



23 **Abstract**

24

25 Saccadic eye movements cause rapid retinal-image shifts that go perceptually unnoticed  
26 several times per second. The mechanisms for perceptual saccadic suppression have been  
27 controversial, in part due to sparse understanding of neural substrates. Here we uncovered  
28 an unexpectedly specific neural locus for saccadic suppression in the primate superior  
29 colliculus (SC). We first developed a sensitive behavioral measure of perceptual  
30 suppression in two male macaque monkeys (*Macaca mulatta*), demonstrating known  
31 selectivity to low spatial frequencies. We then investigated visual responses in either  
32 purely visual SC neurons or anatomically-deeper visual-motor neurons, which are also  
33 involved in saccade generation commands. Surprisingly, visual-motor neurons showed  
34 the strongest visual suppression, and the suppression was dependent on spatial frequency  
35 like in perception. Most importantly, visual-motor neuron suppression selectivity was  
36 highly predictive of behavioral suppression effects in each individual animal, with our  
37 recorded population explaining up to ~74% of behavioral variance even on completely  
38 different experimental sessions. In contrast, purely visual SC neurons only had mild and  
39 unselective suppression (only explaining up to ~48% of behavioral variance). These  
40 results run contrary to a hypothesized SC mechanism for saccadic suppression, in which a  
41 motor command in the visual-motor and motor neurons is relayed to the more superficial  
42 purely visual neurons to suppress them, and to then potentially be fed back to cortex.  
43 Instead, our results indicate that an extra-retinal modulatory signal mediating perceptual  
44 suppression is already established in visual-motor neurons.

45

46 **New & Noteworthy**

47

48 Saccades, which repeatedly re-align the line of sight, introduce spurious signals in retinal  
49 images that normally go unnoticed. In part, this happens because of peri-saccadic  
50 suppression of visual sensitivity. Here we discovered that a specific sub-type of superior  
51 colliculus (SC) neurons may play a critical role in saccadic suppression. Curiously, it is  
52 the neurons that help mediate the saccadic command itself that exhibit perceptually-  
53 relevant changes in *visual* sensitivity, not the previously hypothesized purely visual  
54 neurons.

55

56 **Keywords**

57

58 Saccades; Microsaccades; Superior colliculus; Saccadic suppression; Perceptual stability

## 59 **Introduction**

60

61 A long standing question in visual neuroscience has been on the sense of perceptual  
62 stability that we normally experience despite incessant eye movement (Wurtz 2008).  
63 Saccadic eye movements dramatically alter retinal images several times per second.  
64 During each saccade, retinal images undergo rapid motion, which can be beyond the  
65 range of motion sensitivity of many neurons. Such motion ought, at least in principle, to  
66 cause a brief period of “grey out” every time a saccade occurs (Campbell and Wurtz  
67 1978; Matin 1974; Wurtz 2008; Wurtz et al. 2011), much like the grey out experienced  
68 while standing near train tracks and high-speed trains sweep by.

69

70 Several fiercely debated theories on why we do not experience saccade-related visual  
71 disruptions have emerged. On the one hand, purely visual mechanisms, such as masking  
72 (Matin et al. 1972), can be sufficient to suppress perception of saccade-induced grey out  
73 and/or motion (Wurtz 2008). Consistent with this, people are not entirely “blind” during  
74 saccades, as long as spatio-temporal properties of peri-saccadic stimuli remain within  
75 sensitivity ranges of visual neurons (Burr and Ross 1982; Castet et al. 2001; Castet and  
76 Masson 2000; Garcia-Perez and Peli 2011; Ilg and Hoffmann 1993; Matin et al. 1972;  
77 Ross et al. 1996). On the other hand, extra-retinal mechanisms (Sperry 1950; von Holst  
78 and Mittelstaedt 1950) for perceptual suppression are supported by the lack of  
79 suppression during simulated image displacements (Diamond et al. 2000), the  
80 dependence of suppression on spatial frequency (Burr et al. 1982; Burr et al. 1994; Hass

81 and Horwitz 2011; Volkmann et al. 1978), and the observation of saccade-related  
82 modulation of neural excitability in the absence of visual stimulation (Rajkai et al. 2008).  
83  
84 While it is likely that a combination of visual and extra-retinal mechanisms co-exist  
85 (Wurtz 2008), controversies surrounding saccadic suppression will not be resolved  
86 without further understanding of neural mechanisms. We were particularly interested in  
87 potential mechanisms for extra-retinal suppression, whose sources remain elusive. For  
88 example, it was suggested from behavioral studies that selective perceptual suppression  
89 of low spatial frequencies is evidence for selective magno-cellular (achromatic) pathway  
90 suppression (Burr et al. 1994). However, in lateral geniculate nucleus (LGN) and primary  
91 visual cortex (V1), the two earliest visual areas, selective magno-cellular suppression is  
92 not established (Hass and Horwitz 2011; Kleiser et al. 2004; Ramcharan et al. 2001;  
93 Reppas et al. 2002; Royal et al. 2006). In addition, a popular hypothesis about a source of  
94 saccadic suppression is that a “corollary” of saccade commands in visual-motor and  
95 motor neurons of the superior colliculus (SC) is fed back to superficial purely visual  
96 neurons to suppress their sensitivity, and to jumpstart a putative feedback pathway for  
97 cortical suppression through pulvinar (Berman and Wurtz 2008; 2010; 2011; Isa and Hall  
98 2009; Lee et al. 2007; Phongphanphane et al. 2011; Wurtz 2008; Wurtz et al. 2011).  
99 However, evidence for an SC saccadic suppression pathway from visual-motor/motor  
100 neurons to visual neurons comes primarily from rodent SC slices (Isa and Hall 2009; Lee  
101 et al. 2007; Phongphanphane et al. 2011). In the awake, behaving primate, findings of  
102 stronger suppression in visual-motor rather than visual neurons cast doubt on this  
103 hypothesis (Chen et al. 2015; Hafed et al. 2015; Hafed and Krauzlis 2010).

104

105 We visited the question of neural loci for saccadic suppression by explicitly testing the  
106 predictions of a perceptually-relevant suppressive pathway from SC motor-related  
107 neurons to purely visual ones. We have previously shown that SC neurons exhibit time  
108 courses of saccadic suppression remarkably similar to those of perceptual effects (Hafed  
109 and Krauzlis 2010). Here, we adapted our sensitive behavioral paradigm (Hafed and  
110 Krauzlis 2010) to first establish *selectivity* in saccadic suppression, and we then asked  
111 whether *visual* neural modulations in either purely visual or visual-motor SC neurons  
112 would reflect such selectivity. Contrary to the hypothesis about a suppressive pathway  
113 from deep to superficial layers (Isa and Hall 2009; Lee et al. 2007; Phongphanphane et  
114 al. 2011), we observed perceptually-relevant and spatial-frequency specific saccadic  
115 suppression only in the deeper visual-motor neurons. Our results suggest that the SC is  
116 indeed relevant for perceptually-relevant saccadic suppression, but that the putatively  
117 extra-retinal modulatory signal mediating suppression may already be established in the  
118 visual-motor neurons, without the need for a relay through purely visual neurons.

119

120

## 121 **Materials and Methods**

122

123 We exploited microsaccades to study saccadic suppression because they offer important  
124 experimental advantages while at the same time being mechanistically similar to larger  
125 saccades (Hafed 2011; Hafed et al. 2015; Hafed et al. 2009; Zuber et al. 1965). First,  
126 microsaccades are small (median amplitude in our data:  $\sim 7.5$  min arc). Thus, pre- and  
127 post-movement visual response fields (RF's) are not displaced by much, minimizing the  
128 problem of dramatic spatial image shifts caused by saccades (Wurtz 2008; Wurtz et al.  
129 2011). Experimentally, this meant presenting the exact same stimulus at the exact same  
130 screen location with and without microsaccades to isolate suppression effects. Second,  
131 microsaccades have velocities significantly  $< 100$  deg/s (median peak velocity in our data:  
132  $\sim 17.7$  deg/s). Thus, image motion caused by microsaccades is well within the range of  
133 motion sensitivity, even for small features (Thiele et al. 2002), allowing us to study  
134 suppression even when no motion-induced grey out is expected to occur. Third, we have  
135 previously shown that SC visual sensitivity exhibits pre-, peri-, and post-microsaccadic  
136 suppression that is very similar in time course and amplitude to perceptual saccadic  
137 suppression in humans, and we have also demonstrated a sensitive behavioral paradigm  
138 for the same phenomenon (Hafed and Krauzlis 2010). Fourth, and most importantly, we  
139 avoided potential masking effects by only presenting stimuli immediately *after*  
140 microsaccades. This allowed us to study a potential intrinsic reduction in neural  
141 excitability after saccades (Chen et al. 2015; Hafed and Krauzlis 2010; Zuber et al. 1966),  
142 and to ensure comparing “no-microsaccade” to “microsaccade” conditions without the  
143 latter involving saccade-induced retinal image motion. Thus, the logic of all of our

144 experiments was to present high-contrast gratings (80% contrast), which were highly  
145 visible and well within the saturation regime of SC contrast sensitivity curves (Chen et al.  
146 2015; Hafed and Chen 2016; Li and Basso 2008), and to ask whether either behavioral or  
147 visual neural responses to these gratings were altered if the gratings appeared  
148 immediately after a microsaccade.

149

### 150 **Animal Preparation**

151 Ethics committees at regional governmental offices in Tuebingen approved experiments.  
152 Monkeys P and N (male, *Macaca mulatta*, aged 7 years) were prepared earlier (Chen and  
153 Hafed 2013; Chen et al. 2015; Hafed and Chen 2016; Hafed and Ignashchenkova 2013).  
154 We used scleral search coils to record eye movements (Fuchs and Robinson 1966; Judge  
155 et al. 1980).

156

### 157 **Behavioral Tasks**

158 In all tasks, monkeys initially fixated a small, white spot presented over a gray  
159 background (Chen and Hafed 2013; Chen et al. 2015; Hafed and Ignashchenkova 2013).

