the vertical FF line but
444 instead more closely parallels the tilted saccade onset vertical line. This is supported in
445 Figure 7B which now aligns the same neuronal activity as in 7A on saccade onset (blue
446 vertical line). The neuronal discharge on the raster occurs long after the visual latency of
447 the neuron and parallels the now vertical line of saccade onset. The relationship between
448 the onset of the FF activity and the saccade is confirmed in Figure 7C. The onset of the
449 FF activity is plotted against the onset of the saccade for the data presented in Figure 7A.
450 In this case the onset times are with respect to the onset of the FF stimulus and added
451 stimuli. There was a clear relationship between the onset of the FF activity and the onset
452 of the saccade ($R=0.44$, $P<0.001$). (The onset of the FF activity was determined by
453 finding the maximum instantaneous firing rate within the interval plotted in Figure 7A.) For
454 all the neurons studied, we found the FF stimulus and added stimuli activity to have a
455 much longer latency than the visual latency of the neuron (across the population the
456 mean visual latency and FF activity latency were 52 ± 14 ms and 158 ± 55 ms
457 respectively), and the same parallel relation of the FF activity and the saccade onset. We
458 were only able to perform the test displayed in Figure 7C on four neurons in our sample
459 due to the need for a substantial number of trials, for variability of the interval between
460 onset of the saccade and FF stimulus and for a sufficient number of spikes/trial to
461 determine the instantaneous rate. However, for the four neurons there was a significant
462 linear relationship between the onset of the FF activity and the onset of the saccade
463 ($R>0.25$, $P<0.001$). In addition there was no significant correlation between the FF onset
464 and the stimulus onset ($R<0.1$, $P>0.4$). We conclude that activity related to the FF

465 stimulus does not have the characteristics of a visual response and that the FF field
466 activity is not due to the onset of stimuli within the RF of the neuron.

467

468 *Does any change in the variability of saccade amplitude or latency account for the*
469 *decrease in the FF activity?*

470 A factor that could contribute to the general decrease in the FF response with
471 added stimuli is a change in the amplitude or latency of the saccade and we investigated
472 the extent of the changes in each.

473 A difference in the average saccadic endpoint and its variability would be important
474 if the saccade went to a substantially different location in the two experimental conditions,
475 resulting in a significantly different saccade vector and therefore a potentially different
476 corollary discharge signal. Figure 8A shows the mean eye-movement position and
477 endpoint variability (95% confidence intervals) of saccades made to the same target with
478 and without added stimuli (black and blue traces and ellipses respectively) during a
479 session for the example neuron in Figure 3. There was no significant difference in mean
480 saccade endpoints in the presence of added stimuli. However, there was an increase in
481 the saccade endpoint variability with the added stimuli. This increase could result in
482 different trial-to-trial stimulation of the FF by the stimulus and lead to a decrease in FF
483 activity. We therefore determined whether the increased variability was large enough to
484 account for the decrease in FF activity with the added stimuli. Because for each neuron
485 we selected a stimulus size that when placed in the center of the FF would optimally
486 activate the neuron, any displacement of the stimulus as a result of changed saccade
487 amplitude would lead to a reduction of the visual activity. We can estimate magnitude of
488 the reduction from saccade displacement by seeing how such displacement of the
489 stimulus from the center of the RF would reduce the response. Figure 8B shows the
490 results that such a displacement would produce on the two dimensional map of the RF
491 (see Methods). The vertical axis shows the percent change in FF activity with added
492 stimuli that we observed across our sample of neurons (Figure 4D). The horizontal axis
493 shows the change in activity that would result if we moved the stimulus spot from the
494 center (as would occur with different saccade amplitudes). As shown in the figure, there
495 was minimal change in the activity that can be attributed to the variability of the saccade

496 compared to the change with the added stimuli. There was no significant correlation
497 ($R=0.2$, $P=0.21$). Therefore, such a small increase in saccade endpoint variability was
498 unlikely to account for the decrease in FF activity. This analysis, however, does assume
499 that the FF has the same organization as the RF - a point that needs to be tested in future
500 investigations.

501 Changes in saccade latency with the addition of stimuli is of greater concern
502 because the FF stimulus was flashed just before the saccade and occurred with a delay
503 after the offset of the fixation point (which was the cue for the saccade). Therefore, if the
504 latency of the saccade changed, the time at which the FF stimulus flash occurred would
505 change with respect to saccade onset. Because the FF activity in the FEF is dependent
506 upon the proximity to the FF stimulus to the saccade onset (see Sommer and Wurtz
507 2008) this latency change itself could alter the FF activity. For the neuron shown in Figure
508 8A, the added stimuli did alter the saccade latency from $203 \text{ ms} \pm 22 \text{ ms}$ without added
509 stimuli to $225 \pm 18 \text{ ms}$ with the added stimuli, a mean difference of 22 ms. This 22 ms
510 increase in mean saccade latency could *reduce* the FF activity and could be the source of
511 the reduced FF activity we see with added stimuli. We therefore performed an additional
512 analysis on the neural activity to determine if this was the case. Figure 8C displays the
513 distribution of the intervals between FF stimulus onset and saccade onset for the example
514 neuron. The two distributions overlap, but note that there was more variability in the
515 interval distribution with added stimuli (black trace) than without them (blue trace). We
516 therefore reanalyzed a subset of trials where this interval was the same in both conditions
517 (within the vertical dashed red lines). For this subset of trials, the presence of the added
518 stimuli still significantly reduced the FF activity by 9.8 spikes/s on average (Figure 8D,
519 41% reduction, two-tailed t -test, $P<0.001$). These results were consistent for our neurons
520 in our sample that had sufficient variability in the stimulus-saccade interval to perform the
521 above analysis (two-tailed t -test, $P<0.001$, same four neurons as above). The reduction
522 was comparable to that seen for all trials as shown in Figure 3. Importantly, the neuronal
523 activity on the non overlapping trials (those outside the dashed red lines) was not
524 significantly different from the neural activity on the overlapping trials (two-tailed t -test,
525 $P=0.64$). We conclude that the change in saccade latency did not produce the reduction
526 in FF activity with added stimuli.

527 *Is the FF activity dependent on both the FF stimulus and the saccade?*

528 The above analysis shows that the FF activity in FEF requires the presence of the
529 FF stimulus but that its latency is fixed to the onset of the saccade. However, the
530 analysis does not demonstrate that the FF activity is not simply a saccade related
531 response; we show it occurs in association with saccades. We verified that the FF activity
532 was not just a saccade related response by using control trials embedded in every
533 experiment. In this control, when the monkey made saccades to the target but in the
534 absence of the stimulus, there was no FF activity. Figure 9A shows the example neuron
535 in which the absence of the FF stimulus eliminated the visual activity. This was true for all
536 cells in our sample of neurons that had shifting RFs, as has been demonstrated
537 previously for FEF neurons (Sommer and Wurtz 2008; Umeno and Goldberg 1997). The
538 saccade only activity within the same window that the FF activity was determined (see
539 Methods) was significantly less than the FF activity for the sample of neurons (one-tailed
540 t -test, $P < 0.05$). Therefore the saccade alone was not producing the FF activity. The FF
541 stimulus without the saccade also produced no response. In Figure 9B for the same
542 neuron, presenting the FF stimulus in the absence of the saccade produced no response
543 while the same stimulus when presented in the RF did produce a visual response. This
544 was also tested on all neurons, with the same result; in no case did the activity when
545 presenting the FF stimulus in the absence of the saccade meet the criteria for a response
546 (see Methods). Therefore, the FF activity was dependent on the combination of the FF
547 stimulus and the generation of the saccade.

548

549 **DISCUSSION**

550

551 **Visual salience effect on shifting RF activity**

552 The major explanation of visual stability in spite of displacement of the visual image
553 with each saccade is that advanced knowledge of the impending saccade is available from
554 an internal copy of the motor command to move the eye (a corollary discharge or efference
555 copy). This advanced knowledge makes it possible to recognize that the displacements are
556 self generated. First in parietal area LIP (Duhamel et al. 1992) and then in FEF region of
557 frontal cortex (Umeno and Goldberg 1997), neurons have been shown to become sensitive
558 to visual stimuli at the spatial location that their receptive field (RF) would occupy after the
559 saccade, the future field of the neuron (FF). Most of the experiments studying FF activity
560 have used a highly salient stimulus, an isolated flash against a uniform background, to
561 determine whether a neuron had FF activity. In the present experiments we explored the
562 effect of reducing this salience by adding the onset of other stimuli in the visual field at the
563 same time as the FF stimulus appeared. In a sample of 50 neurons with shifting RFs, we
564 found that 30% of the neurons had reduced FF activity, with a reduction averaging 16%.
565 This is consistent with a reduction in the FF activity observed in an LIP neuron in the
566 experiments of Gottlieb et al. (1998) as described in the Introduction. Thus, in the usual
567 shifting RF experiment, the activity resulting from the onset of the FF stimulus can be
568 regarded as resulting both from the anticipatory nature of the FF stimulus and the relative
569 salience of that stimulus.

