
Research Article: New Research | Sensory and Motor Systems

Dynamic contextual modulation in superior colliculus of awake mouse

<https://doi.org/10.1523/ENEURO.0131-20.2020>

Cite as: eNeuro 2020; 10.1523/ENEURO.0131-20.2020

Received: 4 April 2020

Revised: 25 June 2020

Accepted: 17 July 2020

This Early Release article has been peer-reviewed and accepted, but has not been through the composition and copyediting processes. The final version may differ slightly in style or formatting and will contain links to any extended data.

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- 1 **1. Title: Dynamic contextual modulation in superior colliculus of awake mouse**
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3 **2. Abbreviated title:** Context in the superior colliculus
4
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13 to the accuracy or integrity of any part of the work are appropriately investigated and
14 resolved. G.D.F. performed the experiments. All persons designated as authors qualify
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23 **6. Figures:** 7
24 **7. Tables:** 0
25 **8. Multimedia:** 0
26 **9. Abstract:** 212 words
27 **10. Significance statement:** 109 words
28 **11. Introduction:** 734 words
29 **12. Discussion:** 2123 words
30
31 **13. Acknowledgments:** The authors thank A. Perry and N. Dhruv for help in early
32 experiments.
33
34 **14. Conflict of interest:** Authors report no conflict of interest.
35
36 **15. Funding sources:** S.G.S. received support from a project grant from the Biotechnology
37 and Biological Sciences Research Council (BB/R004765/1), and an International
38 Collaboration Award (with Adam Kohn) from the Stavros Niarchos Foundation /
39 Research to Prevent Blindness. G.D.F. was also supported by an Impact studentship from
40 UCL.
41

42 **ABSTRACT**

43 The responses of neurons in the visual pathway depend on the context in which a stimulus is
44 presented. Responses to predictable stimuli are usually suppressed, highlighting responses to
45 unexpected stimuli that might be important for behaviour. Here we established how context
46 modulates the response of neurons in the superior colliculus, a region important in orienting
47 towards or away from visual stimuli. We made extracellular recordings from single-units in
48 the superficial layers of superior colliculus in awake mice. We found strong suppression of
49 visual response by spatial context (surround suppression) and temporal context (adaptation).
50 Neurons showing stronger surround suppression also showed stronger adaptation effects. In
51 neurons where it was present surround suppression was dynamic, and was reduced by
52 adaptation. Adaptation's effects further revealed two components to surround suppression:
53 one component that was weakly tuned for orientation and adaptable, and another component
54 that was more strongly tuned but less adaptable. The selectivity of the tuned component was
55 flexible, such that suppression was stronger when the stimulus over the surround matched that
56 over the receptive field. Our results therefore reveal strong interactions between spatial and
57 temporal context in regulating the flow of signals through mouse superior colliculus, and
58 suggest the presence of a subpopulation of neurons that might signal novelty in either space or
59 time.
60

61 **SIGNIFICANCE STATEMENT**

62 Our senses provide enormous amounts of information, and the central nervous system needs
63 to filter this information to focus on potentially important objects. Here we study two visual
64 mechanisms that might highlight unexpected or surprising objects for further analysis:
65 surround suppression and adaptation. We show that both mechanisms work to filter the neural
66 signals provided by the superior colliculus, a mid-brain area important for directing
67 behaviour. We also show that the two mechanisms are unexpectedly intertwined, endowing
68 rich dynamics on neural signals at the first central stage of sensory processing. Finally, our
69 results suggest a subpopulation of neurons that is specialised for signalling the presence of
70 potentially important objects.

71

72

73 **INTRODUCTION**

74 Unexpected objects are likely to be important for behaviour, and predictable objects less
75 important. Many aspects of the functional organisation of the visual system can be explained
76 by supposing that neuronal activity is suppressed when the image falling on a receptive field
77 is predictable. For example, inhibitory inputs to retinal neurons can be thought of as providing
78 predictions about the intensity of the image over the receptive field, suppressing responses
79 unless the intensity deviates from those predictions (Srinivasan et al., 1982). The functional
80 consequences of this predictive inhibition are the classical centre-surround organisation and
81 transient responses of receptive fields in the retina and its targets (Hartline, 1940; Kuffler,
82 1953; Barlow, 2001).

83 In the classical model of an early receptive field, inhibition provides predictions about the
84 average intensity of the image over the receptive field, but not the variance, or pattern, of
85 intensity in that image. Two additional mechanisms are needed to explain how responses to
86 predictable patterns are suppressed. Spatial interactions (often called surround suppression)
87 can suppress responses when the pattern over the classical receptive field is similar to that in
88 the surrounding region. Temporal interactions (often called adaptation) can suppress
89 responses when the pattern is similar over time. The spatial and temporal suppression are
90 thought to reflect the action of ‘gain controls’, mechanisms that regulate the responses
91 generated by the classical receptive field (Solomon and Kohn, 2014; Webster, 2015; Shapley
92 and Victor, 1978; Bonds, 1989; Carandini and Heeger, 2011).

93 While most work on spatial and temporal gain controls has concentrated on visual cortex
94 (Allman et al., 1985; Solomon and Kohn, 2014; rodent: Adesnik et al., 2012; Vaiceliunaite et
95 al., 2013; Self et al., 2014; cat: Movshon and Lennie, 1979; Carandini and Ferster, 1997;
96 monkey: Mayo and Sommer, 2008; Patterson et al., 2013), gain controls are also known to be
97 important in the retina and early stages of central visual processing (rodent: Zhang et al.,