160

161 *Behavioral tests.* Trials started with an initial fixation interval of random duration  
162 (between 600 and 1500 ms). After this interval, we initiated a real-time process to detect  
163 microsaccades (Chen and Hafed 2013). If a microsaccade was detected within 500 ms, a  
164 stationary vertical Gabor grating appeared at 3.5 deg to the right or left of fixation, and  
165 the fixation spot was removed simultaneously. Monkeys oriented to the grating as fast as  
166 possible using a saccadic eye movement, and saccadic reaction time (RT) served as a

167 sensitive behavioral measure of SC visual response strength (Boehnke and Munoz 2008;  
168 Hafed and Chen 2016; Hafed et al. 2015; Hafed and Krauzlis 2010; Tian et al. 2016).  
169 Grating onset occurred ~25, 50, 75, 100, 150, or 200 ms after online microsaccade  
170 detection, and we later measured precise times of microsaccade onset during data  
171 analysis for all results presented in this paper (see Data Analysis below). If no  
172 microsaccade was detected during our 500 ms online detection window, a grating was  
173 presented anyway, and the data contributed to “baseline” measurements (i.e. ones with  
174 the stimulus appearing without any nearby microsaccades). The grating was 2 deg in  
175 diameter. Spatial frequency in cycles per degree (cpd) was one of five values: 0.56, 1.11,  
176 2.22, 4.44, 11.11 (Hafed and Chen 2016), and phase was randomized. Our monitor  
177 resolution allowed displaying the highest spatial frequency without aliasing and  
178 distortion. We collected 8153 and 7117 trials from monkeys N and P, respectively. We  
179 removed trials with an intervening microsaccade between fixation spot removal and the  
180 orienting saccade.

181

182 *Neural recordings.* We isolated single neurons online, and we identified their RF  
183 locations and sizes using standard saccade tasks (Chen et al. 2015; Hafed and Chen  
184 2016). We then ran our main experimental paradigm. In each trial, monkeys fixated while  
185 we presented a similar vertical grating to the one we used in behavioral tests above, but  
186 the grating was now inside the recorded neuron’s RF. Grating size was optimized for the  
187 recorded neuron, and was specifically chosen to fill as much of the RF as possible (and  
188 showing >1 cycle of the lowest spatial frequency). Task timing was identical to that in  
189 (Chen et al. 2015); briefly, a grating was presented for 250 ms while monkeys fixated,

190 and the monkeys never generated any saccadic or manual responses to the grating (they  
191 simply maintained fixation, during which they generated microsaccades, and they were  
192 rewarded at the end of the 250 ms stimulus presentation phase for maintaining fixation).  
193 We collected data from 90 neurons, covering 1-24 deg eccentricities. We classified  
194 neurons as purely visual neurons or visual-motor neurons using previous criteria from  
195 visually-guided and memory-guided saccade tasks (Chen et al. 2015; Hafed and Chen  
196 2016). To ensure sufficient microsaccades for statistical analyses (i.e. with sufficient  
197 trials having stimulus onset within the critical post-movement intervals that we analyzed),  
198 we collected >800 trials per neuron. We then separated trials as ones having no  
199 microsaccades within +/- 100 ms from grating onset (>100 trials per neuron; mean: 289  
200 trials per neuron) or ones with grating onset within 50 ms *after* microsaccades (>25 trials  
201 per neuron; mean: 79 trials per neuron). For some analyses, we considered grating onsets  
202 up to 100 ms after microsaccades.

203

204 It is important to note here that for all neurons reported in this paper, we never observed a  
205 microsaccade-related movement burst (Hafed et al. 2009; Hafed and Krauzlis 2012).

206 Thus, even for stimuli appearing immediately after a microsaccade, the neural responses  
207 that we analyzed were *visual* bursts in response to stimulus onset, and not movement-  
208 related saccade or microsaccade bursts. The only difference between purely visual and  
209 visual-motor neurons in this study was that visual-motor neurons would, in principle,  
210 exhibit a saccade-related burst if the monkeys were to hypothetically generate saccades  
211 towards the RF location (but not if they generated smaller microsaccades during  
212 fixation). Thus, any neural modulations that we report in this study are not direct

213 microsaccade-related motor bursts. It is also important to note that our monkeys did not  
214 generate any targeting saccades to the gratings during recordings. We were simply  
215 studying *visual* sensitivity if a stimulus appeared near an eye movement (which happened  
216 to be small due to our experimental choice). Our approach was thus similar to classic  
217 ways of studying neural correlates of saccadic suppression (i.e. monkeys make saccades  
218 while neurons are visually stimulated; e.g. Zanos et al. 2016; Hafed and Krauzlis 2010;  
219 Bremmer et al. 2009).

220

## 221 **Data Analysis**

222 *Behavioral analyses.* For behavior, we measured RT as a function of spatial frequency  
223 and time of grating onset relative to microsaccades. We detected microsaccades using  
224 previously described methods (Hafed et al. 2009), and we used such detection to identify  
225 grating onset time relative to microsaccade onset or offset. We defined no microsaccade  
226 trials as trials with no microsaccades <250 ms from grating onset. RT on these trials  
227 constituted our baseline.

228

229 *Firing rate analyses.* For neural data, we measured stimulus-evoked firing rate after the  
230 onset of a given spatial-frequency grating under two scenarios: (1) when the grating  
231 appeared without any nearby microsaccades within +/- 100 ms, and (2) when the grating  
232 appeared immediately after a microsaccade. Baseline, no-microsaccade spatial frequency  
233 tuning curves (i.e. responses for each given spatial frequency) were described recently  
234 (Hafed and Chen 2016), but here we analyzed microsaccadic influences on these curves.  
235 We did not analyze trials with grating onset immediately before or during microsaccades,

236 to avoid pre-movement modulations (Chen et al. 2015; Hafed 2013) and retinal-image  
237 shift effects caused by movement of the eyes.

238

239 To analyze stimulus-evoked firing rate, we measured peak visual response 20-150 ms  
240 after grating onset. In some analyses, we also measured mean firing rate within an  
241 interval after grating onset. In this case, we tailored the averaging window to each spatial  
242 frequency, because visual burst latency depended on spatial frequency (e.g. Fig. 3, see  
243 cyan bars on x-axes). Our averaging windows for mean firing rate were all 100-ms long  
244 windows starting at 20 ms (for 0.56 cpd), 25 ms (for 1.11 cpd), 30 ms (for 2.22 cpd), 40  
245 ms (for 4.44 cpd), or 80 ms (for 11.11 cpd). We chose these intervals after inspecting all  
246 neurons as follows. For each neuron and spatial frequency, we found the time at which  
247 firing rate became  $>3$  s.d. from a pre-stimulus baseline (mean activity 0-100 ms before  
248 stimulus onset). We then chose our window start time as the average start time of the first  
249 quartile of the entire population (rounded to the nearest 5 ms).

250

251 To compare visual sensitivity on microsaccade and no-microsaccade trials, we created a  
252 “normalized firing rate” modulation index for each individual spatial frequency. We  
253 measured firing rate on microsaccade trials (i.e. trials with grating onset within 50 ms  
254 after microsaccades) and divided it by rate on no-microsaccade trials (i.e. trials with no  
255 microsaccades within  $<100$  ms from grating onset). A value  $<1$  indicates suppression.  
256 Note that we only considered neurons with  $>5$  spikes/s stimulus-evoked response (even  
257 on 11.11 cpd trials, which frequently had the lowest firing rates), thus avoiding “divide  
258 by zero” problems. Also, note that this modulation index isolates changes in visual

259 sensitivity associated with microsaccadic suppression, regardless of how visual  
260 sensitivity itself might depend on spatial frequency without microsaccades. For example,  
261 visual responses in general are expected to be weaker for high spatial frequencies (Hafed  
262 and Chen 2016); however, our modulation index would normalize activity within a given  
263 spatial frequency in order to isolate any further suppression of visual sensitivity due to  
264 saccadic suppression.

265

266 In our analyses (including behavioral analyses), we also combined microsaccades  
267 towards or away from the grating because microsaccadic suppression is not direction-  
268 dependent in the post-movement interval that we focused on (Chen et al. 2015). We also  
269 confirmed this when analyzing the present data set (data not shown). We additionally  
270 considered a potential confound in our data. Specifically, because microsaccade trials  
271 were usually fewer than no-microsaccade trials for a given stimulus, it could be argued  
272 that the measured firing rates on microsaccade trials may have been biased relative to the  
273 no-microsaccade trials as a result of fewer trial repetitions. We thus checked whether the  
274 smaller numbers of trials for the microsaccade condition somehow explained our neural  
275 modulation results. For each neuron and spatial frequency, we subsampled the no-  
276 microsaccade trials, such that we kept only the same number of trials as in the  
277 corresponding microsaccade condition. We repeated such subsampling 10000 times with  
278 replacement, and we confirmed that all of our statistical results were not due to the  
279 microsaccade condition having fewer trials than the no-microsaccade condition (e.g. see  
280 Fig. 3). Finally, we combined neurons representing different eccentricities in our  
281 population analyses. We did so because we found that suppression is independent of

282 eccentricity during the post-movement interval that we focused on (also see Chen et al.  
283 2015).

284

285 To investigate the relevance of neural modulations to behavioral effects, we correlated  
286 behavioral patterns of saccadic suppression from the behavioral tests to neural  
287 modulations obtained from the recordings. For example, we related visual response  
288 strength to RT as a function of time of grating onset after microsaccades. We also did this  
289 for neural modulations of “first-spike latency”. This latency was defined as the time of  
290 visual burst onset after grating onset, and we investigated whether this time was affected  
291 by saccadic suppression. For neurons with no baseline activity (the majority), first-spike  
292 latency is trivially obtained as the first occurring spike after stimulus onset. For neurons  
293 with baseline activity, we used Poisson spike-train analysis to estimate visual burst onset  
294 (Legendy and Salcman 1985).

295

296 For all analyses with time courses, we used bin steps of 10 ms and bin widths of 50  
297 ms (except for Fig. 2C, F with both bin steps and bin widths of 25 ms).

298

299 *Local field potential (LFP) analyses.* To analyze LFP’s, we sampled neurophysiological  
300 activity at 40 KHz. The signal was first filtered in hardware (0.7-6 KHz). We then  
301 removed 50, 100, and 150 Hz line noise using an IIR notch filter and then applied a zero-  
302 phase-lag lowpass filter (300 Hz cutoff). We finally down-sampled to 1 KHz. We  
303 analyzed filtered LFP traces like firing rates (Hafed and Chen 2016; Ikeda et al. 2015),

304 and we classified electrode track locations as visual or visual-motor according to the  
305 neurons isolated from these tracks in the same sessions (Hafed and Chen 2016).

306

307 To obtain a measure of intrinsic peri-microsaccadic modulation of LFP's independent of  
308 visual stimulation, we took all microsaccades occurring in a pre-stimulus interval (20-100  
309 ms before grating onset). We then aligned LFP traces on either microsaccade onset or  
310 end. To compare this data to a baseline, we took identically-long analysis intervals, again  
311 from pre-stimulus periods, but with no microsaccades occurring anywhere within these  
312 intervals.