570 Our experiments have a striking similarity to two human psychophysical experiments
571 that studied the effect of attention drawn by an abrupt onset of a stimulus flashed near the
572 time of a saccade (Golomb et al. 2008; Mathot et al. 2010; Mathot and Theeuwes 2011). In
573 one set of these experiments (Experiment 3 Mathot et al. 2010) the subject made a
574 saccade from one point to another and a cue stimulus was flashed just before the saccade
575 – identical to our paradigm. The subject was instructed to remember the cue location in
576 order to make a discrimination based on a stimulus appearing briefly at that point after the
577 saccade. The discrimination was better when the cue was located at what we refer to as
578 the FF location rather than other areas of the visual field, indicating that attention had
579 shifted to the FF even before the saccade was made. This behavioral measure of a shift of

580 attention to the FF before a saccade parallels our interpretation of the flash in the FF of a
581 neuron benefiting from the salience of the stimulus. At this point, the demonstration of the
582 neuronal changes in the monkey and the attention discrimination benefit in humans provide
583 at least an indication that attention is likely to be involved in both cases.

584 As in the previous experiments studying the effects of exogenous attention on the
585 response of neurons, our current experiments did not measure attention. We did not have
586 any behavioral measure of the monkey's attention to gauge the magnitude of the added
587 stimuli effect; we inferred the reduction of attention with the addition of stimuli from related
588 behavioral experiments. We think our observations are highly likely to result from the
589 effects of visual attention drawn to the salient stimulus onset because of three related
590 observations. First, psychophysical experiments have shown a decrease in performance
591 with the addition of visual stimuli in the visual field during search (Duncan and Humphreys
592 1989; Kim and Cave 1999) and on cued attention tasks (such as Kahneman et al. 1983;
593 Wright and Richard 2003). Of course, these search and attention experiments on humans
594 do not directly relate to shifting RFs in monkeys; they simply provide the only guidance
595 available on the consequence of adding visual stimuli. Second, visual search tasks have
596 shown the reduction of neuronal responses in both FEF (Cohen et al. 2009) and LIP (Balan
597 and Gottlieb 2006; Balan et al. 2008) with the addition of visual stimuli in the visual field.
598 Third, our experiments are remarkably parallel to those described above (Golomb et al.
599 2008; Mathot et al. 2010; Mathot and Theeuwes 2011) which did measure and find
600 exogenous attention effects. None of these experiments, however, can substitute for the
601 needed direct measurement simultaneously of the FF response and the effect of salience
602 on exogenous attention.

603

604 **Visual factors affecting the magnitude of salience on FF activity**

605 The strength of stimulus salience leading to exogenous or onset attention effects in
606 our experiments is almost certainly reduced by two factors. First, the FF stimuli were
607 presented repeatedly in the same region of the visual field, although at multiple locations
608 within this region on successive trials. It is reasonable to expect that the onset effect we
609 saw had habituated at least somewhat over the training and experimental periods
610 preceding the particular neuronal experiment. Added stimuli presented for the first time

611 might produce an even greater reduction in the FF activity with added stimuli. Second, we
612 always placed the added stimuli at a substantial distance from the FF stimulus in order to
613 minimize direct visual stimulation generated by the stimuli falling in the presumed FF of the
614 neuron. The consequence of this was that the added stimuli were pushed off to the side of
615 the monkey's visual field. This might also change the magnitude of the effect of the added
616 stimuli (Hagenaar and van der Heijden 1986).

617 Probably the most important questions on the addition of visual stimuli in the shifting
618 field experiments are related to the organization of the FF, particularly the extent of its
619 visual surround, and whether the added stimuli fell in a FF suppressive surround. At the
620 start of the experiment, we had established the presence of a suppressive surround and
621 had estimated its extent using the annulus test for the RF (see Methods). We then placed
622 the added stimuli about 5° beyond the outer edge of the surround so as to minimize the
623 direct visual activation of the neuron. The more important question, however, is the size
624 and organization of the FF. In each experiment, it would be challenging to both map in
625 detail the FF and do the added stimuli experiment so we relied on information about the
626 organization of the FF from other ongoing experiments. In experiments on FEF (personal
627 communication, Joiner, Cavanaugh, and Wurtz), we found that the beginning of the
628 surround for the RF and FF were within a few degrees of each other. In LIP neurons
629 (Phillips and Goldberg 2010), a comparison of the RF and FF showed that the FFs were
630 somewhat more narrowly tuned than RFs. Both observations imply that there may be
631 differences in the RF and FF, but the differences are small compared to our placement of
632 the added stimuli well beyond the estimated surround. We therefore interpret the reduction
633 of the FF response with the added stimuli as a reduction of salience rather than an effect of
634 a suppressive surround.

635 Our observations emphasize the visual modulation of FF activity. This is the second
636 component of the FF activity, the other being the temporal proximity to the saccade and its
637 accompanying corollary discharge (Kusunoki and Goldberg 2003; Sommer and Wurtz
638 2008). Thus the FF activity results from the conjunction of the visual stimulus in the right
639 part of the visual field and the corollary discharge associated with the right saccade
640 directed to that part of the visual field. It is not a FF visual response, but FF activity. The
641 present experiments emphasize that the magnitude of the FF activity is dependent on the

642 characteristics of the stimulus, particularly the salience of the stimulus, just as it is
643 dependent on the temporal proximity to the saccade. The difference in the composition of
644 the RF visual response and the FF activity, may account for the absolute differences in the
645 size of the effect of added stimuli on the RF responses and FF activity.

646 .

647 **Salience and its relation to visual stability**

648 Change blindness experiments emphasize the key role that attention plays in
649 determining what we see in the visual world. This attention has also been shown to be
650 relevant for our stable visual perception; attended objects are critical for maintenance of
651 visual stability (Mathot and Theeuwes 2011). The implication of this for visual stability is
652 that stability might not be maintained for the entire visual scene but just for attended parts.

653 One possibility is that stability is maintained just for those regions in and around the
654 fovea to which attention is directed during each visual fixation (see discussion in Wurtz et
655 al. 2011). Such a concentration of stabilization near the target of the saccade has been
656 demonstrated for the suppression of target motion during saccades (Deubel et al. 1996;
657 2002). If the shifting RFs are related to visual stability, then they too might be expected to
658 have a higher frequency near the center of the visual field. Our population of 171 FEF
659 neurons sampled across varying eccentricities within the central 35° of the visual field
660 seemed adequate for addressing this question. We found no evidence of a difference in
661 frequency of shifting RFs with eccentricity. The proportion of neurons with shifting RFs
662 tracked the proportion of neurons with visual RFs with remarkable precision (Figure 5). We
663 also found no systematic difference in the magnitude of the FF activity with increasing
664 eccentricity (Figure 6A). The limitation to these observations is that none were made
665 within the fovea so that if the frequency of FF activity in the fovea soars we would have
666 missed it. Within the visual field studied, our results in FEF are consistent with the finding
667 in LIP that there was no difference in the strength of FF activity in neurons with central,
668 intermediate and peripheral RFs (Heiser and Colby 2006). In both FEF and LIP, we have
669 no evidence that the shifting receptive fields are concentrated in the central visual field.

670 Another possibility is that stability across saccades is maintained for attended stimuli
671 regardless of the region of the visual field in which they fall. Stimulus salience would draw
672 attention and be included in what remains stable during a saccade. Our finding of a larger

673 magnitude of FF activity in FEF when the stimulus is a salient one is consistent with that
674 possibility. We did not have enough data to determine whether the salience effect on the
675 FF or its magnitude was related to eccentricity in the visual field (Figures 5 and 6B).

676 In summary, so far as FF activity contributes to visual stability, our evidence
677 indicates that the salience of an object is probably more important than its location in the
678 visual field for determining whether the object is included in what is perceptually stable
679 across saccades.