98 2012; Jacoby and Schwartz, 2017; lagomorphs: Oyster and Takahashi, 1975; Smirnakis et al.,
99 1997; cat: Sterling and Wickelgren, 1969; Jones et al., 2000; Bonin et al., 2005; Fisher et al.,
100 2017; monkey: Solomon et al., 2002; Solomon et al., 2004; Solomon et al., 2006; Boehnke et
101 al., 2011). In most animals the major target of the retina is the superficial layers of the mid-
102 brain superior colliculus (SC, homologous to the optic tectum) (May, 2006; Ellis et al., 2016).
103 The superficial layers of SC project to, among other areas, the deeper layers of SC, which are
104 important in organising movements towards or away from potentially important objects (Dean
105 et al., 1989; Basso and May, 2017; rodent: Comoli et al., 2012; Hoy et al., 2019). The
106 receptive fields of superficial SC neurons are often remarkably selective for image features:
107 for example, neurons in superficial SC of mouse can be tightly tuned for contour orientation,
108 even in the absence of visual cortex (Wang et al., 2010; Shi et al., 2017). The receptive fields
109 of neurons in superficial SC also show prominent surround suppression (rodent: Girman and
110 Lund, 2007; Wang et al., 2010; Ahmadlou et al., 2017; Barchini et al., 2018; monkey:
111 Davidson and Bender, 1991) and adaptation (Dutta and Gutfreund, 2014; monkey: Boehnke et
112 al., 2011;). How gain controls influence the response of SC neurons is less clear, particularly
113 in awake animals. For example, we do not know if surround suppression and adaptation's
114 effects are ubiquitous, whether they are independent, or how they interact.

115 Here we made extracellular recordings from the superficial layers of SC in awake mice. We
116 characterised surround suppression from the response to drifting gratings of varying size, and
117 characterised adaptation from the time-course of the response to drifting gratings of optimal
118 size. We find profound impact of surround suppression and adaptation in many but not all
119 neurons, and show that neurons with strong suppressive surrounds are also more susceptible
120 to adaptation. Further, the suppressive surrounds themselves are susceptible to adaptation, and
121 adaptation's effects reveal at least two components of suppression – an untuned component
122 that is adaptable, and a tuned component that is less adaptable. The selectivity of the tuned

123 component was not static, but flexible: that is, suppression depended on what was shown to
124 the receptive field, and was stronger when the stimulus over the surround matched that over
125 the receptive field. The spatial and temporal gain controls may therefore allow neurons in the
126 superficial SC the capacity to dynamically signal unexpected events in either space or time.
127

128 **METHODS**129 **Ethical approval.**

130 All animal procedures were performed in accordance with the UK Animals Scientific
131 Procedures Act (1986). Experiments were performed at University College London in
132 accordance with its animal care committee's regulations, under personal and project licenses
133 released by the Home Office following appropriate ethics review, and in accordance with the
134 ethical policy under which *eNeuro* operates.

135

136 **General**

137 Adult C57BL/6 male mice (8-12 weeks at the start of experiments, 20-35 g) were obtained
138 from Charles River Laboratories. Animals were housed with *ad libitum* food and water, on an
139 inverted 12-hour light/dark cycle. Measurements were obtained during the dark phase. To
140 prevent damage to implanted devices, animals were singly housed after the preparatory
141 surgeries described below.

142 *Preparation for recordings:* anaesthesia was induced with 3% isoflurane in O₂ and the animal
143 transferred to a stereotaxic apparatus. Anaesthesia was subsequently maintained with 1-1.5%
144 isoflurane in O₂, and adjusted as necessary by monitoring the breathing rate and absence of
145 reflex responses to paw pinch. The scalp was retracted and a craniotomy was made in one
146 hemisphere, centred 3.5-3.7 mm posterior to bregma, 0.7-1.1 mm lateral to the midline suture.
147 A metal head post fixed to the skull and a ground screw implanted over frontal cortex. In six
148 animals the brain was covered with a layer of Kwik-Cast Sealant (WPI), which was replaced
149 with artificial cerebrospinal fluid (Bio-technie Ltd, UK) during recording sessions; in these
150 cases, recordings were subsequently made using quartz/platinum-tungsten electrodes (Thomas
151 Recordings; impedance 4-5 M Ω) or tetrodes (impedance 0.5-0.8 M Ω). In two animals the
152 dura mater was instead removed and a 16-channel microdrive (arranged as 4 tetrodes, Axona

153 Ltd, UK) was implanted. Animals recovered from surgery for at least one week and were then
154 habituated to head-restraint before recordings started. Typical duration of a recording session
155 was 90-120 minutes. At the end of the experiments, animals were euthanized by overdose of
156 sodium pentobarbital I.P..

157 *Recordings and spike sorting:* The analogue signal from each electrode was amplified and
158 filtered (0.3 kHz -7/10 kHz), then digitised and recorded at 48 or 44 kHz. All recordings
159 obtained at one site on one day were analysed together. Putative single-units were identified
160 off-line using Plexon Offline Sorter (Version 3.3.2, for single electrode recordings) or
161 KlustaSuite (Rossant *et al.*, 2016). Single-units were identified by clustering in principal
162 component (PCA) space, followed by manual inspection of spike shape, auto- and cross-
163 correlograms. In no putative single unit did the fraction of ISIs under 0.5 ms exceed 2%.

164 *Visual stimuli:* Visual stimuli were generated using Expo (P. Lennie, Rochester, NY) on an
165 Apple Macintosh computer, and presented on a LCD monitor (Iiyama ProLite E1890SD,
166 mean luminance 35-45 candela/m²; 38 cm wide, 29 cm high) refreshed at 60 Hz and
167 displaying a grey screen of the mean luminance, positioned 20 cm from the animals' eye. The
168 monitor was gamma-corrected by measuring the luminance of the red, green and blue
169 elements with a photometer (Konica Minolta, Chroma meter CS-100A). Neural recordings
170 were aligned to the visual stimulus by the output of a photodiode scanning a small corner of
171 the stimulus monitor shielded from the animal. The coarse location of receptive fields was
172 manually identified and the monitor location adjusted to approximately centre them while
173 making the monitor normal to the animal. Receptive field position estimates were
174 subsequently refined by on-line analysis of responses to 'sparse-noise', where black or white
175 squares (size 15°; duration 0.2s) were presented pseudo-randomly at each location of a 9x9
176 grid centred in the monitor. Our recordings were made from a variety of elevations in the
177 nasal visual field, or from the lower temporal visual field, and were not distributed

178 sufficiently for us to characterise the relationship between receptive field location and
179 functional properties. We did not correct the display for the distortions in visual angle or
180 changes in illumination that the short viewing distance produces at the edges of the monitor.
181 Stimuli lasted for 2 s with an inter-stimulus interval of 0.5 s. Each set of stimuli included a
182 blank condition (during which the screen was held at the mean luminance) from which
183 ‘spontaneous’ or maintained firing rates were estimated. Each set of stimuli was presented in
184 pseudo-randomised order for 3-15 repetitions.