313

314 To correlate LFP responses to behavioral dynamics of saccadic suppression (similar to  
315 what we did with firing rates), we measured peak transient LFP deflection as the  
316 minimum in the stimulus-evoked LFP trace 20-150 ms after grating onset. We created a  
317 "field potential index" by dividing this measurement on microsaccade trials by that on  
318 no-microsaccade trials. An index  $>1$  indicates enhancement. For a control analysis, we  
319 computed the index after correcting for a microsaccade-related LFP level shift that may  
320 have happened due to intrinsic peri-microsaccadic modulation of the LFP independent of  
321 visual stimulation. We did this according to the following procedure. On microsaccade  
322 trials, we measured the average LFP value -25 to 25 ms from grating onset. We then  
323 subtracted the peak stimulus-evoked LFP deflection from this baseline measurement  
324 before dividing by the no-microsaccade trials. If an intrinsic peri-microsaccadic LFP  
325 modulation explained our results of LFP enhancement with increasing spatial frequency  
326 (see Results), then the baseline-shifted index should show no enhancement.

327

328 We also analyzed transient stimulus-evoked LFP deflection latency (analogous to first-  
329 spike latency). We found the first time at which the LFP was  $>2$  s.d. away from baseline  
330 LFP (calculated as the mean LFP value -25 to 25 ms from grating onset), and there also  
331 had to be  $>5$  ms of continuous  $>2$  s.d. deviation from baseline. We did this separately for  
332 microsaccade and no-microsaccade trials, and we subtracted the measurements to obtain  
333 the influences of saccadic suppression on stimulus-evoked LFP deflection latency. If the  
334 LFP transient deflection occurs faster on microsaccade trials, then the subtraction gives a  
335 negative value.

336

337

338 **Results**

339

340 **Selective Microsaccadic Suppression of Low Spatial Frequencies in Behavior**

341 Isolation of perceptually-relevant saccadic suppression requires demonstrating a selective  
342 form of suppression in behavior, and subsequently asking which neurons reflect such  
343 selectivity. We thus first developed a sensitive behavioral measure demonstrating  
344 selective suppression, which was based on our earlier results (Hafed and Krauzlis 2010).  
345 We did so for microsaccades because they are mechanistically similar to larger saccades,  
346 while at the same time providing important experimental advantages (Materials and  
347 Methods). Monkeys fixated, and we initiated a computer process for real-time  
348 microsaccade detection (Chen and Hafed 2013). After such detection by a programmable  
349 delay, we presented a stationary vertical Gabor grating (80% contrast). The monkeys  
350 oriented towards the grating as fast as possible. Because SC *visual* bursts are strongly  
351 correlated with RT (Boehnke and Munoz 2008; Chen et al. 2015; Hafed and Chen 2016;  
352 Hafed et al. 2015; Hafed and Krauzlis 2010; Tian et al. 2016), we used RT changes in  
353 this task as a sensitive measure of microsaccadic influences on visual sensitivity (Hafed  
354 and Krauzlis 2010; Tian et al. 2016).

355

356 Similar to previously reported perceptual effects with large saccades (Burr et al. 1994)  
357 and microsaccades (Hass and Horwitz 2011), grating onset after microsaccades had a  
358 strong, yet selective, impact on behavior in our monkeys. Figure 1A shows example eye  
359 position (left) and velocity (right) traces from one monkey while we presented a 1.11 cpd  
360 grating. The black traces show trials without microsaccades <250 ms from grating onset,

361 and the gray traces show trials with grating onset ~20-100 ms after microsaccades. There  
362 was a marked increase in RT during microsaccade trials (Fig. 1A). However, when we  
363 presented 4.44 cpd gratings, RT's on microsaccade and no-microsaccade trials were  
364 similar (Fig. 1B; compare gray and black distributions). Thus, the microsaccadic  
365 suppressive effect (causing slower RT's) was diminished for higher-frequency gratings.  
366 These sample-trial results demonstrate a microsaccadic correlate of selective perceptual  
367 suppression of low spatial frequencies by large saccades and microsaccades (Burr et al.  
368 1982; Burr et al. 1994; Hass and Horwitz 2011; Volkman et al. 1978).

369

370 Across sessions, both monkeys showed selective RT increases for low spatial frequencies  
371 (Fig. 2A, D). On no-microsaccade trials (black curves), RT increased with increasing  
372 spatial frequency, as expected from dynamics of the early visual system (Breitmeyer  
373 1975) and SC (unpublished observations). This effect was statistically significant ( $p < 0.01$   
374 for monkey N and  $p < 0.01$  for monkey P, 1-way ANOVA with spatial frequency as the  
375 main factor). However, with gratings appearing ~20-100 ms after microsaccades, the RT  
376 cost relative to no-microsaccade trials (i.e. the difference in RT between microsaccade  
377 and no-microsaccade trials) was strongest for the lowest spatial frequencies (Fig. 2B, E;  
378  $p < 0.01$  for monkey N and  $p < 0.01$  for monkey P, 1-way ANOVA with spatial frequency  
379 as the main factor). This effect was not a ceiling effect on RT (because of the baseline  
380 increase with increasing spatial frequency). For example, at 4.44 cpd, RT on  
381 microsaccade and no-microsaccade trials was similar (Fig. 2A, D; magenta rectangles),  
382 but it got even slower for 11.11 cpd regardless of eye movements. Thus, the reduction in  
383 RT differences between microsaccade and no-microsaccade trials for high spatial

384 frequencies (Fig. 2B, E) was indicative of a selective suppression of low spatial  
385 frequencies, and not necessarily a ceiling effect on RT.  
386  
387 Our behavioral paradigm also provided rich information about saccadic suppression  
388 dynamics, which we could later use to identify a behaviorally-relevant SC neural  
389 modulation. For example, we evaluated microsaccadic suppression time courses across  
390 different spatial frequencies. Figure 2C, F illustrates this by plotting RT as a function of  
391 when a 1.11 or 4.44 cpd grating appeared after microsaccades. Microsaccadic  
392 suppression had a clear time course of RT costs for each spatial frequency, with both  
393 monkeys showing lower suppression for the higher spatial frequency immediately after  
394 microsaccades, and then a gradual return towards the baseline no-microsaccade  
395 performance for a given frequency.

396  
397 Therefore, using a behavioral measure sensitive to SC visual response strength (Boehnke  
398 and Munoz 2008; Hafed and Chen 2016; Hafed et al. 2015; Hafed and Krauzlis 2010),  
399 we demonstrated a robust and selective pattern of microsaccadic suppression, which is  
400 directly analogous to perceptual suppression with large saccades (Burr et al. 1982; Burr et  
401 al. 1994; Hass and Horwitz 2011; Volkmann et al. 1978). We were now in a position to  
402 evaluate neural correlates of this suppression, and to specifically test a previously  
403 published hypothesis that perceptually-relevant suppression may emerge in purely visual  
404 SC neurons (Berman and Wurtz 2008; 2010; 2011; Isa and Hall 2009; Lee et al. 2007;  
405 Phongphananee et al. 2011; Wurtz 2008; Wurtz et al. 2011).  
406

407 **Selective Suppression of Low Spatial Frequencies in Visual-Motor but not Visual**

408 **SC Neurons**

409 Using the same animals but in completely different experimental sessions not requiring  
410 any saccadic responses at all (Materials and Methods), we recorded the activity of purely  
411 visual SC neurons (24 neurons; located  $680 \pm 95$  s.e.m.  $\mu\text{m}$  below SC surface) or  
412 visual-motor neurons (66 neurons;  $1159 \pm 66$  s.e.m.  $\mu\text{m}$  below SC surface). Both types  
413 of neurons exhibit robust *visual* responses, but the question remains as to which would  
414 show perceptually-relevant suppression. We presented gratings similar to those used in  
415 Figs. 1-2 inside each neuron's RF (Materials and Methods). However, the task was now a  
416 pure fixation task, and we only analyzed either no-microsaccade trials or trials in which  
417 the gratings appeared immediately *after* microsaccades (Materials and Methods).

418

419 Ensuring pure fixation was especially important to demonstrate behavioral relevance of  
420 our neural modulations. Specifically, one of our primary goals was to directly correlate  
421 neural dynamics to behavior in each animal (as will be presented later). Showing that a  
422 specific SC cell class is highly correlated with behavior compared to another cell class,  
423 *even* when the correlations are made across completely independent sessions and tasks,  
424 would demonstrate the behavioral relevance of the cell class. Moreover, demonstrating  
425 that neural suppression dynamics appear on *visual* responses, even in the complete  
426 absence of an overt response, shows that it is *sensory* responses that matter during  
427 saccadic suppression. Finally, ensuring fixation avoided saccade preparation influences  
428 on visual sensitivity (Li and Basso 2008).

429

430 Visual-motor SC neurons showed the strongest saccadic suppression, and in a spatial-  
431 frequency selective manner. Figure 3A shows the activity of two sample pure visual  
432 neurons (one per row) during presentations of different spatial frequencies (across  
433 columns), and Fig. 3B shows the activity of two sample visual-motor neurons (in the  
434 same format). In each panel, saturated colors show activity with no microsaccades <100  
435 ms from grating onset, and unsaturated colors show activity when the same grating was  
436 presented within 50 ms after microsaccades. In no-microsaccade trials, all neurons  
437 showed expected visual bursts, but burst strength varied with spatial frequency (Fig. 3,  
438 saturated colors). This is suggestive of spatial-frequency tuning (Hafed and Chen 2016),  
439 but our purpose here was to investigate suppression relative to no-microsaccade  
440 responses; thus, we scaled the y-axis in each panel such that across panels, no-  
441 microsaccade curves visually appeared to be roughly equal in height. Using such scaling,  
442 visual-burst suppression (unsaturated colors) was rendered clearer (and quantitatively, we  
443 always measured suppression relative to the no-microsaccade responses *within* each  
444 given spatial frequency independently and not across spatial frequencies; Materials and  
445 Methods). Importantly, there were differences in suppression patterns between visual and  
446 visual-motor neurons. For the visual neurons (Fig. 3A), suppression was mild and  
447 relatively inconsistent across spatial frequencies; for the visual-motor neurons (Fig. 3B),  
448 there was strong suppression for the lowest spatial frequency (Neuron #3: ~32%; Neuron  
449 #4: ~38%;  $p < 0.01$  for each neuron, Mann-Whitney U-test), and there was also a  
450 systematic reduction in suppression strength with increasing frequency (by 4.44 and  
451 11.11 cpd, there was practically no suppression left at all;  $p = 0.49$  for 4.44 cpd and  $p = 0.41$   
452 for 11.11 cpd in Neuron #3, and  $p = 0.15$  for 4.44 cpd and  $p = 0.99$  for 11.11 cpd in Neuron

453 #4, Mann-Whitney U-test). Importantly, the eye movement associated with suppression  
454 in all panels had ended before grating onset. Thus, the suppression cannot be attributed to  
455 blurring of the gratings by eye movements. Moreover, the suppression cannot also be due  
456 to a reduced number of trial repetitions in the microsaccade condition: the shaded curves  
457 in Fig. 3 show no-microsaccade firing rates after we subsampled the no-microsaccade  
458 condition to match trials with the microsaccade condition (Materials and Methods); the  
459 firing rates were statistically indistinguishable from our original full set of no-  
460 microsaccade trials.