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803 **FIGURE LEGENDS**

804

805 **Figure 1. Potential onset and goal directed attention actions on shifting receptive**
806 **field activity.** (A) While the monkey looks at a fixation point (red cross) a receptive field
807 (RF) can be mapped (dotted red circle). As the monkey prepares to make a saccade
808 from the fixation point to a peripheral target (blue cross), there is an anticipatory shift of
809 the RF of the neuron to a future spatial location. This future field (FF) location (blue circle)
810 is at the same location with respect to the final eye position after the saccade (blue dotted
811 circle to blue cross) as the RF is to the current fixation point (red dotted circle to red
812 cross). (B) Two types of attention act at the time of the RF shift. First, as the monkey
813 makes the saccade to the target, there is a shift in goal directed or endogenous attention
814 to the target. Second, the single stimulus flashed against a dark background at the FF
815 location produces an onset or exogenous attention effect.

816

817 **Figure 2. Task for studying exogenous attention (onset attention) on the shifting**
818 **receptive field activity.** (A) The location of the RF, FF and added stimuli during the
819 shifting receptive field saccade task. The task has two conditions: a shift without added
820 stimuli (top line) and one with added stimuli (bottom line). In both conditions, after fixating
821 a central point (red cross) a RF stimulus (red spot in dotted circle) was flashed, and then
822 following a variable delay, the fixation point was extinguished as the target (blue cross)
823 came on. Before the saccade began (dashed arrow), a 50ms flash probed the sensitivity
824 at the FF location (blue spot in blue dotted circle). Two points to note: on every trial there
825 was a 50 ms flash in the RF and then just before the saccade a 50 ms flash in the FF; the
826 FF flash was over before the saccade began. In trials with added stimuli, eight added
827 visual stimuli came on at locations that did not evoke a visual response. The same spatial
828 configuration of the added stimuli was presented for the RF and FF, but shifted by the
829 vector between the initial and future fixation points (the saccade vector). (B) The timing of
830 the task events. The length of the colored bars represent the duration of the respective
831 event. See Methods for further details.

832

833 **Figure 3. Reduction of the future field activity by added stimuli for an example FEF**
834 **neuron.** The left column depicts the stimulus configuration and results for the RF
835 response and the right column depicts the equivalent for the FF activity. In trials with no
836 added stimuli, a single visual stimulus (red and blue spots) was flashed in the RF (A) and
837 FF (B). The RF, including excitatory center and suppressive surround, is represented by
838 the red dashed circle; the possible FF by the blue circle. The stimuli were at the same
839 location with respect to the initial fixation point (red cross at $0^{\circ}, 0^{\circ}$, with the RF stimulus at
840 $27^{\circ}, 19^{\circ}$) and future fixation point (blue cross at $-30^{\circ}, 0^{\circ}$, with the FF stimulus at $-3^{\circ}, 19^{\circ}$). In
841 the trials with added stimuli, the RF and FF stimulus was accompanied by eight added
842 visual spots (C and D, respectively), all 6° in diameter. The stimuli added to the RF spot
843 did not significantly alter the visual response (E, two-tailed *t*-test, $P=0.93$), but the addition
844 of the stimuli reduced the FF activity significantly (F, 44% reduction, two-tailed *t*-test,
845 $P<0.001$).

846
847 **Figure 4. Change in the RF response and FF activity with added stimuli for the**
848 **sample of neurons.** The RF response (A) and FF activity (B) with added stimuli (vertical
849 axis) is plotted against the respective responses without them (horizontal axis). Filled
850 circles represent neurons that had a significant decrease in the visual activity with added
851 stimuli (two-tailed *t*-test, $P<0.05$). The red and blue circles show the example neuron from
852 Figure 3, and the dashed line is the unity line. C and D display histograms of the percent
853 change of the RF response and FF activity with added stimuli. Black markers are the
854 average percent change for the sample, red (RF) and blue (FF) markers are the percent
855 change values for the example cell. There were significant decreases with added stimuli:
856 a small 4% decrease for the RF response and a larger 16% decrease for the FF activity.
857 Panels E and F display histograms for only those neurons showing a significant change
858 (two-tailed *t*-test, $P<0.05$) in the FF activity which shows a non-significant decrease for
859 the RF response (6%) and a larger significant decrease for the FF activity (34%).

860
861 **Figure 5. Cumulative distribution for the sample of neurons as a function of**
862 **receptive field eccentricity.** The cumulative distribution of the sample of neurons tested
863 (black circles, $n=171$) and the sub-sample of these cells that demonstrated a shifting RF

864 (blue circles, $n=52$) are plotted as a function of receptive field eccentricity. The orange
865 circles represent the shifting RF neurons that demonstrated a significant decrease (two-
866 tailed t -test, $P<0.05$) in the FF activity in the presence of added stimuli ($n=15$).

867

868 **Figure 6. Magnitude of FF activity across receptive field eccentricity.** (A) The
869 distribution (bin width 5°) of the magnitude of FF activity as a function of receptive field
870 eccentricity ($n=52$). The height of each bar represents the average FF activity for the cells
871 that fell within that bin. (B) The distribution (bin width 5°) of the FF activity with (orange
872 bars) and without added stimuli (blue bars) as a function of RF eccentricity. The black
873 trace represents the difference in the mean FF activity with and without added stimuli.
874 Only cells with a significant decrease (two-tailed t -test, $P<0.05$) in FF activity with added
875 stimuli are displayed ($n=15$). The height of each bar represents the average activity for
876 the cells that fell within that bin. The gaps at the three eccentricity ranges are due to a
877 lack of cells that demonstrated a significant decrease in the FF activity with added stimuli.

878

879 **Figure 7. Future field activity is better aligned to saccade onset than FF stimulus**
880 **onset.** (A) Each row on the raster plot represents spikes on one trial for the example cell
881 with the trials plotted in ascending order of saccade latency with the shortest latency at
882 the bottom. The neuronal activity is aligned to the onset of the FF stimulus and added
883 stimuli (green vertical line). The increased activity occurs long after the visual latency for
884 this neuron (47 ms, indicated by the dashed vertical red line) and follows the saccade
885 onset (blue line). (B) Same neuronal activity but now aligned to the saccade onset. Note
886 the difference in time scales between A and B. (C) The onset of the FF activity is plotted
887 against the onset of the saccade for the data presented in panel A. Onset times are with
888 respect to the onset of the FF stimulus and added stimuli. There was a significant linear
889 relationship between the onset of the FF activity and the onset of the saccade ($R=0.44$,
890 $P<0.001$).

891

892 **Figure 8. Changes in saccade endpoint scatter and latency with added stimuli do**
893 **not account for the FF activity decrease.** (A) For the example neuron presented in
894 Figure 3, the mean position of the saccade endpoint with and without added stimuli did

895 not increase but the scatter did increase (black and blue traces and ellipses respectively).
896 The ellipses represent 95% confidence intervals around the mean endpoint. (B) The
897 percent change in FF activity with added stimuli (vertical axis) is plotted against the
898 percent change in FF activity due to saccade endpoint variability (horizontal axis). There
899 was no significant relationship between the percent change in FF activity with added
900 stimuli and the percent change due to saccade endpoint variability ($R=0.2$, $P=0.21$). (Note
901 that positive percent changes on the horizontal axis represent cases where the saccade
902 endpoint variability for the added stimuli condition was *less* than the variability in the
903 without added stimuli condition.) (C) The distribution of the intervals between the FF
904 stimulus onset and saccade onset with (black trace) and without added stimuli (blue
905 trace). The 0 on the x axis represents saccade onset and the red dashed lines represent
906 the points where the interval distributions overlap (between -167 ms and -107 ms). (D)
907 The FF activity with (black trace) and without added stimuli (blue trace) for the trials within
908 the red dashed lines in panel C. The presence of the added stimuli reduced the FF
909 activity significantly (41% reduction, two-tailed t -test, $P<0.001$) even when the intervals
910 were matched.

911

912 **Figure 9. The future field activity is not saccade-related activity or a receptive field**
913 **response.** (A) For the example neuron presented in Figure 3, when the monkey made a
914 saccade without a FF stimulus the neuron did not respond (black trace) in contrast to the
915 case with the FF stimulus present (blue trace). (B) For the same neuron, a FF stimulus
916 flashed while the monkey fixated without making a saccade did not activate the neuron
917 (black trace). This activity is different from that elicited by a visual stimulus placed in the
918 RF (red trace).