185 In some experiments we presented a drifting sinusoidal grating in a circular patch of varying
186 diameter (2° - 90°), outside of which the screen was held at the mean luminance. The spatial
187 and temporal frequency of the gratings was determined by initial measurements at each site.
188 We used a spatial frequency near the optimal for the neurons under consideration (usually
189 0.05 cycles/degree; μ 0.09, range 0.04-0.30); temporal frequency was usually 4 Hz (μ 3.5 Hz;
190 0.7 Hz, $n = 2$ units; 2 Hz, $n = 33$; 4 Hz, $n = 56$; 7.5 Hz, $n = 6$); Michelson contrast was 0.99
191 (hereafter normalized to 1.0) unless varied. In additional experiments we presented a central
192 patch of grating with a surrounding (abutting) annular grating. The central patch was of fixed
193 size, and of the spatial and temporal frequency defined above; the annular grating was of the
194 same spatial frequency, and a temporal frequency 0.5 Hz higher. In one experiment we varied
195 the contrast of the annular grating, and in another experiment, we varied the
196 orientation/direction of the annular grating. Each set of stimuli included trials in which the
197 central patch or an annular grating was presented in isolation. Measurements were drawn
198 from a large set of units, some of which have been reported previously (De Franceschi and
199 Solomon, 2018).

200 **Data analysis**

201 *Analysis.* Offline analysis was performed in the Matlab environment (R2019a; Mathworks,
202 Natick, MA). Peristimulus time histograms (PSTHs, bin width 0.016 s) were constructed for

203 each trial, from which we extracted the mean firing rate. Unless stated, we define response as
 204 stimulus evoked activity, that is, the change in activity from that measured during presentation
 205 of a blank screen (the ‘spontaneous’ or maintained firing rate).

206 *Inclusion criteria.* We considered neurons visually responsive if their maximal response
 207 exceeded the maintained rate by at least 1.5 S.D. of that rate, and further required that their
 208 response exceed 2 impulses/s in the relevant analysis. We also required the centre of a units’
 209 receptive field (estimated from responses to the sparse-noise stimulus) to be within 10° of the
 210 stimulus centre.

211 *Size tuning:* To characterise the dependence of response on the size of a grating patch we
 212 assumed that both the classical receptive field and a suppressive surround could be described
 213 by concentric circular Gaussians (Cavanaugh et al., 2002a). The excitatory classical receptive
 214 field (L_e) to a grating of diameter d is proportional to the integrated volume of a Gaussian:

$$L_e(d) = \frac{2}{\sqrt{\pi}} \int_0^d e^{-(x/r_e)^2} dx \quad (1)$$

215 where r_e is the width of the Gaussian envelope. A similar expression can be derived for the
 216 larger surround Gaussian (L_i). We assumed that the surround has divisive influence on the
 217 activity of the classical receptive field (Sceniak et al., 2001;Cavanaugh et al., 2002a), such
 218 that response is:

$$R(d) = \frac{K_e L_e(d)}{1 + K_i L_i(d)} \quad (2)$$

219 Where K_e and K_i are respectively the excitatory and the suppressive gains. We found the set of
 220 parameters that maximised the log-likelihood (LL) of the model given the responses (El-
 221 Shamayleh & Movshon, 2011) using the Matlab function *fmincon*. We compared the model
 222 LL to an upper bound (LL_u ; obtained by fitting the responses to themselves) and a lower
 223 bound (LL_l ; obtained by fitting the responses to the average response across all stimuli). The

224 normalized log-likelihood [$LLn = (LL-LLl)/(LLu-LLl)$] was used to decide whether to include
225 the resulting model parameters in subsequent analyses ($LLn \geq 0.5$). In addition to the
226 parameters described above we included an additional parameter that allowed for a
227 maintained discharge rate, and included in the set of responses to be modelled the activity
228 during presentation of a blank grey screen. We estimated the preferred size from the model fit
229 as the smallest size reaching 95% of the maximal response.

230 *Suppression index*: To quantify the suppression observed in size-tuning curves we calculated
231 a suppression index (SI) as:

$$SI = 100 \times \frac{R_{opt} - R_{large}}{R_{opt}} \quad (3)$$

232 where R_{opt} is the response amplitude at the preferred size and R_{large} is the response amplitude
233 at the largest tested size; both were extracted from the best predictions of the model above.
234 We used the same expression to quantify suppression in centre-surround experiments,
235 substituting R_{opt} with the response to a central patch alone, and R_{large} with the response to the
236 relevant combination of central patch and annular grating.

237 *Adaptation index*. We calculated an adaptation index (AI) to characterise the change in
238 response to a stimulus over time:

$$AI = 100 \times \frac{R_{early} - R_{late}}{R_{early}} \quad (4)$$

239 where R_{early} and R_{late} are the average evoked activity during the first and last 0.5 s of stimulus
240 presentation respectively (the stimuli lasted for 2 s).

241 *Orientation/direction tuning*: We calculated the direction tuning of stimulus-evoked responses
242 or SI as the amplitude of the vector sum of responses or SI to different directions:

$$gDSI = \frac{\sum R_{\theta} e^{i\theta}}{\sum R_{\theta}} \quad (5)$$

243 where R_{θ} is the response to a grating of direction θ . A global index of orientation selectivity is
244 defined in the same way, but after doubling θ . The preferred direction or orientation is the
245 angle of the relevant vector sum. We used the same expression to orientation/direction tuning
246 of surround suppression by substituting R_{θ} with the suppression index (SI_{θ}) measured for an
247 annular grating of direction θ .