461

462 Across neurons, there was selective suppression of visual sensitivity as a function of  
463 spatial frequency, but only in visual-motor neurons. Figure 4 summarizes these findings  
464 by plotting a suppression index (Materials and Methods) as a function of spatial  
465 frequency. Visual bursts were suppressed in both visual and visual-motor neurons  
466 (suppression index  $< 1$ ). However, the suppression was not spatial-frequency selective,  
467 and it was weaker, in visual neurons; in visual-motor neurons, there was strong  
468 suppression only for the lowest spatial frequencies, and the effect gradually dissipated  
469 away with increasing frequency. We confirmed these observations statistically for both  
470 peak and mean visual response (i.e. both Fig. 4A and Fig. 4B). One-way ANOVA's  
471 revealed a main effect of spatial frequency in visual-motor ( $p < 0.01$ ) but not visual  
472 ( $p = 0.29$ ) neurons. Also, the average suppression in visual neurons was 11% across spatial  
473 frequencies ( $p = 0.1$ , Mann-Whitney U-test), and it was 22% in visual-motor neurons  
474 ( $p < 0.01$ , Mann-Whitney U-test). A difference between visual and visual-motor neurons  
475 also appeared in suppression temporal dynamics (Fig. 5). Thus, there are differences in

476 saccadic suppression strength between visual and visual-motor SC neurons, and visual-  
477 motor neuron suppression selectivity appears more similar to behavioral effects, both in  
478 our own experiments (Figs. 1-2) as well as in the literature of human perceptual effects  
479 (Burr et al. 1982; Burr et al. 1994; Volkman et al. 1978).

480

481 **Better Correlation Between Visual-Motor Neuron Dynamics and Behavior than**  
482 **Between Visual Neuron Dynamics and Behavior**

483 To further explore the apparent similarity between visual-motor neuron suppression  
484 patterns (Fig. 4) and behavior (Fig. 2), we used the dynamics of our recorded population  
485 as a proxy for how the SC might be engaged in our behavioral task of Figs. 1-2. We  
486 plotted the time course of behavioral suppression (similar to Fig. 2C, F) for each spatial  
487 frequency and each monkey individually (Fig. 6A, E), and we also plotted the neural time  
488 course of visual-motor neuron suppression, again for each monkey individually (Fig. 6B,  
489 F; an example time course for purely visual neurons can also be seen in Fig. 5A). For this  
490 comparative analysis, we used the same binning windows in both behavioral and neural  
491 data (50-ms bin widths in steps of 10 ms starting at 0 ms after microsaccade end), and we  
492 next correlated the two time courses: we plotted all samples of the behavioral time course  
493 against all samples of the neural time course irrespective of spatial frequency or time  
494 after microsaccades (Fig. 6C, G). There was high correlation between visual burst  
495 strength in SC visual-motor neurons and the behavioral effect of microsaccadic  
496 suppression: whenever visual bursts were weaker, RT costs increased, and vice versa,  
497 regardless of spatial frequency or time after microsaccades. This high correlation is

498 particularly remarkable given that the behavioral and neural data were collected in  
499 completely different sessions and with different behavioral tasks.  
500  
501 The highest correlation between neural patterns and behavior was observed only when we  
502 used peak visual response of visual-motor SC neurons as the behavioral predictor (Fig.  
503 6C, G). When we correlated behavioral time courses with peak visual response of purely  
504 visual neurons, the correlations were significantly worse (Fig. 6D, H;  $p=0.02$  for monkey  
505 N and  $p=0.02$  for monkey P, Steiger's Z-test). We also tried to correlate behavior to mean  
506 visual response after stimulus onset (within a certain time window; Materials and  
507 Methods) or first-spike latency (whether of visual or visual-motor neurons), but peak  
508 visual response of visual-motor neurons always provided the best predictor. Specifically,  
509 even though there was a modest change in first-spike latency when visual bursts were  
510 suppressed (e.g. see Fig. 3), the effect was not as consistent as the effect of visual  
511 response magnitude, and it meant that neural response latency was not as good a correlate  
512 of behavioral effects as peak visual response.  
513  
514 The results of Fig. 6 suggest that saccadic suppression in visual-motor neurons is more in  
515 line with behavioral effects than for purely visual neurons. This is inconsistent with a  
516 hypothesized role of a feedback pathway from visual-motor to visual neurons in  
517 perceptually-relevant saccadic suppression in the SC (Isa and Hall 2009; Lee et al. 2007;  
518 Phongphanphane et al. 2011). However, one possible confound could be in the  
519 distribution of preferred spatial frequencies in visual-motor neurons. For example, if only  
520 the preferred spatial frequency of a neuron experiences the strongest suppression, and if

521 visual-motor neurons only had low preferred spatial frequencies, then the selective  
522 suppression of Fig. 4 would emerge. However, we found no clear differences in patterns  
523 of preferred spatial frequencies between visual and visual-motor neurons. Moreover, we  
524 explicitly analyzed suppression profiles of visual-motor neurons as a function of the  
525 neurons' preferred spatial frequencies. For each spatial frequency, we took only neurons  
526 preferring this spatial frequency, and we checked how these neurons were suppressed.  
527 Figure 7A-D shows the results of this analysis. There was indeed a tendency for the  
528 preferred spatial frequency of a neuron to experience the strongest suppression relative to  
529 other frequencies (e.g. black arrows). However, this strongest suppression still became  
530 progressively weaker and weaker with increasing spatial frequency (e.g. compare Fig.  
531 7A, B to Fig. 7C, D). This is further demonstrated by Fig. 7E, in which we took the  
532 maximal suppression frequency from each of the panels in Fig. 7A-D and plotted them  
533 with an indication of the behavioral microsaccadic suppression profile (obtained as the  
534 inverse of RT profiles from Fig. 2B, E, with arbitrary y-axis scaling). Importantly, we  
535 again made sure that the neural suppression data in this figure were analyzed in an  
536 identical manner to behavioral analyses (i.e. we considered the same interval of stimulus  
537 onsets happening 20-100 ms after microsaccade end as in the behavioral analyses). As  
538 can be seen, there was a clear match between neural and behavioral effects in both  
539 animals (the correlation between neural suppression and behavioral suppression in this  
540 figure was 0.99 for monkey N and 0.89 for monkey P). Thus, the selective suppression of  
541 Figs. 3-6 was not an artifact of potential biased spatial-frequency tuning properties of  
542 only visual-motor neurons.  
543

544 Taken together, our results so far suggest that perceptually-relevant SC saccadic  
545 suppression (i.e. selective for spatial frequency as in perception) is localized in the visual-  
546 motor neurons, with visual neurons only showing modest and non-selective modulations.

547

## 548 **Influence of a Putative Microsaccadic Source Signal on Local SC Population**

### 549 **Activity During Suppression**

550 To demonstrate that there may indeed be a saccadic source signal associated with  
551 suppressed SC visual bursts (i.e. putative corollary discharge), we analyzed local field  
552 potentials (LFP's) around our electrodes (Materials and Methods). Stimulus onset in no-  
553 microsaccade trials caused a negative-going “stimulus-evoked” LFP deflection for both  
554 visual and visual-motor electrode tracks (Hafed and Chen 2016; Ikeda et al. 2015). For  
555 example, Fig. 8 shows LFP traces (in a format similar to Fig. 3) as a function of spatial  
556 frequency for an example superficial track (i.e. among visual neurons; Fig. 8A) and an  
557 example deeper track (among visual-motor neurons; Fig. 8B). Remarkably, on  
558 microsaccade trials (unsaturated colors), stimulus-evoked LFP response was not  
559 suppressed. In fact, for the visual-motor electrode track (Fig. 8B), LFP response was  
560 enhanced, and more so with increasing spatial frequency (Fig. 9A;  $p < 0.01$ , 1-way  
561 ANOVA on the modulation index with spatial frequency as the main factor). Given that  
562 LFP's reflect not just local population spiking activity, but also putative synaptic inputs,  
563 these results suggest the existence of a possible microsaccade-related input modulating  
564 visual bursts, and this effect was again stronger in visual-motor than visual electrode  
565 tracks (Fig. 9A). However, it is important to emphasize here that this signal was not a

566 direct microsaccade command because none of our neurons at all electrode locations in  
567 this study exhibited microsaccade-related movement bursts (Materials and Methods).

568

569 Our interpretation of a modulatory movement-related input mediating firing rate  
570 suppression effects is consistent with the enhanced LFP effect seen in Figs. 8 and 9A for  
571 high spatial frequencies. These frequencies evoke the weakest visual activity (Figs. 3, 8;  
572 saturated colors), meaning that the influence of a saccadic source signal for suppression  
573 (which is dependent on the movement and not the stimulus) should become increasingly  
574 more obvious in the LFP with increasing spatial frequency (Fig. 9A). Thus, combined  
575 with earlier firing rate results, our LFP analyses reveal that visual-motor SC neurons may  
576 be closely associated with a movement-related source for perceptually-relevant saccadic  
577 suppression.

578

579 One possible confound with the above result is that microsaccades (even though they  
580 ended before stimulus onset) might cause long-lasting LFP modulations, which would be  
581 superimposed on a stimulus-evoked LFP deflection in Fig. 8. In other words, the evoked  
582 response could potentially still be suppressed, but it could be level-shifted because it rides  
583 on a microsaccade-induced LFP modulation. Indeed, during simple fixation without any  
584 other visual stimuli, both visual and visual-motor SC electrode locations exhibited  
585 prolonged microsaccade-related LFP modulations, involving a subtle negativity after  
586 microsaccade end (Fig. 10). It is intriguing that this effect happens even in extra-foveal  
587 SC (i.e. with no microsaccade-related bursting neurons), and in purely visual layers as  
588 well, because it suggests that the modulation is not a direct motor command. Instead, it is

589 a modulatory effect that is far-reaching across the SC, potentially explaining previously  
590 observed peri-microsaccadic modulations in neural activity and behavior (Chen et al.  
591 2015; Hafed 2013; Hafed et al. 2015; Tian et al. 2016). The modulation is also similar to  
592 saccade-related LFP modulations in human SC (Liu et al. 2009). In any case, what this  
593 modulation (Fig. 10) means for Fig. 8 is that an LFP negativity following microsaccades  
594 might alter the baseline on top of which the stimulus-evoked deflection rides on.  
595 However, we found that the low amplitude of peri-microsaccadic LFP modulation (Fig.  
596 10) was not sufficient to explain the lack of LFP suppression in stimulus-evoked LFP's  
597 (Fig. 8). Specifically, we corrected for a baseline shift at grating onset (Materials and  
598 Methods), and we still found no suppression in the strength of the stimulus-evoked LFP  
599 response (Fig. 9A). Thus, in Figs. 8-10, we believe that we have uncovered evidence for a  
600 putative microsaccade-related modulatory input at the time of visual burst suppression in  
601 both SC visual and visual-motor neurons. Moreover, this input shows differential  
602 modulation between superficial and intermediate electrode tracks (Fig. 9A), consistent  
603 with our firing rate results.  
604  
605 Enhanced stimulus-evoked LFP response amplitudes (Fig. 9A) were also accompanied by  
606 slightly faster LFP responses (Fig. 9B), again consistent with a movement-related source  
607 modulating neural firing rates at the time visual burst occurrence (because the movement  
608 happened before stimulus onset). It is also interesting to note that, like firing rate time  
609 courses, time courses of stimulus-evoked LFP modulations for stimuli appearing after  
610 microsaccades were also correlated with behavioral microsaccadic suppression dynamics  
611 (as in Fig. 6). In the LFP's, the best behavioral predictor was the latency of stimulus-