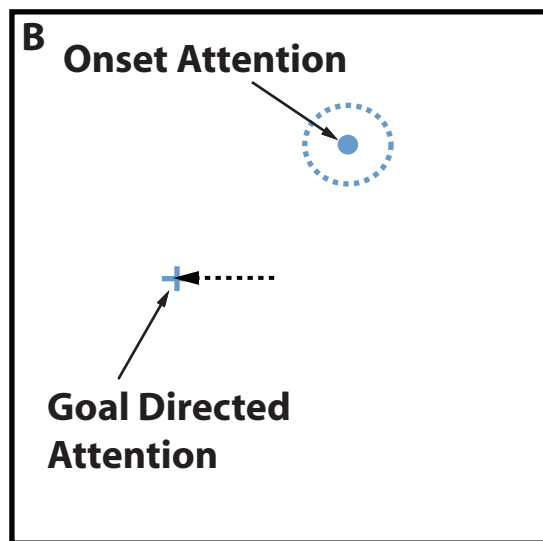
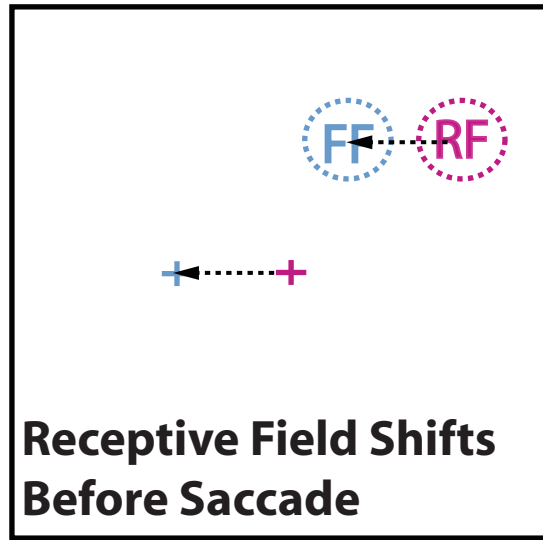
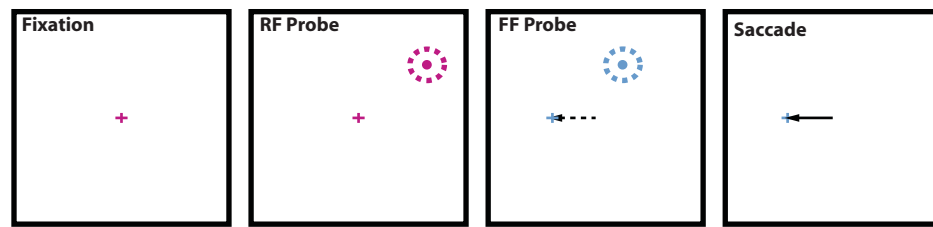
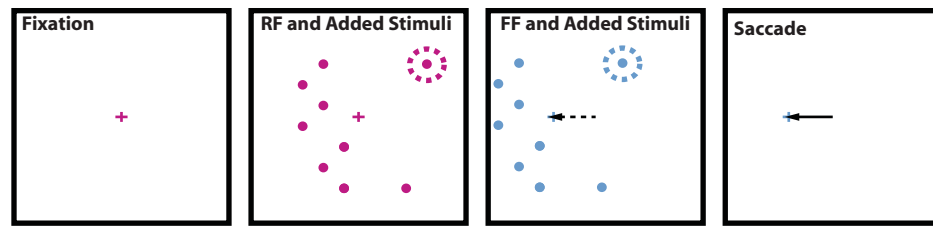
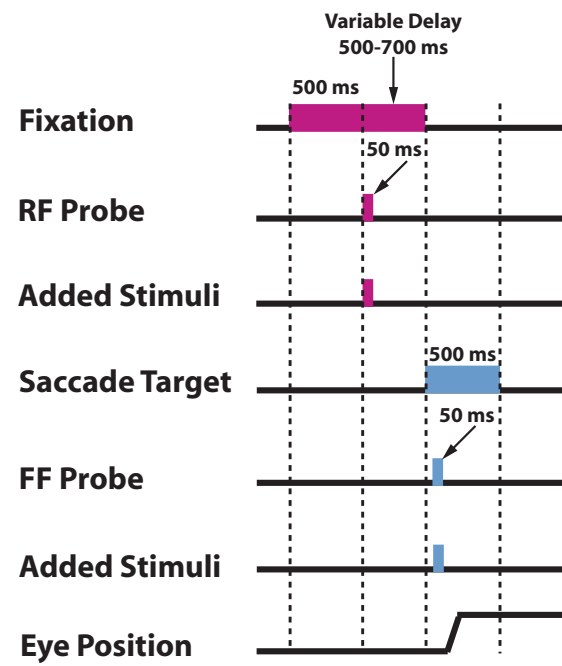