248 **Statistics**

249 All statistical comparisons were performed in Matlab. Correlations are the Pearson's
250 correlation coefficient, r . Statistical tests are Student's paired t-tests unless noted.

251

252 **RESULTS**

253 Most models of receptive fields early in the visual pathway suppose that the signals of
254 different photoreceptors are given appropriate weight (which may be excitatory or inhibitory)
255 and then summed to provide a receptive field that drives spiking output. These models can be
256 used to characterise neurons with centre-surround receptive fields as well as those neurons
257 with more complex response properties, such as orientation tuning (for example: Cheong et
258 al., 2013). These models are, however, unable to explain why the response of neurons often
259 depends on the structure of the image beyond the receptive field, or the previous history of
260 stimulation. Explaining these dependencies requires supposing additional spatial and temporal
261 gain controls, which regulate the sensitivity of the receptive field.

262 The presence of spatial gain controls can be established by measuring the tuning of neurons to
263 the size of a pattern. We therefore varied the diameter of a patch of drifting grating that was
264 centred on the receptive field of the neuron under study (Fig 1A-D). The response of most
265 neurons was suppressed as the grating extended beyond the receptive field and into the
266 surrounding region, showing the presence of a spatial gain control, or suppressive surround.
267 The presence of temporal gain controls can be established from the time course of response to
268 a visual stimulus. All neurons responded robustly at the onset of a small stimulus. In some
269 neurons the response was sustained throughout the stimulus duration (Fig 1B,D), but in others
270 it was rapidly suppressed (Fig 1A,C). This adaptation effect shows the presence of a temporal
271 gain control.

272 *Prevalence of spatial and temporal gain controls*

273 We characterised the impact of the spatial gain control as the proportional reduction in
274 response to a large grating (a suppression index, or SI; Equation (3)). Here values of 0
275 indicate neurons in which there was no discernible suppression at large sizes, while values of
276 100 indicate neurons that only responded to small stimuli, and were completely suppressed by

277 larger ones. On average this suppression index was 76.9% (median 70.4, S.D. 147.9, $n = 93$;
278 Fig 2A-C) but there was substantial variability across the population of neurons. The absence
279 of suppression in some neurons might arise if their receptive fields are very large, and the gain
280 control was beyond the extent of the stimulus monitor. Our sample included neurons that
281 responded best to the largest grating we could produce and the filled bars in Fig 2C show that
282 neurons preferring large gratings (diameter greater than 30°) showed little suppression. Most
283 neurons, however, preferred gratings $10\text{-}30^\circ$ in diameter (geometric mean 16.3° , median 15.6° ,
284 $n = 93$) and in many of these neurons we saw little suppression even though the preferred size
285 was well within the monitor gamut. The measurements above were obtained for patterns of
286 high contrast. To establish the sensitivity of suppression in a sample of neurons we measured
287 the response to a patch of grating of optimal size, and varied the contrast of an annular grating
288 (not shown). In these neurons, suppression at 25% annulus contrast was on average 21.6%
289 (s.d. 15.7, $n = 12$), about half that at 100% annulus contrast (38.3, s.d. 22.0; $p = 0.0139$, paired
290 Students t-test). Spatial gain controls can therefore be engaged at low image contrast, and
291 their impact increases with contrast.

292 To characterise temporal gain control independently from spatial gain control we examined
293 responses to a patch of drifting grating of the preferred size for the neuron under study. We
294 measured the impact of temporal gain controls as the proportional reduction in response from
295 early (the first 0.5s) to late (the last 0.5s) time points, producing an adaptation index (AI;
296 Equation (4)) similar to the suppression index above. On average, later responses were
297 suppressed by 37.4% (median 36.0, S.D. 33.3, $n = 98$; Fig 2D-F) but as for surround
298 suppression we saw substantial variability across the population of neurons (Fig 2F). This
299 variability in AI was not explained by variation in temporal frequency of the grating (2 Hz: μ
300 33.1%, s.d. 23.8%, $n = 33$; 4 Hz: μ 38.4%, s.d. 36.1, $n = 56$). In a sample of neurons we
301 measured AI for a small patch of grating at low or high contrast (not shown): the adaptation

302 index at 25% contrast was on average 47.9% (s.d. 35.0, $n = 27$), if anything stronger than at
303 100% contrast (25.0%, s.d 72.1, $n = 28$; $p = 0.13$, paired Student's t-test). Thus temporal gain
304 controls are also sensitive to low image contrast.

305 The substantial variability in surround suppression and adaptation's effects raises the question
306 of whether the spatial and temporal gain controls are co-expressed in individual neurons. To
307 establish this, we compared the shape of the size-tuning curves for drifting gratings (provided
308 by the SI) and the time course of response for small patches of drifting grating (provided by
309 the AI). We found strong surround suppression in neurons that showed strong adaptation
310 effects (e.g. Fig 1A,C), and weak surround suppression in neurons that showed weak
311 adaptation effects (e.g. Fig 1B,D). Consequently, when we compared the index of surround
312 suppression (SI) and the index of adaptation (AI) we found a positive correlation (Fig 2G, $r =$
313 0.51 , $p < 0.00001$, Pearson's correlation coefficient). Spatial and temporal gain controls
314 therefore appear to be co-expressed in individual neurons.

315 Many, but not all, neurons in SC are tuned for the orientation or motion direction of a grating.
316 We therefore asked if this tuning might predict the expression of surround suppression or
317 adaptation effects (not shown). We found little relationship between adaptation's effects (AI)
318 and global measures of orientation or direction tuning (respectively $r = 0.08$, 0.16 ; $p = 0.47$,
319 0.17 ; $n = 78$). We found more of a relationship for surround suppression (SI; respectively $r =$
320 0.33 , 0.36 ; $p = 0.0028$, 0.0014). Units with little surround suppression were usually weakly
321 tuned for orientation or direction, while units with strong surround suppression included units
322 with a range of tuning for orientation/direction.