612 evoked LFP deflection, and visual-motor electrode tracks again showed higher  
613 correlation values with behavior than visual electrode tracks. These results are shown in  
614 Fig. 11, which is formatted similarly to Fig. 6, except that the neural data in this figure  
615 was now based on LFP measurements instead of firing rates.  
616  
617 Our results combined demonstrate that visual-motor neurons are more in line with  
618 selective perceptual effects of saccadic suppression, both in humans (Burr et al. 1982;  
619 Burr et al. 1994; Volkman et al. 1978) and monkeys (Fig. 2), than purely visual neurons.  
620 This calls for recasting of a hypothesized SC pathway for saccadic suppression, relying  
621 on a relay to superficial SC layers from deeper centers of the saccade motor command.  
622  
623

624 **Discussion**

625

626 We found spatial-frequency selective saccadic suppression in SC visual-motor neurons,  
627 and the neural dynamics of visual-motor neuron suppression were well correlated with  
628 behavior. Our results are in line with interpretations of saccadic suppression as a  
629 reduction in response gain (Chen et al. 2015; Guez et al. 2013; Hafed and Krauzlis 2010).  
630 Consistent with this, we have recently found that neural contrast thresholds in the SC are  
631 altered around the time of microsaccades (Chen et al. 2015). We have also found that for  
632 SC neurons possessing some baseline activity in the absence of a visual stimulus, there  
633 was very modest peri-microsaccadic modulation of activity (see Fig. S2 of Chen et al.  
634 2015) when compared to the modulations in stimulus-evoked visual bursts that we have  
635 observed here and earlier (Chen et al. 2015; Hafed and Krauzlis 2010). We believe that  
636 observations like these place constraints on the potential sources and mechanisms of  
637 extra-retinal modulation that is often invoked in theories of saccadic suppression.

638

639 There have been few successful demonstrations of perceptually-relevant patterns of  
640 saccadic suppression in neural activity. In the earliest visual areas, selective magno-  
641 cellular pathway suppression is not clear (Hass and Horwitz 2011; Kleiser et al. 2004;  
642 Ramcharan et al. 2001; Reppas et al. 2002; Royal et al. 2006), even though behavioral  
643 effects strongly predicted them (Burr et al. 1982; Burr et al. 1994; Hass and Horwitz  
644 2011; Volkman et al. 1978). Rather, there is mild suppression throughout these early  
645 areas, regardless of magno- or parvo-cellular pathway. Higher areas, primarily in the  
646 dorsal stream, do show saccadic suppression dynamics (Zanos et al. 2016; Bremmer et al.

647 2009; Han et al. 2009; Ibbotson et al. 2008; Ibbotson et al. 2007; Thiele et al. 2002), but  
648 the origins of such suppression remain elusive. In fact, it has been suggested that  
649 suppression in motion-related areas MT and MST (Bremmer et al. 2009; Ibbotson et al.  
650 2008; Ibbotson et al. 2007; Thiele et al. 2002) may be inherited from earlier visual areas  
651 (Ibbotson et al. 2008; Ibbotson et al. 2007), which themselves have weak and unselective  
652 suppression. Thus, there is a pressing need for better understanding of saccadic  
653 suppression mechanisms.

654

655 The fact that primarily motion areas have been shown to exhibit the most convincing  
656 suppression additionally does not help account for the fact that saccadic suppression may  
657 be useful for perception even if the “motion problem” (Wurtz 2008) caused by saccades  
658 is solved. For example, suppression could help regularize processing of stimuli after  
659 saccades, regardless of the image shift itself. Consistent with this, we saw SC suppression  
660 for microsaccades, even though both the retinal-image motion and displacement caused  
661 by these eye movements are quite mild. Moreover, we saw suppression even with purely  
662 stationary gratings.

663

664 Related to the above, the fact that we saw any effects with microsaccades at all is  
665 interesting in its own regard, but the real advantage from studying microsaccades was  
666 that they allowed better experimental control. Microsaccades are mechanistically similar  
667 to larger saccades (Hafed 2011; Hafed et al. 2015; Hafed et al. 2009; Zuber et al. 1965),  
668 making them an extremely viable tool to understanding saccadic suppression. However,  
669 these movements simplify several challenges associated with large saccades. For

670 example, studies with large saccades have to contend with large image shifts caused by  
671 eye movements. As a result, full field stimuli become necessary (Ibbotson et al. 2008;  
672 Ibbotson et al. 2007). However, in our case, we could use stimuli identical to how normal  
673 experiments might stimulate RF's.

674

675 Another experimental advantage here was the fact that SC shows suppression *after*  
676 saccades in our type of paradigm (Chen et al. 2015; Hafed and Krauzlis 2010). This  
677 allowed us to avoid probing neurons during the eye movements themselves; we always  
678 presented stimuli *after* microsaccades, such that no-microsaccade and microsaccade trials  
679 both had the exact same stimulus, location, and eye-state. Of course, saccadic suppression  
680 in the SC would be even stronger *during* the microsaccades themselves, as we have  
681 recently shown (Chen et al. 2015; Hafed and Krauzlis 2010), which is further evidence of  
682 a consistency between our visual-motor neural modulations and classic perceptual effects  
683 of saccadic suppression in humans. That is, our choice to focus in this paper on post-  
684 movement modulations was one of exploiting the experimental advantages of doing so as  
685 opposed to one of a conceptual difference between our visual-motor neural modulations  
686 and the perceptual phenomenon itself.

687

688 Concerning superficial visual neurons, one question arises on the sources of mild and  
689 unselective suppression that we saw. This could reflect retinal effects. For example,  
690 retinal outputs show transient perturbations in response to saccade-like image  
691 displacements (Roska and Werblin 2003). Additionally, the effect could be inherited  
692 from V1, which also does not show selectivity (Hass and Horwitz 2011). Regardless of

693 the source, what is clear is that suppression in visual neurons is not selective as in  
694 perception. However, it could still be functional. For example, a collicular-cortical  
695 pathway from superficial SC may selectively target motion-related areas (Berman and  
696 Wurtz 2008; 2010; 2011; Wurtz et al. 2011). As a result, superficial SC may still  
697 contribute to saccadic suppression of motion (Bridgeman et al. 1975; Burr et al. 1982); in  
698 this case, selectively suppressing motion by superficial SC neurons would arise not  
699 necessarily because the neurons themselves are selective in their suppression profiles, but  
700 instead because of selectivity in their connections to cortical targets.

701

702 Our observation of a lack of suppression selectivity in purely visual neurons also helps  
703 address an important question regarding the nature of our selective visual-motor neuron  
704 modulations. Specifically, it may be argued that (peripheral) SC neurons may  
705 preferentially over-sample low spatial frequencies in their tuning curves (Hafed and Chen  
706 2016), meaning that they exhibit higher baseline sensitivity for low spatial frequencies  
707 even without microsaccades. This, in turn, could mean that we only saw stronger  
708 suppression at low spatial frequencies (in the visual-motor neurons) simply because the  
709 baseline visual responses were stronger; suppression could in reality be constant across  
710 spatial frequencies, but its effect on absolute firing rate would scale with visual response  
711 sensitivity. However, in our mappings of SC tuning curves, we found that purely visual  
712 neurons, like visual-motor neurons, also tend to be more sensitive to low spatial  
713 frequencies. If our effects are explained by the dependence of suppression on baseline  
714 visual sensitivity in the absence of microsaccades, then our purely visual neurons should  
715 have shown the same patterns of selective suppression as the visual-motor neurons. They

716 did not (Figs. 3, 4). Second, we specifically examined suppression within each spatial  
717 frequency relative to the no-microsaccade baseline of the same frequency, in order to  
718 isolate the suppression effect independent of baseline response strength. This avoided  
719 questions of absolute firing sensitivity across spatial frequencies. Third, in Fig. 7, we  
720 explicitly examined suppression as a function of preferred spatial frequency and still  
721 found diminishing returns in suppression strength with increasing spatial frequency even  
722 when each spatial frequency bin only included the neurons preferring that frequency.  
723 Finally, because the visual system is inherently generally low pass anyway (especially in  
724 the periphery), then even a mechanism in which suppression simply scales with visual  
725 sensitivity of a given spatial frequency would still explain the well known perceptual  
726 phenomenon of selective suppression of low spatial frequencies in humans.

727

728 There may also be an additional potential counter-interpretation of our results.  
729 Specifically, it may be argued that we uncovered a highly specific effect only modulating  
730 saccadic RT's, and that visual-motor neuron modulations are irrelevant for other forms of  
731 behavior (e.g. not requiring saccadic responses). However, this is highly unlikely. First,  
732 the SC contributes to behavior even with non-saccadic outputs. For example, during  
733 attentional tasks with button presses, SC lesions impair performance (Sapir et al. 1999),  
734 suggesting that it is sensory and/or cognitive modulations that are relevant. Consistent  
735 with this, the SC contributes to attentional paradigms with a variety of response  
736 modalities (Lovejoy and Krauzlis 2010; Zenon and Krauzlis 2012). Second, we only  
737 looked at the earliest visual responses and uncovered strong correlations to behavior  
738 observed in separate experiments. This indicates that it was the *sensory response* that

739 mattered. Consistent with this, we have recently found that microsaccades have a  
740 virtually identical impact on either saccadic or manual responses (Tian et al. 2016).  
741 Third, our behavioral effects on RT are themselves remarkably similar to perceptual  
742 effects of saccadic suppression in humans, but using different perceptual measures and  
743 response modalities (Burr et al. 1982; Burr et al. 1994; Volkman et al. 1978). Fourth, we  
744 found that monkey P had a stronger suppression effect in behavior than monkey N at the  
745 low spatial frequencies (compare the cyan curves in Fig. 2C and Fig. 2F) even though  
746 monkey P had significantly longer saccadic RT's to begin with (compare the black no-  
747 microsaccade curves in Fig. 2A and Fig. 2D). If our behavioral and neural effects were  
748 restricted to limits on saccadic RT, perhaps due to potential saccadic refractory periods  
749 between successive saccades and microsaccades, then monkey P should have shown  
750 weaker behavioral suppression than monkey N since this monkey's saccadic system had  
751 plenty of time to recover from the previous generation of a microsaccade before having to  
752 generate the next saccadic RT. Given all of the above, we find it highly unlikely that our  
753 modulations are only specific to modulating saccadic RT's.