Figure 1

A**Without Added Stimuli Trials****With Added Stimuli Trials****Figure 2****B**

Receptive Field Response

Future Field Activity

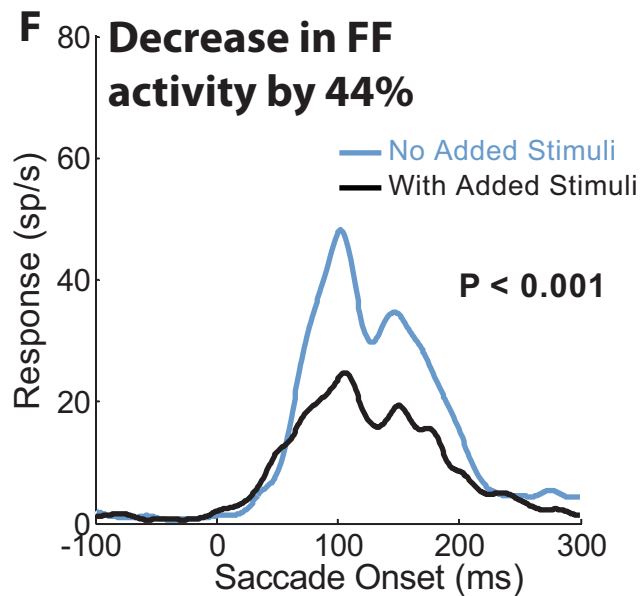
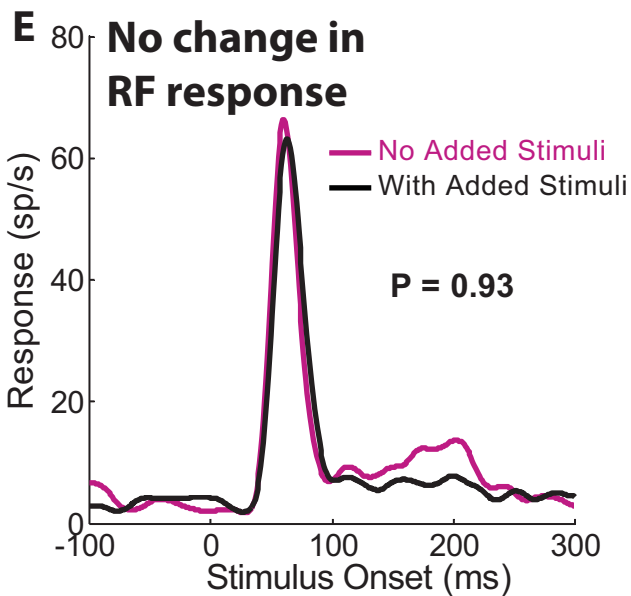
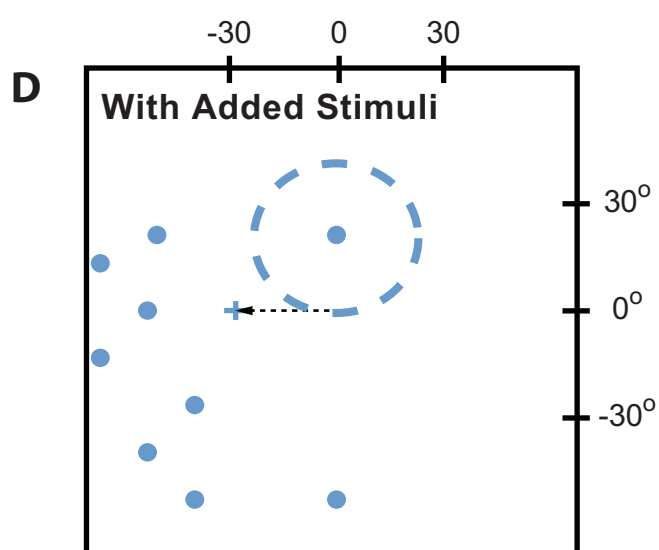
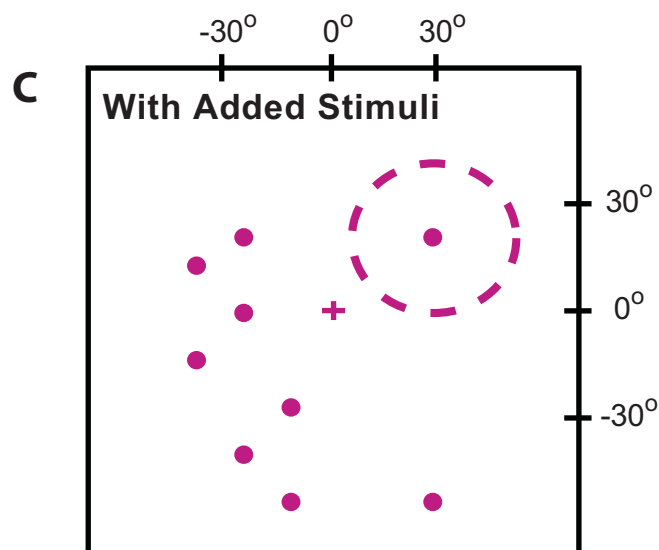
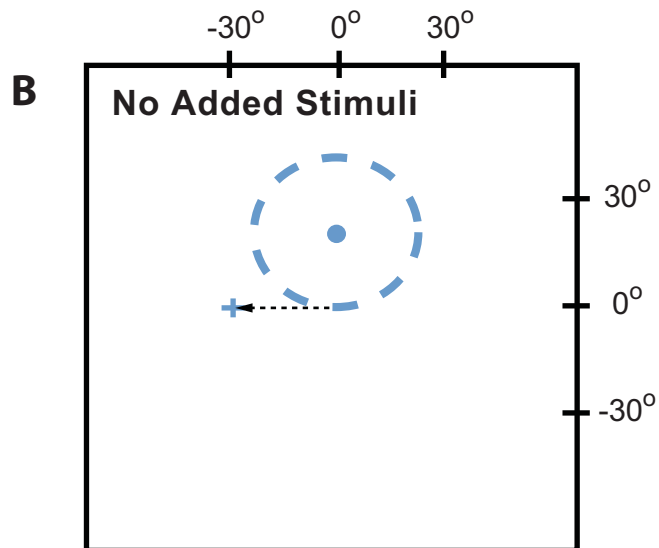
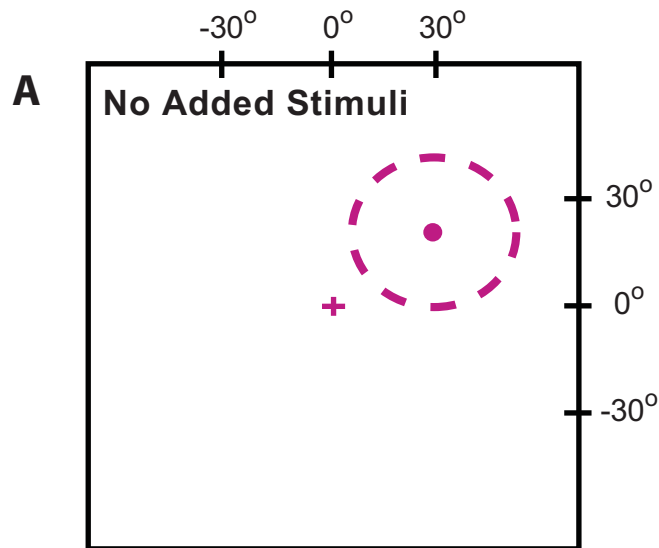
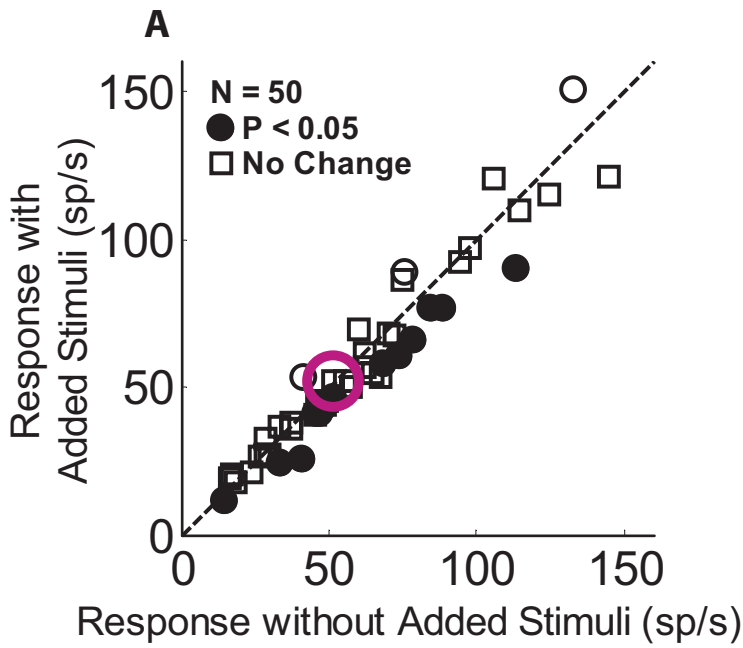