323 *Tuned and untuned contributions to spatial gain controls revealed by adaptation*

324 Inspection of PSTHs for small and large stimuli showed that responses to small stimuli were
325 more transient – that is, adaptation's effects were stronger for small stimuli (Fig 3A). This

326 suggests that spatial and temporal gain controls interact in shaping neural response. We
327 characterised this interaction by generating size tuning curves for early and late responses. We
328 found less surround suppression at late time points (Fig 3B), and our index of suppression
329 consequently reduced over time (Fig 3C; on average from 69.0% to 51.2%, $n = 73$, $p <$
330 0.00001 , paired Student's t -test). The reduced suppression at late time points suggests that
331 surround suppression is also adaptable.

332 If adaptation changes the sensitivity of surround suppression it may also change the tuning of
333 surround suppression. Previous work shows that surround suppression in mouse SC can be
334 sensitive to the orientation and/or direction of a pattern (Ahmadlou et al., 2017; Barchini et
335 al., 2018). We confirmed that suppression in SC was usually strongest when the orientation
336 and direction of the annular grating matched that over the receptive field (Fig 4A,B). In many
337 neurons (for example, the unit in Fig 4B), and in the population average (Fig 4E), suppression
338 was similar for either direction of motion of a parallel annular grating. In other neurons
339 suppression was clearly stronger when the direction of the annular grating also matched that
340 in the central patch, and in others surround suppression was untuned. We therefore asked if
341 suppression was more tuned in neurons in which spiking response (Fig 4A,D) was also
342 strongly tuned. We used a global index of orientation or direction selectivity (see Methods) to
343 compare the tuning of neuronal responses to a single large grating, with the tuning of
344 suppression elicited by the annular gratings. In both cases, values of 0 indicate no tuning,
345 while values of 1 indicate spiking response or suppression for only one stimulus. There was
346 little correlation (Fig 4C, $r = -0.02/0.09$, $p = 0.90/0.53$, Pearson's correlation coefficient):
347 suppression was often tuned even when spiking response was untuned, and vice versa.
348 Nevertheless, in neurons where the tuning of suppression was strong enough to define a
349 preferred stimulus (tuning index greater than 0.1), the preferred orientation/direction of
350 suppression was generally aligned with the stimulus shown in the central patch (Fig 4F).

351 To establish if the tuning of suppression is changed by adaptation we measured the tuning of
352 suppression in the first 0.5s following the onset of the stimulus, and in the last 0.5s. The
353 population average showed strong suppression at early time points, but this suppression was
354 only weakly tuned for annulus orientation (Fig 5B). At later time points the overall strength of
355 suppression was reduced and was largely confined to gratings of the same orientation /
356 direction as the central patch, resulting in increased selectivity of suppression (Fig 5F). To
357 illustrate how tuning changed in individual neurons we compared suppression for annular
358 gratings of the same orientation and motion direction as the central patch, with that for
359 gratings tilted by 45° (average of $\pm 45^\circ$; Fig 5C,G). Parallel gratings generated stronger
360 suppression at both time points, but their advantage was less pronounced at early (parallel
361 gratings generated μ 21.1% more suppression than tilted gratings, S.D. 22.3, $n = 58$; Fig 5C-
362 D) than late timepoints (μ 32.6%, S.D. 31.8, $n = 36$; Fig 5G-H) ($p = 0.0059$, paired Students
363 t-test, for 35 units that could be characterised at both time points). We conclude that the
364 overall strength of surround suppression reduces over time, and the selectivity of suppression
365 increases.

366 The pattern of results in Figs 5B&F might be explained if spatial gain controls constitute two
367 mechanisms – one that is narrowly tuned for orientation / direction and less susceptible to
368 adaptation, and one that is more broadly tuned and more susceptible to adaptation. One
369 potential source of suppression is the response of other neurons in SC and we therefore
370 conducted similar analyses of spiking response to large drifting gratings (Fig 5A,E). As for
371 suppression, the population spiking response has both tuned and untuned components, and as
372 for suppression the population spiking response reduced substantially at later time points,
373 showing the presence of adaptation effects. This reduction in response was similar for the
374 preferred grating and a grating tilted by 30° ($p = 0.0985$, $n = 34$). Similar results were
375 obtained if we compared responses to preferred and orthogonal gratings, examined direction

376 tuning curves in a larger dataset including additional units ($n = 155$; not shown), or compared
377 the global orientation and direction selectivity indices. We conclude that adaptation's effects
378 on spiking activity in SC may be sufficient to explain why the overall strength of suppression
379 is reduced at late time points, but additional mechanisms may be required to explain why the
380 tuning of suppression increases at late time points.

381 *Flexible tuning selectivity of spatial gain controls*

382 The tuning selectivity of spatial gain controls could either be static, or depend on the
383 parameters of the stimulus over the receptive field. In other words, the tuning selectivity may
384 be 'fixed' or 'flexible'. In a sample of neurons that were suppressed by annular gratings we
385 therefore repeated the measurements after rotating the orientation/direction of the central
386 patch by 45 degrees. Suppression is relatively broadly tuned, and we therefore expected to see
387 similar tuning curves for suppression across the two measurements. This was the case (Fig
388 6A,E). Nevertheless, the most suppressive surround did depend on the orientation/ direction
389 of the central patch, at both early (Fig 6A,B) and late (Fig 6E,F) time points.