754

755 Given the above, it might be additionally asked why the SC should be among the neural  
756 substrates for perceptually-relevant saccadic suppression? We think that the SC has  
757 several appealing features to place it well within a hypothetical saccadic suppression  
758 system. For example, the SC contributes to triggering the saccade command. Thus, a  
759 source of corollary discharge is already present in the visual-motor layers, as  
760 demonstrated by our differential firing rate (Figs. 3-7) and LFP (Figs. 8-10) effects.  
761 Second, proximity of the SC to motor outputs confers an additional advantage: SC

762 suppression, besides having perceptual effects, could help to regularize how often  
763 subsequent saccades are made to sample the visual world. That is, in reality, suppression  
764 could serve to control the temporal structure of saccades, which can be very important  
765 both behaviorally (Tian et al. 2016) and cortically (Lowet et al. 2016). Finally, our results  
766 are in line with an early hypothesis that the primary output of SC may be the visual-motor  
767 layers (Mohler and Wurtz 1976).

768

769 In all, our results will motivate further investigation of a classic, yet highly controversial  
770 topic in systems neuroscience.

771

772

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774

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779

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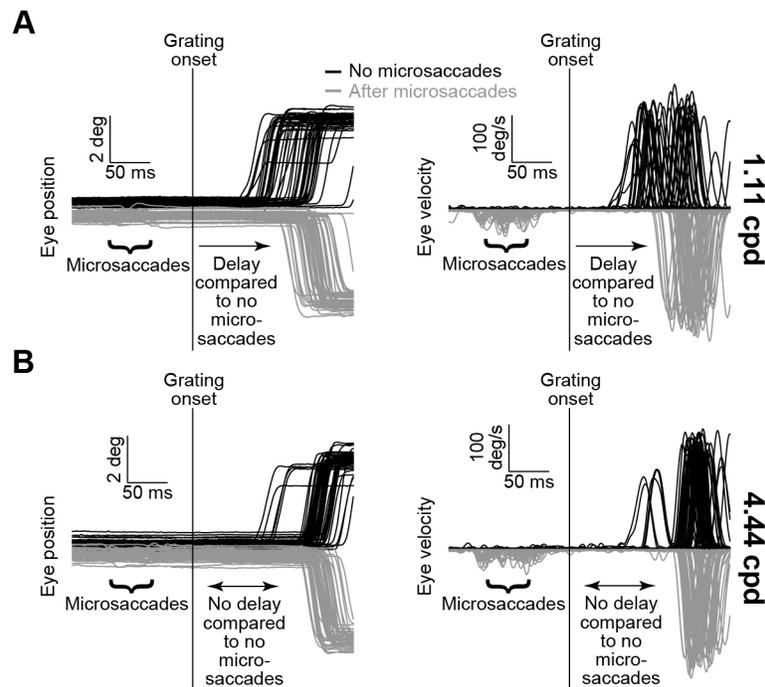
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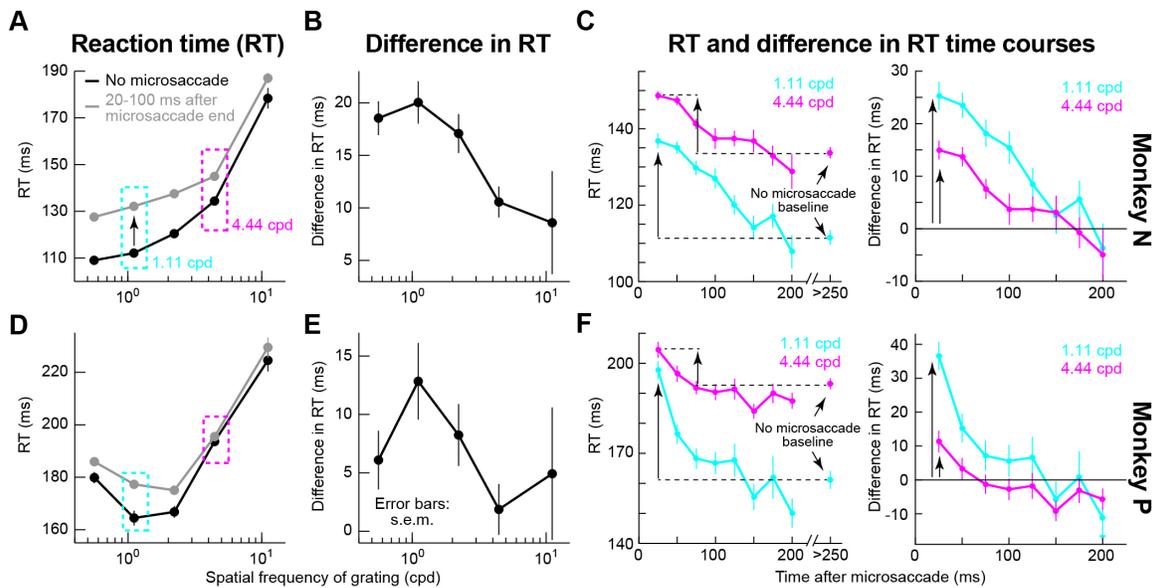
922 **Figures and Figure Legends**

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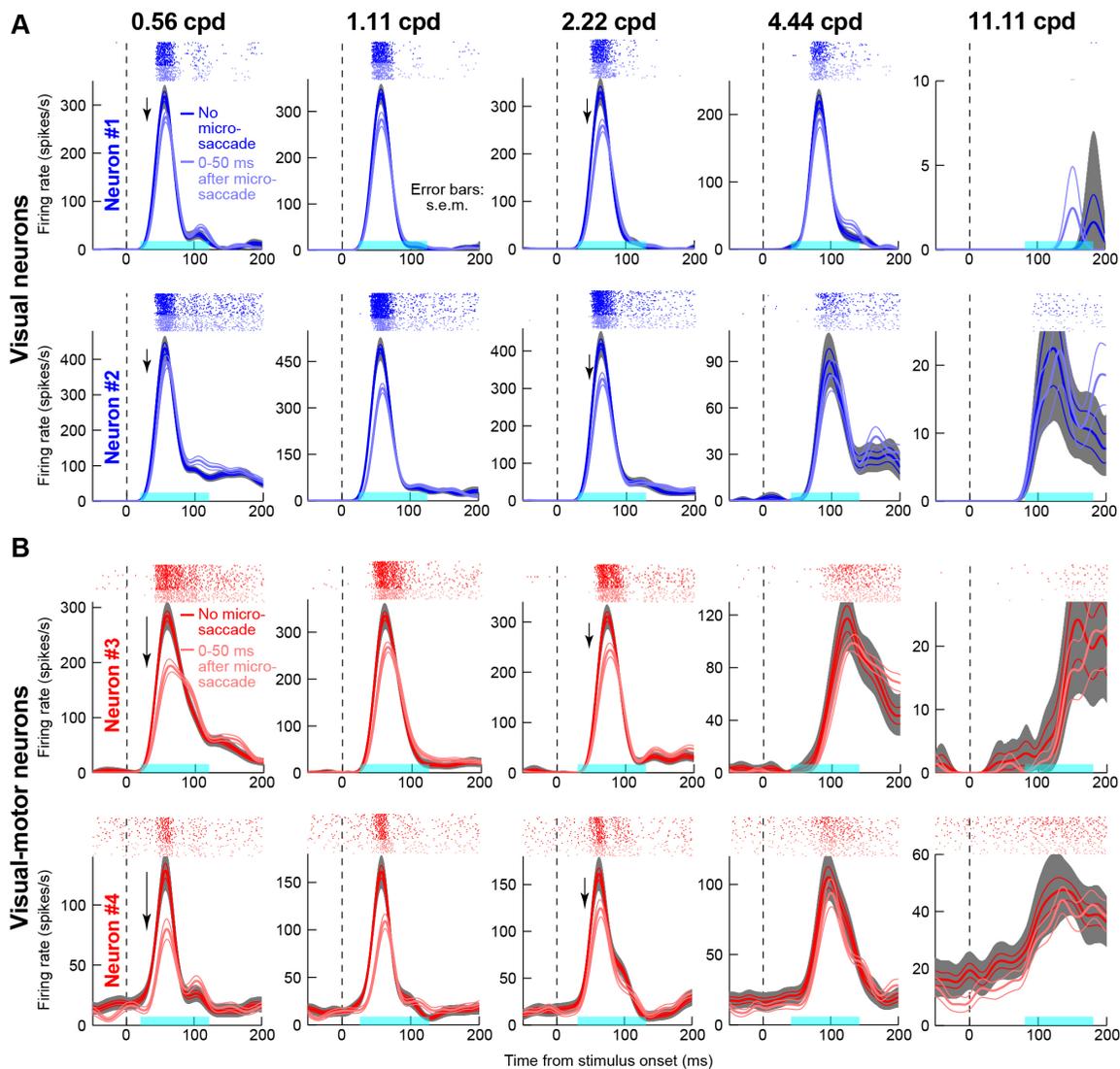
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925 **Figure 1** Behavioral measure of microsaccadic suppression across spatial frequencies.  
926 (A) Eye position (left) and radial eye velocity (right) traces from 100 sample trials from  
927 monkey N during a stimulus detection task. A 1.11 cpd grating appeared during fixation  
928 either with no nearby microsaccades (black, n=50 randomly selected trials) or ~20-100  
929 ms after microsaccades (gray, n=50 randomly selected trials), and the monkey had to  
930 orient as fast as possible to the grating. Reaction time (RT) on the microsaccade trials  
931 was slower than on the no-microsaccade trials. Note that we flipped the gray position and  
932 velocity traces around the horizontal axis to facilitate comparison to the black traces, and  
933 we also displaced the initial fixation position in the position traces. The microsaccades  
934 are more visible in the velocity traces, because they constitute spikes of eye velocity. (B)  
935 Same analysis, but from 100 randomly selected trials having a higher spatial-frequency  
936 grating (4.44 cpd). RT's in this case were more similar between the microsaccade and no-  
937 microsaccade trials, suggesting that the effect in A disappears with increasing spatial  
938 frequency.  
939