Figure 3

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Receptive Field Response



Future Field Activity

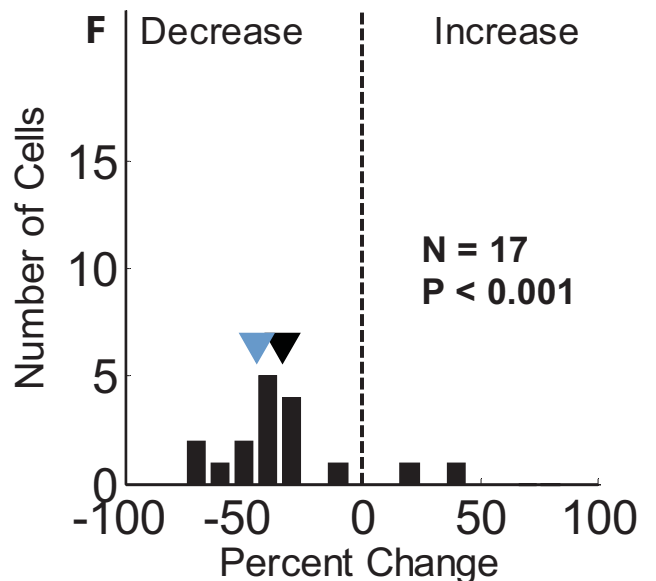
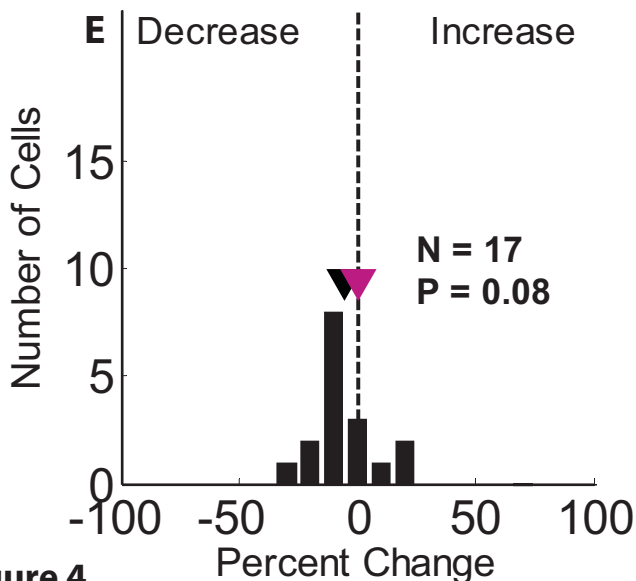
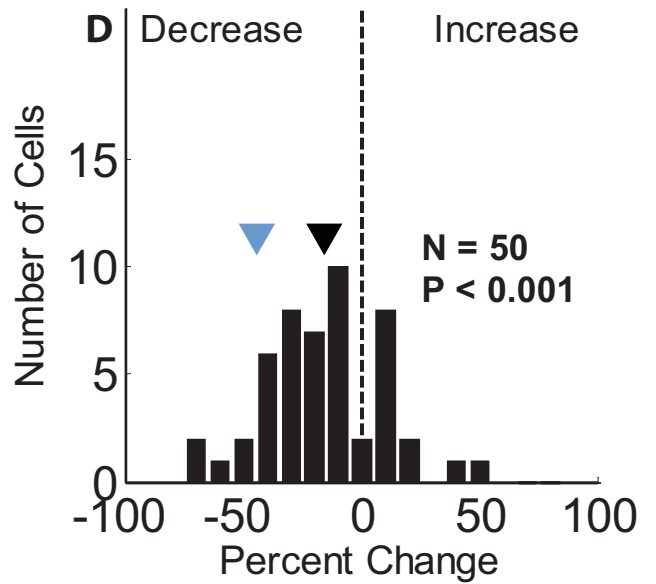
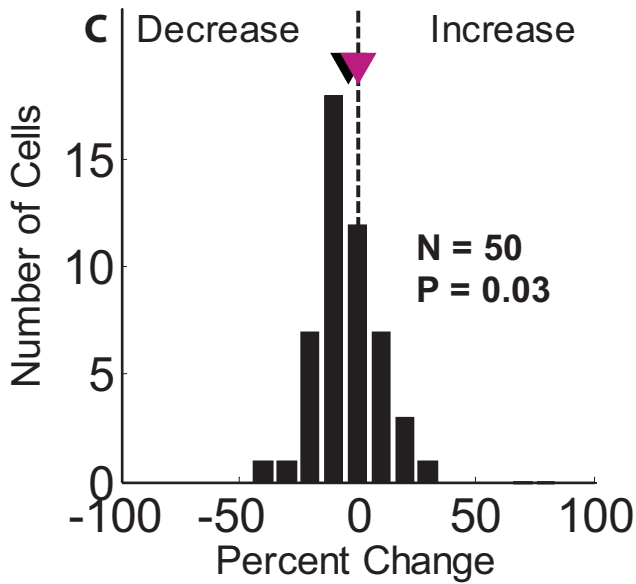
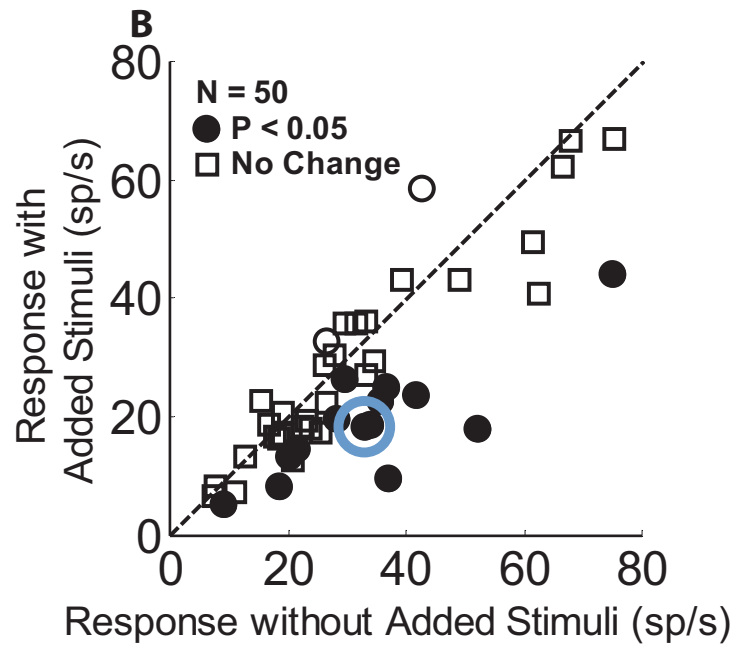