390 To establish how surround suppression depended on what was shown over the receptive field
391 we focused our analyses on suppression evoked by the pair of annular gratings that matched
392 the orientations/directions of the pair of gratings shown to the receptive field. The orientations
393 of the central gratings over the receptive field are labelled C1 and C2 in Fig 6, and the annulus
394 orientations that matched them are respectively S1 and S2. The analyses in Fig 6C,G show
395 that annular gratings were relatively more effective when they matched the central patch. That
396 is, when C1 was the central grating, suppression at S1 was stronger than suppression at S2
397 (points lie below the diagonal in Fig 6C,G), and when C2 was the central grating the pattern
398 was reversed (points lie above the diagonal). To compare the suppression that was evoked by
399 S1 and S2 at each of the centre orientations we calculated the difference in suppression for the
400 two conditions - that is, for C1 we calculated $SI_{S1} - SI_{S2}$, and for C2 we also calculated $SI_{S1} -$

401 SI_{S2} . This subtraction collapsed the data along the diagonal in Fig 6C,G while preserving sign,
402 and produced the distributions in Fig 6D,H.

403 The advantage of matched annular gratings appeared to increase with time: suppression
404 indices lie further away from the diagonal at later time points (Fig 6G) than they do at early
405 time points (Fig 6C). Similarly, the distributions in Fig 6H lie further from 0 than do the
406 distributions in Fig 6D. To provide a statistical comparison across early and late time points,
407 we computed an additional index, $[MI = (SI_{C1,S1} - SI_{C1,S2}) - (SI_{C2,S1} - SI_{C2,S2})]$ for each unit at
408 each time point. If suppression was fixed, and thus the same for any particular annulus
409 orientation, regardless of centre orientation, then this MI should be 0, but it was not (early: μ
410 40.4, s.d. 33.1, $n = 28$; late: μ 85.4, s.d. 60.1, $n = 22$). Comparison of the indices at early and
411 late time points, for units that responded in both, showed that the index increased at later time
412 points ($p = 0.000459$, $n = 22$; paired Students' t-test). We conclude that the tuning selectivity
413 of suppression in SC can be flexible, and that this flexibility is most apparent at later time
414 points, when the untuned gain control is less effective.

415

416 **DISCUSSION**417 *Functional impact of temporal gain controls*

418 Adaptation's effects allow neurons to adjust their activity to the recent stimulus history. The
419 reduction in response to a stimulus that is unchanging might be used by neurons to better
420 signal changes over time. We have shown that many neurons in the mouse superior colliculus
421 show adaptation effects: responses are characterized by a large initial response that is quickly
422 suppressed. This suppression cannot be explained by retinal light adaptation, because we
423 presented drifting gratings, where the spatial pattern is constantly modulated.

424 The timescales of adaptation effects that we have characterised are on the order of 10s-100s of
425 milliseconds, shorter than most earlier characterisations of adaptation effects in SC, which
426 were primarily conducted in anaesthetised animals (e.g. rabbit: Horn and Hill, 1966; monkey:
427 Cynader and Berman, 1972; mouse: Drager and Hubel, 1975; pigeon: Woods and Frost,
428 1977). That work emphasised a large and long-lasting suppression of response (often called
429 habituation) by the appearance of a visual stimulus. The habituation was strongest in the
430 intermediate and deeper layers of the SC, but it has also been reported in the superficial layers
431 (rabbit: Oyster and Takahashi, 1975; cat: Binns and Salt, 1995). In anaesthetised rat, more
432 rapid adaptation effects were seen in superficial neurons for flashes of bright spots on a dark
433 background (Bytautiene and Baranauskas, 2018), but those effects may have included a
434 contribution of light adaptation. Our stimuli were interleaved, and were preceded by other sets
435 of stimuli, so it is difficult to establish the effect of long-term habituation from these
436 measurements. Nevertheless, we did not see a clear impact of position in the stimulus
437 sequence on response amplitude, even when we only considered units with high adaptation
438 indices (not shown). Recordings in superficial layers of awake monkey also show lack of
439 long-term adaptation effects (e.g. Goldberg and Wurtz, 1972), and more substantial short-term
440 adaptation effects (Mayo and Sommer, 2008; Boehnke et al., 2011).

441 Previous measurements of adaptation's effect in SC have often involved repeated presentation
442 of a brief stimulus (e.g. Boehnke et al., 2011), whereas we measured response to a single,
443 longer, continuous stimulus. While the two types of stimuli are likely to engage the same
444 mechanisms, that does not mean they will have the same effect (Solomon and Kohn, 2014).
445 The transients associated with repeated flashes may be more effective at driving the adaptive
446 mechanism(s) and repeated presentations may therefore induce greater changes in activity.
447 Alternatively, the periods of rest between the presentations may allow adaptive mechanisms
448 to recover, and repeated presentations may therefore have less effect. Onset transients appear
449 to be increasingly important for information processing as one ascends through the visual
450 hierarchy (eg. Tovee et al., 1993; Muller et al., 2001), so differences in adaptive responses to
451 repeated and continuous presentations may be more pronounced in later visual processing. SC
452 integrates early and later visual inputs, so comparison of adaptive responses to flashed and
453 continuous presentation may be of interest.

454 Adaptation effects are prominent in retinal ganglion cell response, and likely first emerge in
455 the bipolar cell input to ganglion cells (salamander: Chander and Chichilnisky, 2001;
456 salamander/rabbit: Baccus and Meister, 2002; monkey: Solomon et al., 2004; guinea pig:
457 Zaghoul et al., 2005; mouse: Marco et al., 2013). It is therefore probable that some of the
458 adaptation effects that we see in SCs are inherited from the retinal input, but we are not aware
459 of reports of retinal neurons that show the complete suppression of response that we often
460 encountered in SCs. Additional mechanisms in SCs, potentially mediated by GABA_B
461 receptors and metabotropic glutamate receptors, have been implicated in pre- and
462 postsynaptic adaptation effects in SCs (cat: Binns and Salt, 1995; rat: Cirone and Salt, 2001),
463 and these are likely to enhance or supersede adaptation effects inherited from retinal input. In
464 addition, the sustained response was slightly reduced at large stimulus sizes (cf. Fig. 3A),
465 while the initial transient was strongly reduced. Size-dependence of the sustained response

466 has also been observed in SC of monkey (Chen and Hafed, 2018), though direct comparison is
467 difficult because that work explored shorter time-windows and stimuli confined to the
468 receptive field.