940

941 **Figure 2** Spatial-frequency selective microsaccadic suppression in behavior. (A) RT as a  
 942 function of spatial frequency. On no-microsaccade trials (black), RT increased with  
 943 spatial frequency, consistent with dependence of visual response dynamics on spatial  
 944 frequency (Breitmeyer 1975). If the same gratings appeared ~20-100 ms after  
 945 microsaccades (gray), RT increased relative to no-microsaccade trials (a behavioral  
 946 correlate of suppressed visual sensitivity), but more dramatically for low rather than high  
 947 spatial frequencies (compare gray to black curves at different spatial frequencies). (B)  
 948 Difference in RT between microsaccade and no-microsaccade trials (i.e. difference  
 949 between gray and black curves in A), demonstrating the diminishing effects of  
 950 microsaccades on RT behavioral costs with increasing spatial frequency. (C) Time  
 951 courses of RT (left panel; like in A) or difference in RT (right panel; like in B) as a  
 952 function of the time of grating onset after microsaccade end. The figure shows time  
 953 courses from two sample spatial frequencies (complete time courses from all spatial  
 954 frequencies, and for each animal individually, are also shown in Fig. 6). For the  
 955 difference in RT time course, RT's on trials with no microsaccades within <250 ms from  
 956 grating onset were taken as the baseline. The initial RT cost caused by microsaccades  
 957 was weaker for higher spatial frequency gratings (compare vertical arrows, consistent  
 958 with A). Error bars, when visible, denote s.e.m. (D-F) Same analyses but for a second  
 959 monkey. n=8153 trials for monkey N, and n=7117 for monkey P.  
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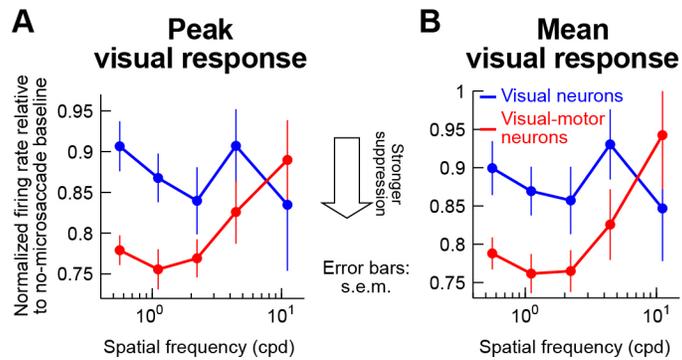


961

962 **Figure 3** Spatial-frequency selective microsaccadic suppression of visual-motor SC  
963 neurons. (A) Neural activity as a function of time after grating onset for two sample  
964 purely visual SC neurons (one per row). Each panel in a row shows activity after  
965 presentation of a specific spatial frequency (indicated above each panel). Rasters above  
966 each firing rate curve show individual action potentials emitted by the neuron across  
967 individual trials. We divided trials into ones in which there was no microsaccade within  
968 <100 ms from grating onset (saturated blue;  $n \geq 38$  trials per spatial frequency in these  
969 sample neurons) and ones in which the grating appeared immediately after microsaccades  
970 (unsaturated blue;  $n \geq 30$  trials per spatial frequency). The y-axis was scaled in each  
971 panel such that the no-microsaccade firing rates visually appeared to have approximately  
972 similar heights across panels, allowing easier comparison of suppression effects. Both  
973 neurons showed moderate microsaccadic suppression, with no clear pattern across spatial  
974 frequencies. (B) Same format as A, but for two sample visual-motor neurons. The  
975 neurons showed stronger suppression at the lowest spatial frequency, and the suppression  
976 gradually decreased in strength with increasing spatial frequency (like in behavior); by  
977 4.44 and 11.11 cpd, there was practically no suppression left at all. For these neurons,

978  $n \geq 28$  trials per spatial frequency for no microsaccade trials (saturated red), and  $n \geq 22$   
979 trials per spatial frequency trials for microsaccade trials (unsaturated red). Error bars  
980 denote s.e.m. In all panels, the gray shaded regions indicate 95% confidence intervals for  
981 the no-microsaccade trials when they were subsampled (and bootstrapped) to match the  
982 numbers of trials in the microsaccade condition (Materials and Methods). Also, the cyan  
983 intervals on x-axes indicate the averaging intervals for measuring mean firing rate  
984 (Materials and Methods).  
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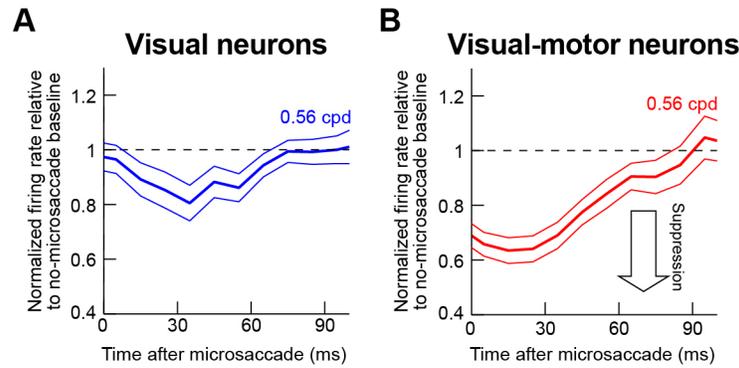
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988 **Figure 4** Spatial-frequency dependent microsaccadic suppression of visual bursts in  
989 visual-motor but not visual SC neurons. **(A)** We measured peak stimulus-evoked visual  
990 burst after grating onset (e.g. from traces like those in Fig. 3) and plotted it as a function  
991 of grating spatial frequency. We grouped neurons as purely visual (blue) or visual-motor  
992 (red). Visual neurons showed only ~10% suppression, and there was no consistent  
993 spatial-frequency dependence of this suppression. Visual-motor neurons showed ~25%  
994 suppression in the low spatial frequencies, and this effect gradually decreased with  
995 increasing spatial frequency (as in behavior). Error bars denote s.e.m. Note that the error  
996 bars for the highest spatial frequency were larger than other frequencies because some  
997 neurons completely stopped responding at 11.11 cpd, which reduced population size in  
998 this spatial frequency (Materials and Methods). **(B)** We repeated the same analysis but  
999 now measuring mean stimulus-evoked response in a certain window after grating onset  
1000 (cyan intervals indicated in Fig. 3; Materials and Methods). Similar observations to those  
1001 in **A** were made. n=66 visual-motor neurons, and n=24 visual neurons.  
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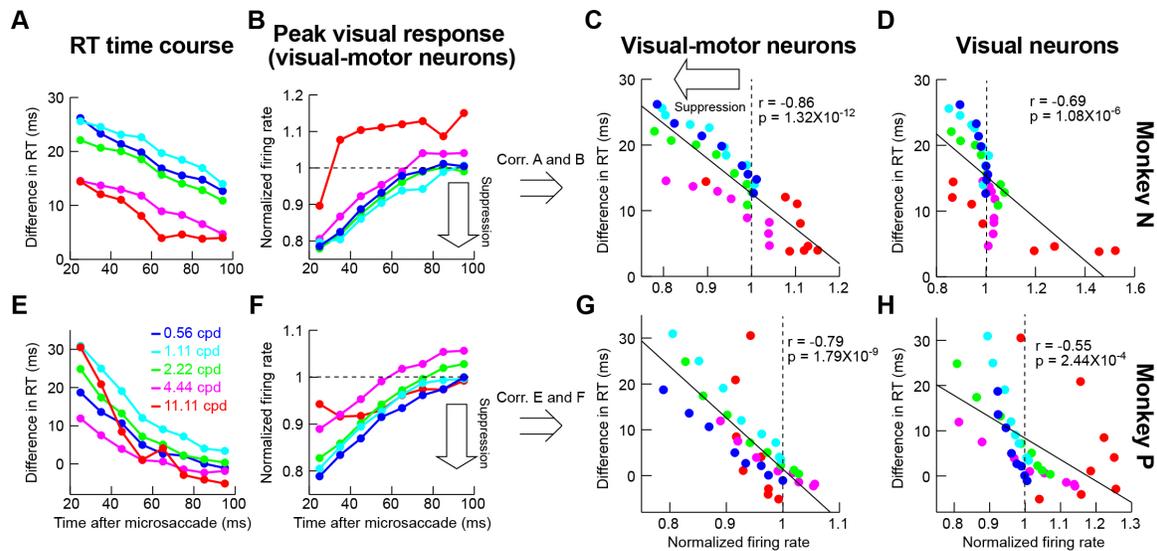


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1005 **Figure 5** Time courses of microsaccadic suppression in visual (A) and visual-motor (B)  
1006 neurons for a sample spatial frequency. We performed an analysis similar to that  
1007 described in (Chen et al. 2015) but aligning on microsaccade end. For each time window  
1008 after microsaccade end in which a grating appeared (x-axis; 50-ms bins in 10-ms steps),  
1009 we measured mean firing rate evoked by grating onset (Materials and Methods), and we  
1010 normalized it by mean firing rate on no-microsaccade trials. Visual-motor neurons  
1011 showed stronger suppression than visual neurons (compare y-axis in both panels; error  
1012 bars denote 95% confidence intervals), and both neuron types experienced recovery with  
1013 increasing time after microsaccades (consistent with behavioral effects). Note that the  
1014 time course of visual-motor neuron suppression is similar to the time course of behavioral  
1015 effects (e.g. Fig. 2C, F) and also similar to the time course of saccadic suppression in the  
1016 earlier literature (e.g. Ibbotson and Krekelberg 2011; Hafed and Krauzlis 2010; Diamond  
1017 et al. 2000). Figure 6 shows individual monkey time courses, other spatial frequencies, as  
1018 well as relationships between neural time courses and the respective monkey's behavioral  
1019 performance dynamics.