Figure 4

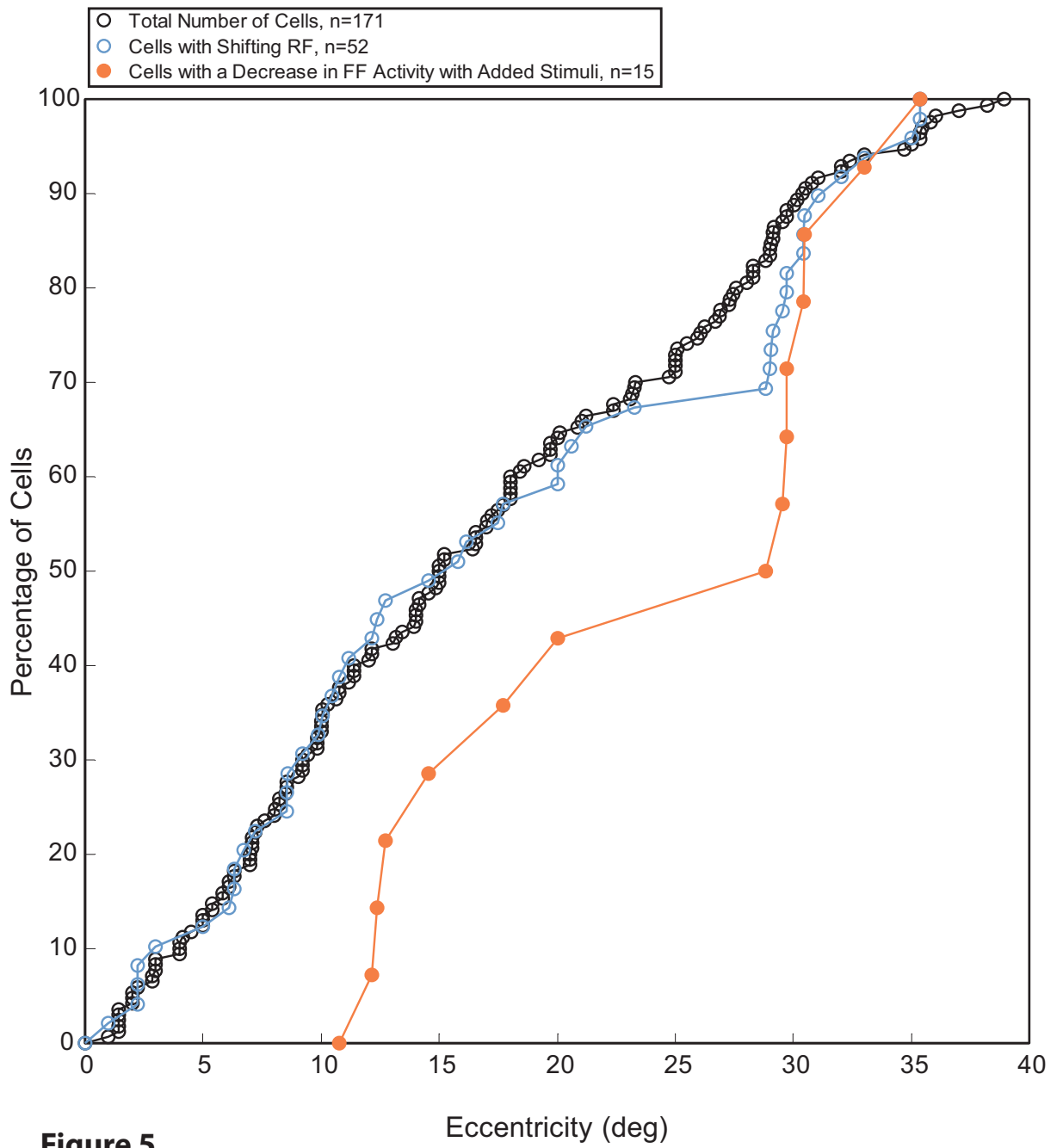


Figure 5

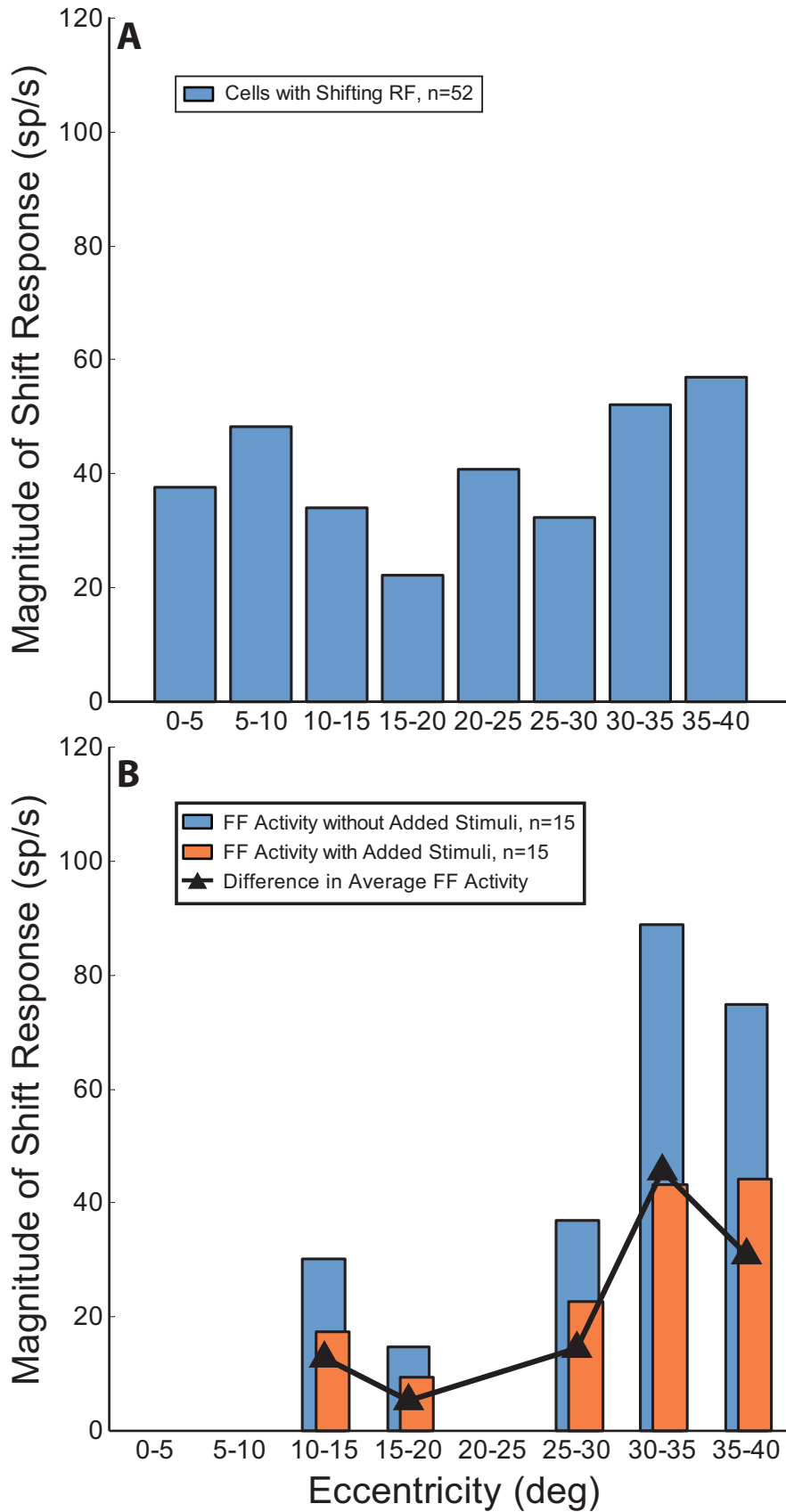


Figure 6

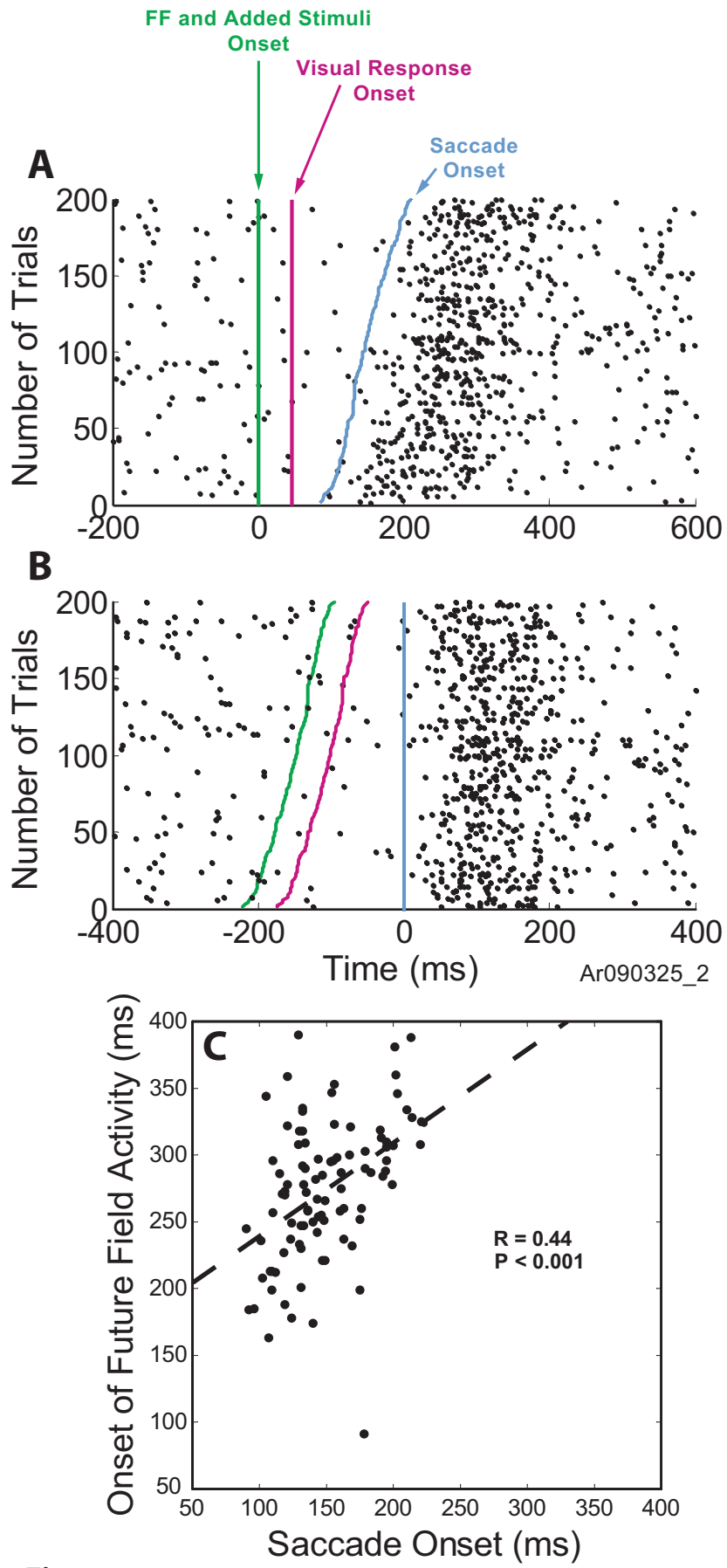


Figure 7

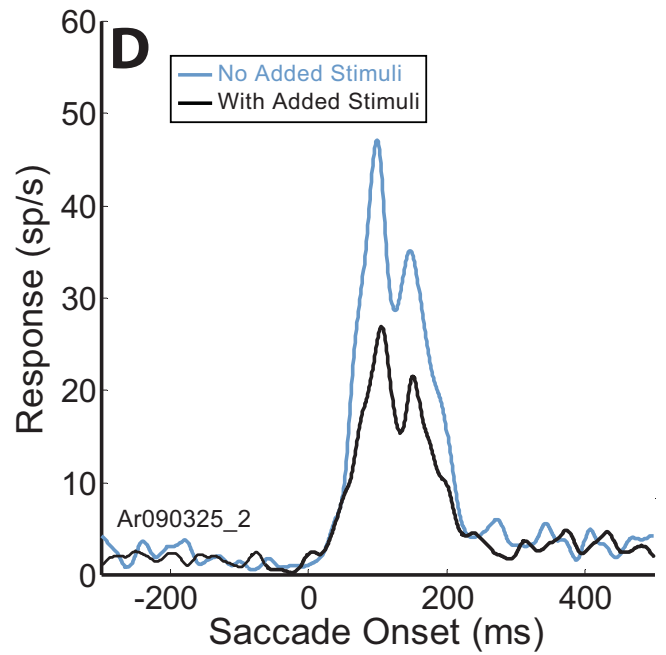