469 *Functional impact of spatial gain controls*

470 Suppressive surrounds have been described in the superior colliculus of many species (cat:
471 Sterling and Wickelgren, 1969; monkey: Cynader and Berman, 1972; Wurtz et al., 1980; rat:
472 Girman and Lund, 2007; zebrafish: Del Bene et al., 2010; barn owl: Mysore et al., 2010;
473 Zahar et al., 2012; Zahar et al., 2018), including mouse (Wang et al., 2010; Gale and Murphy,
474 2014; Ahmadlou et al., 2017; Barchini et al., 2018). We show that in awake mouse that
475 surround suppression consists at least two components – one that is weakly tuned and
476 adaptable, and another that is more tuned and less susceptible to adaptation’s effects. The
477 tuned gain controls appear to have flexible selectivity, such that the most suppressive
478 surrounding stimulus is that which matches the stimulus over the receptive field.

479 Most types of mouse retinal ganglion cell send axons to the SCs (Ellis et al., 2016) and
480 several of these are known to show surround suppression. One is the ON-OFF W3 cell (Zhang
481 et al., 2012), thought to be a homolog of the “net convexity detector” cells in the frog retina
482 (Lettvin et al., 1959) and the local edge detector (LED) cells first described in rabbit (Levick,
483 1967). But size sensitive responses are also found in ‘high definition’ (HD) (Jacoby and
484 Schwartz, 2017) as well as the direction-selective J and BD retinal ganglion cell classes,
485 which also project to SCs (Kim et al., 2010). Thus some of the surround suppression that we
486 observe in SCs may be inherited from the retinal input. Yet while adaptation effects can
487 reduce the amount of inhibition onto retinal ganglion cells (salamander/rabbit: Baccus and
488 Meister, 2002; mouse: Wark et al., 2009; Marco et al., 2013; salamander: Kastner et al.,
489 2019), we are not aware of reports of adaptation effects on suppression in retina at the time
490 scale of the rapid adaptation that we see in SCs. This suggests that lateral interactions within

491 SCs are a strong contributor to the surround suppression that we see, and the simplest
492 conclusion is that adaptation reduces surround suppression in SCs because adaptation reduces
493 spiking activity in SCs.

494 Networks in the superficial layers of mouse SC include inhibitory lateral interactions that
495 suppress the activity of simultaneously activated neurons (Phongphanphanee et al., 2014).
496 Local inhibition from ‘horizontal cells’, which respond to large stimuli (Gale and Murphy,
497 2014), may be particularly important in providing surround suppression (Gale and Murphy,
498 2016), while ‘narrow field’ and ‘wide field’ cells appear particularly susceptible to
499 suppression (Gale and Murphy, 2014). Similar mechanisms for constructing size tuning have
500 been described in the zebrafish optic tectum (Del Bene et al., 2010). In addition, the superior
501 colliculus receives substantial input from visual cortex (May, 2006), though the role(s) of
502 cortico-collicular input remain unclear – these projections modulate gain of SC neurons but
503 their absence seems to have little effect on tuning properties (Wang et al., 2010; Zhao et al.,
504 2014) or surround suppression (Ahmadlou et al., 2017), at least in mouse. Indeed, surround
505 suppression in the SC may precede that in V1 (monkey: White et al., 2017) and inactivation
506 of SC can interfere with surround suppression in V1 of mouse (Ahmadlou et al., 2018).

507 Units that were not selective for pattern orientation/direction were also less likely to show
508 strong surround suppression. This result may reflect a straightforward correlation in the two
509 functional properties, or surround suppression may be important for constructing selectivity
510 for orientation or direction. Regardless, controlling for the size of stimuli is likely to be
511 important in characterising, and therefore understanding, the mechanisms of orientation and
512 direction tuning in SC.

513 We found that tuned surround suppression was less susceptible to adaptation than untuned
514 suppression, with the consequence that suppression was more sharply tuned and more flexible
515 in later activity. Our finding that at least some of the suppression in SCs is flexible is in

516 accord with recent calcium imaging from SCs of anaesthetised mouse (Barchini et al., 2018).
517 That work showed suppression by surrounding gratings of the same motion direction as a
518 central patch, and facilitation by surrounds of the opposite direction, particularly in excitatory
519 cells. The dynamics of calcium signalling make comparison of response time course difficult,
520 but the initial spiking response, where we find weakly tuned suppression, may have
521 contributed less to the calcium signal than the subsequent response, where we find more
522 tuning of suppression and some facilitation. Our finding that tilted surrounds could even
523 become facilitatory in the late phase of responses raises the possibility that the tuning of late
524 suppression may in fact reflect tuned facilitation. Flexible suppression selectivity may
525 therefore reflect input from neurons with large receptive fields that are sensitive to image
526 continuity (if they provide tuned suppression) or sensitive to image discontinuity (if they
527 provide tuned facilitation). These flexible mechanisms may arise in SCs or in its inputs. If
528 they arise in SCs, then one candidate may be the horizontal cells. Regardless, mouse SCs is
529 likely to be a useful model for understanding the mechanisms that enable flexible suppression
530 of neural responses by spatial context (Coen-Cagli et al., 2015).