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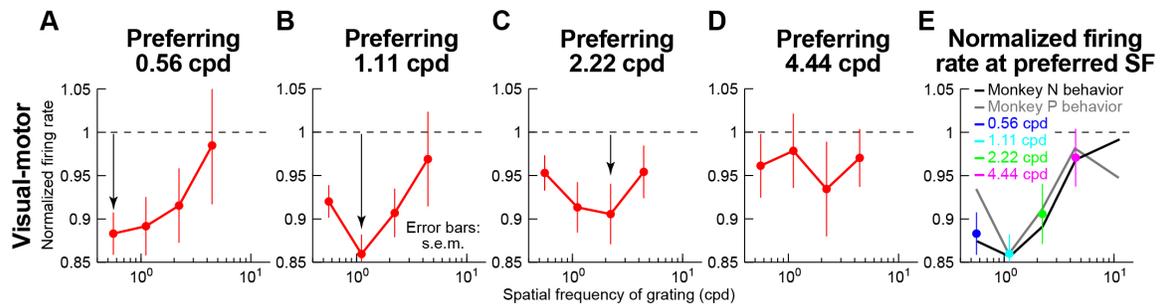
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1023 **Figure 6** Correlating behavioral microsaccadic suppression with neural microsaccadic  
 1024 suppression on completely different experimental sessions. **(A)** Time course of difference  
 1025 in RT from baseline (e.g. Fig. 2C, F; Materials and Methods) as a function of time of  
 1026 grating onset after microsaccade end in our behavioral experiments (monkey N).  
 1027 Different curves show different spatial frequencies. Immediately after microsaccades,  
 1028 there was a strong cost in RT for low spatial frequencies, and a more moderate cost for  
 1029 high spatial frequencies. In all spatial frequencies, the RT cost associated with  
 1030 microsaccadic suppression slowly dissipated in time. **(B)** Similar analysis but for the peak  
 1031 visual response in our neural experiments, on completely different sessions from the  
 1032 behavioral data, and only for visual-motor neurons. **(C)** Correlation between the data  
 1033 points in **A** and those in **B**, regardless of time or spatial frequency. There was strong  
 1034 correlation between visual burst strength and RT cost, even on completely different  
 1035 experimental sessions, suggesting that visual-motor neurons are modulated during  
 1036 microsaccadic suppression in a perceptually-relevant manner. **(D)** This was not the case  
 1037 for purely visual neurons. Here, we correlated the behavioral points in **A** with similar  
 1038 points but for visual neuron time courses (e.g. Fig. 5A). The correlation with behavior  
 1039 was worse than in visual-motor neurons. **(E-H)** Similar observations for a second  
 1040 monkey.  $n=24$  visual-motor neurons for monkey N, and  $n=42$  visual-motor neurons for  
 1041 monkey P;  $n=15$  visual neurons for monkey N, and  $n=9$  visual neurons for monkey P.  
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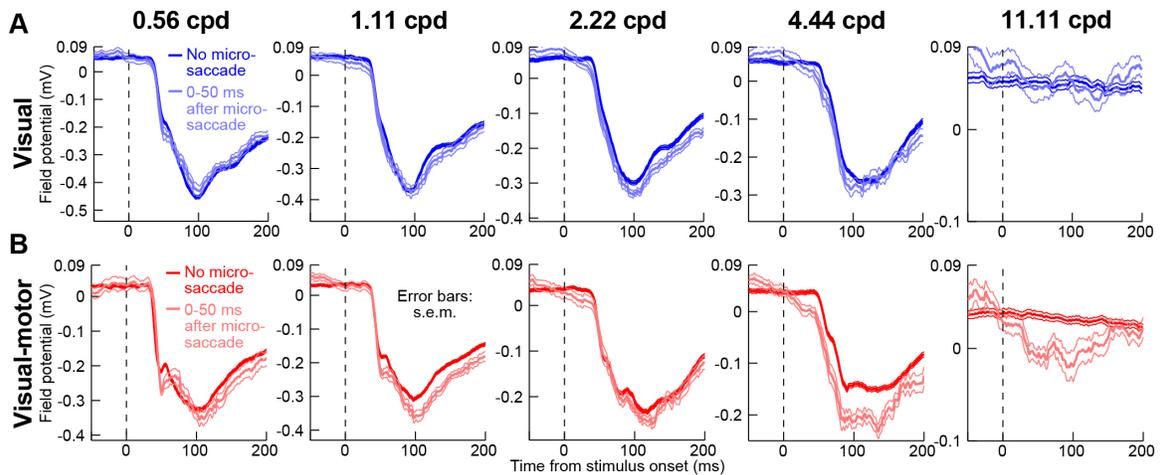


1044

1045 **Figure 7** Selective low-frequency suppression in visual-motor neurons independent of  
1046 preferred spatial frequency. (A-D) In each panel, we selected only neurons preferring a  
1047 single spatial frequency on no-microsaccade trials (Materials and Methods). We then  
1048 repeated the analysis of Fig. 4A. The preferred spatial frequency tended to experience the  
1049 strongest suppression compared to other spatial frequencies (black arrows). However, the  
1050 strength of the suppression even for the preferred spatial frequency consistently  
1051 decreased with increasing spatial frequency (compare the arrows in the individual  
1052 panels). Note that we did not have neurons preferring 11.11 cpd in this analysis, and we  
1053 thus do not show this spatial frequency in this figure. (E) We collected the maximally  
1054 suppressed spatial frequency from each panel in A-D (legend), and we plotted them  
1055 together. The black and gray lines are a copy of the behavioral RT microsaccadic  
1056 suppression curves of Fig. 2B, E, but inverted (and with arbitrary y-axis scaling) to match  
1057 the neural suppression curves. As can be seen, even if the preferred spatial frequency of  
1058 neurons always experienced maximal suppression, this maximal suppression was still  
1059 decreased with increasing spatial frequency. Thus, the spatial-frequency selectivity of  
1060 visual-motor neural suppression was still correlated with behavior. Error bars denote  
1061 s.e.m. n=26, 19, 8, and 5 neurons in each of A, B, C, and D.

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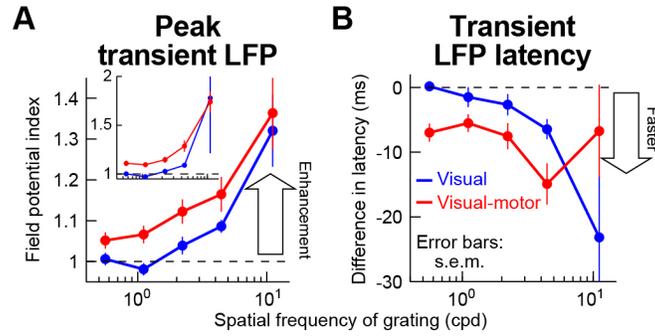


1064

1065 **Figure 8** Local field potential modulations during microsaccadic suppression. This figure  
1066 is formatted similarly to Fig. 3, except that we now plot LFP modulations around a  
1067 sample electrode track near visual (A) or visual-motor (B) neurons. There was *no*  
1068 evidence of a reduced LFP evoked response for trials with grating onset after  
1069 microsaccades (faint colors). If anything, the peak evoked response, and the latency to  
1070 evoked response were stronger and shorter, respectively (see Fig. 9). This effect was not  
1071 explained by an intrinsic peri-microsaccadic modulation of LFP (see Figs. 9A, 10), but it  
1072 is consistent with an additional movement-related modulatory signal associated with  
1073 saccade execution that influences stimulus-evoked spiking activity. Error bars denote  
1074 s.e.m. For the visual track (A),  $n \geq 113$  trials per spatial frequency on no-microsaccade  
1075 trials (saturated blue), and  $n \geq 25$  trials per spatial frequency on microsaccade trials  
1076 (unsaturated blue). For the visual-motor track (B),  $n \geq 140$  trials per spatial frequency on  
1077 no-microsaccade trials (saturated red), and  $n \geq 12$  trials on microsaccade trials  
1078 (unsaturated red).

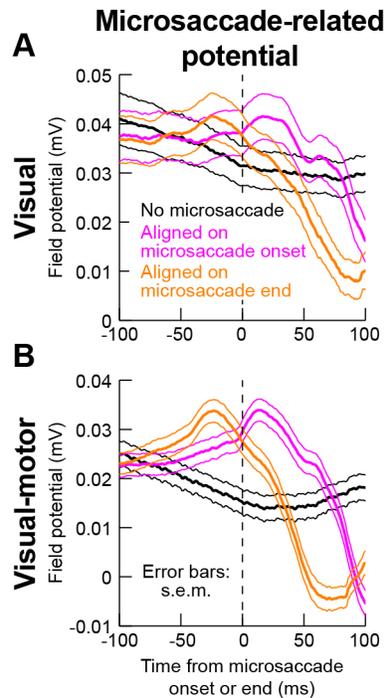
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1081

1082 **Figure 9** Lack of microsaccadic suppression in LFP stimulus-evoked responses. (A) We  
1083 performed an analysis similar to that in Fig. 4 but on LFP's. We measured peak LFP  
1084 response with and without microsaccades, and we then obtained a modulation index  
1085 (Materials and Methods). The inset shows the modulation index from raw measurements,  
1086 and the main panel shows the same analysis but after subtracting a baseline shift from the  
1087 microsaccade trials. Specifically, Fig. 10 suggests that there is a negativity in LFP's after  
1088 microsaccades, and stimulus onset in the microsaccade trials came after a previous  
1089 microsaccade. Thus, we measured the peak LFP stimulus-evoked response on  
1090 microsaccade trials as the difference between the raw LFP stimulus-evoked negativity  
1091 minus the baseline LFP value that was present at the time of grating onset (Materials and  
1092 Methods). In both the inset and the main panel, there was no suppression in the stimulus-  
1093 evoked LFP response, contrary to firing rate results (Fig. 4). Rather, there was response  
1094 enhancement, which progressively increased with increasing spatial frequency, and this  
1095 happened for both visual and visual-motor electrode track locations ( $p < 0.01$  for either  
1096 baseline-corrected or raw measurements and for each of visual-only or visual-motor  
1097 electrode tracks; 1-way ANOVA with spatial frequency as the main factor). (B) Similar  
1098 analyses but measuring the latency to LFP stimulus-evoked response, which decreased on  
1099 microsaccade trials (y-axis values  $< 0$  ms;  $p < 0.01$  for visual electrode tracks and  $p = 0.03$   
1100 for visual-motor electrode tracks; 1-way ANOVA with spatial frequency as the main  
1101 factor). Thus, when a stimulus appeared immediately after a previous microsaccade, the  
1102 stimulus-evoked LFP response started earlier than without a microsaccade. Error bars  
1103 denote s.e.m.  
1104



1105

1106 **Figure 10** Microsaccade-related local field potential modulations in the absence of an RF  
1107 stimulus. We aligned LFP activity to either microsaccade onset (magenta) or  
1108 microsaccade end (orange) during a baseline fixation interval with no RF stimulus at all  
1109 (Materials and Methods). The black curves show LFP activity during equally-long  
1110 control intervals, again with no RF stimulus, but also with no microsaccade occurrence.  
1111 Even though there was no microsaccade-related spiking at all the sites investigated in this  
1112 study, microsaccades caused systematic modulations in both visual (**A**) and visual-motor  
1113 (**B**) electrode locations in the SC, even though our electrodes were primarily placed in  
1114 extra-foveal SC representations far from the movement endpoints. Thus, these LFP  
1115 modulations, similar to previously reported saccade-related LFP modulations (Liu et al.  
1116 2009), reflect a potential microsaccade-related modulatory signal that can mediate  
1117 microsaccadic suppression of firing rates in extra-foveal SC neurons. Also, note how the  
1118 effect on visual-motor layers (**B**) is more systematic and robust than in visual layers (**A**).  
1119 This is further evidence of a putative extra-retinal signal in the SC visual-motor layers  
1120 that might mediate saccadic suppression (and explain Fig. 6), and it also makes it unlikely  
1121 that the LFP modulations in this figure are due to ocular muscle artifacts. Error bars  
1122 denote s.e.m. n=66 electrode tracks for (**B**), and n=24 electrode tracks for (**A**).  
1123