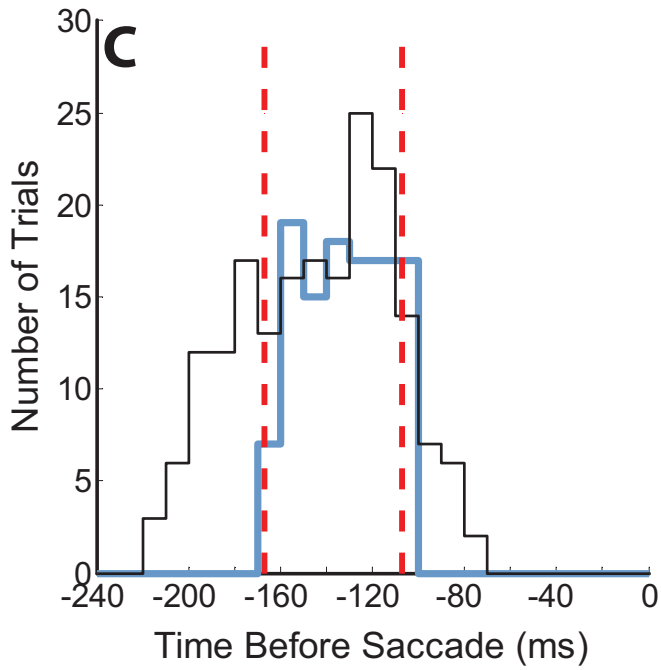
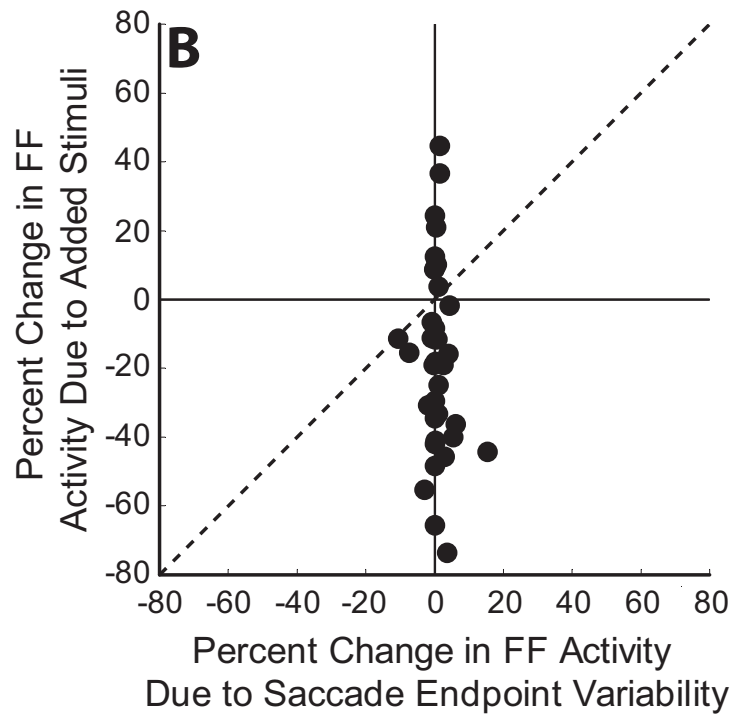
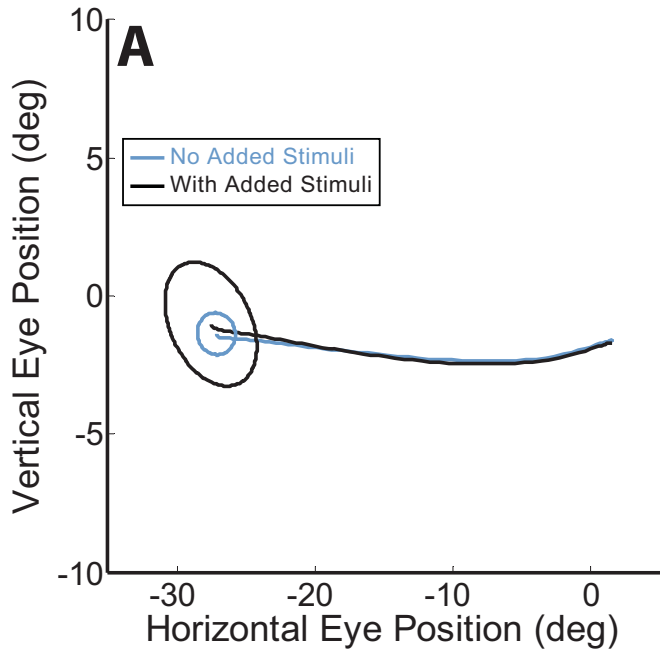
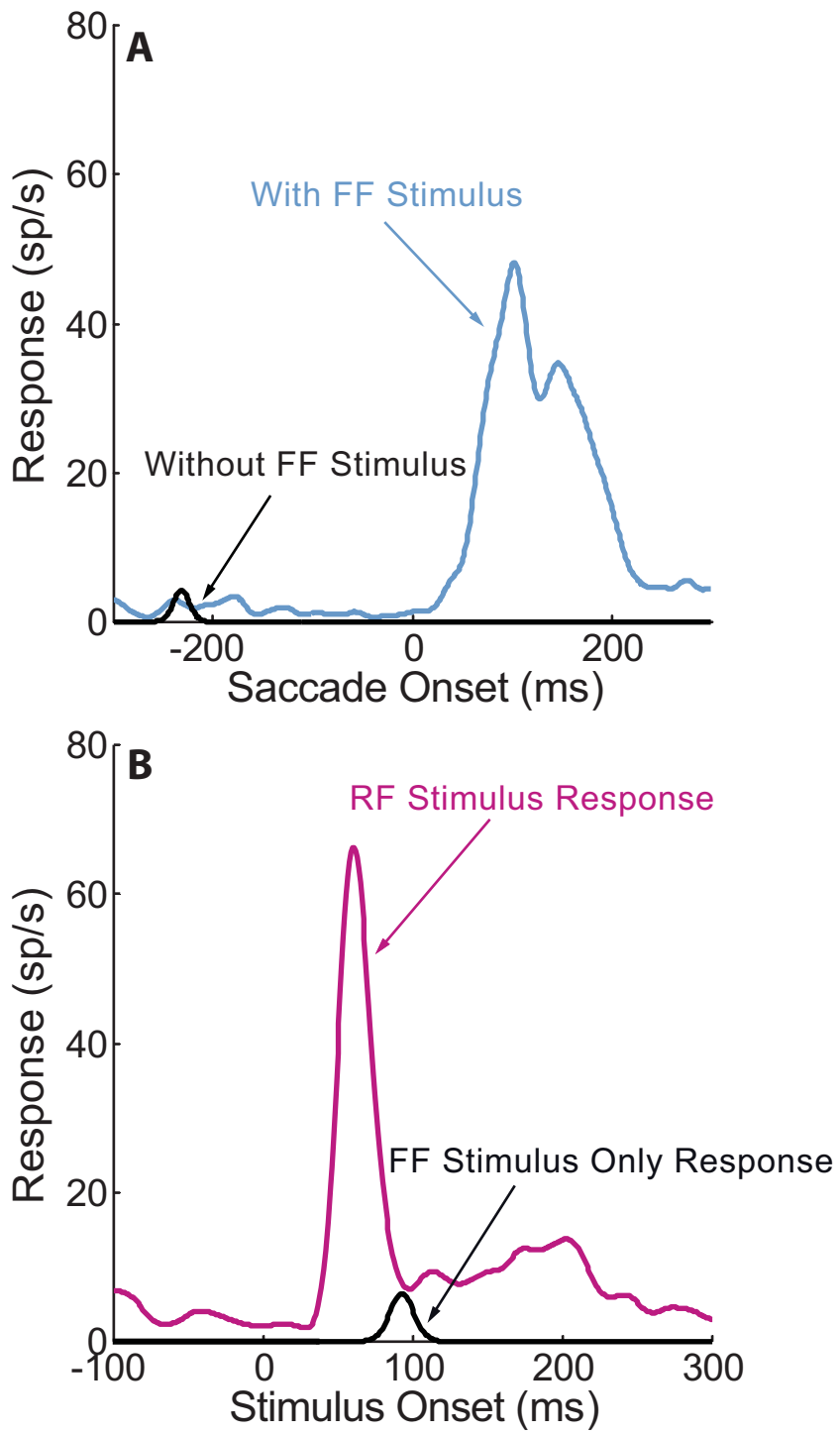


Figure 8



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Figure 9