531 The functional properties of surround suppression in SCs are remarkably similar to that
532 described for primary visual cortex (V1) in many mammals. First, surround suppression in V1
533 is often orientation- and direction selective (mouse: Self et al., 2014; cat: Nelson and Frost,
534 1978; DeAngelis et al., 1994; Ozeki et al., 2004; monkey: Sillito et al., 1995; Levitt and Lund,
535 1997; Cavanaugh et al., 2002b; Webb et al., 2005; Henry et al., 2013), and that tuning
536 selectivity can be flexible (Sillito et al., 1995; Cavanaugh et al., 2002b). Second, in V1 of
537 mouse, monkey and human, this tuned suppression is complemented by an untuned
538 suppression (mouse: Self et al., 2014; monkey: Webb et al., 2005; Henry et al., 2013; human:
539 Schallmo et al., 2019), some of which may be inherited from earlier processing (cat/monkey:
540 Sillito et al., 1993; cat: Ozeki et al., 2004; Bonin et al., 2005; Naito et al., 2007; monkey:

541 Solomon et al., 2002; Camp et al., 2009). Third, some components of surround suppression in
542 V1 of monkey and human are susceptible to adaptation (Cavanaugh et al., 2002a; Wissig and
543 Kohn, 2012; Patterson et al., 2013; Schallmo and Murray, 2016), though in monkey V1 the
544 tuned components of suppression may be more sensitive to adaptation than the untuned
545 components (Webb et al., 2005).

546 *Summary*

547 We have shown the presence of spatial and temporal gain controls in SCs of awake mouse
548 and how they are distributed across neurons. Our results are consistent with the idea that these
549 gain controls provide a predictive signal against which activation of the classical receptive
550 field is compared, thereby suppressing the response to predictable stimuli and highlighting
551 unexpected ones. Our results can be accommodated by a layering of gain controls as
552 illustrated in Fig 7. Fig 7A shows the standard model of early visual processing (e.g.
553 Carandini and Heeger, 2011; Solomon and Kohn, 2014). The output of the classical receptive
554 field (CRF), which filters the visual image, is subject to a spatial gain control, or suppressive
555 surround, before driving spiking activity. The suppressive surround is constructed from
556 nearby neurons with similar characteristics. Adaptation's effects can be thought of as
557 changing the output function of the neuron, as shown by the red-line in Fig 7B. This accounts
558 for the results in Fig 5, because similar neurons contribute to the surround, and the surround is
559 therefore relatively broadly tuned for orientation/direction and susceptible to adaptation's
560 effects. To account for the advantage of surrounds that match the centre stimulus (Fig 6), and
561 the apparent resilience of this suppression to adaptation's effects, a second mechanism seems
562 to be required (Fig 7C). This is sensitive to the relationship between features over the CRF
563 and surround, and is less adaptable.

564 We also found that the strength of adaptation's effects and strength of surround suppression
565 were correlated among neurons. Our results therefore show that neurons characterized by a

566 transient, adapting response are more likely to also be affected by spatial context, and may
567 therefore signal the presence of unexpected objects in either the spatial and the temporal
568 domain. This suggests the presence of a subpopulation of ‘novelty’ or ‘saliency’ neurons
569 within the SC that are sensitive to unexpected events in the visual diet. Whether this
570 functional subgroup has an anatomical correlate would be of interest. In monkey, the
571 amplitude of the initial transient response in anatomically deeper visual-motor SC neurons,
572 which receive direct input from the superficial purely visual neurons studied here, is known to
573 be particularly important in the nature and latency of orienting behaviours such as saccades
574 (Boehnke and Munoz, 2008; Chen and Hafed, 2017).

575

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772 **FIGURE LEGENDS**

773

774 **Figure 1. Expression of spatial and temporal gain controls in neurons in superior**
775 **colliculus of awake mouse. A-D.** Responses of four representative neurons. The left panel in
776 each case shows the average firing rate of the neuron during a 2 s presentation of a circular
777 patch of drifting grating at a spatial frequency near the preferred for the neuron (0.05-0.07
778 cycles/°), and centred on the receptive field. The right panel in each case shows the
779 peristimulus time histogram (PSTH, bin width 0.016 s) during presentation of a patch of
780 grating near the preferred size for that neuron, which is indicated by the arrow in the left
781 panel. Dashed horizontal lines show the maintained rate in absence of patterned visual
782 stimulus. Solid line shows the predictions of the size-tuning model described in Methods
783 (Equation (2)). Error bars show ± 1 SEM across trials. The insets show a spatial map of
784 responses (white indicates no activity and darker colours indicate stronger responses) to a
785 black square, 15° wide, flashed at each of 81 positions on the monitor. Calibration bars are
786 30°. The schematic below panel (A) shows the relative size of two patches of grating, and
787 how a grating of 0.05 cycles/° would appear in each of them.

788

789 **Figure 2. Correlated variability in surround suppression and adaptation effects. A.**
790 Population size-tuning for patches of drifting gratings. Each row of the image shows the
791 predictions of the size-tuning model for a single neuron (as in Fig 1), normalized to its
792 maximum response. Only units in which the normalized log-likelihood of the model was at
793 least 0.5 are shown. The units are ordered, from bottom-to-top, by the preferred size. **B.**
794 Mean size-tuning for a drifting grating, obtained by averaging across the rows in (A). Dashed
795 lines show ± 1 SEM across neurons. Dashed horizontal line shows the maintained rate,
796 normalized to the unit's maximum visual response before averaging. Arrow indicates the
797 definition of the suppression index, SI, which is the proportional reduction in response from a

798 grating of preferred size to a large grating. **C.** Distribution of the suppression index across the
799 population of units in (A). The filled bars show SI for neurons with preferred diameter greater
800 than 30° . **D.** Population time-course for drifting gratings of preferred size. The units are
801 ordered, from bottom-to-top, by the adaptation index, AI. Colour bar as in (A). **E.** Mean time-
802 course for a drifting grating, obtained by averaging across the rows in (D). Conventions as in
803 (B). Arrow indicates the definition of the adaptation index, AI, which is the proportional
804 reduction in response from the first 0.5s to the last 0.5s. **F.** Distribution of the adaptation
805 index across the population of units in (D). **G.** Comparison of the suppression index and
806 adaptation index in individual neurons ($n = 93$). Dashed line is the best linear fit to the data.

807

808 **Figure 3. Surround suppression is susceptible to adaptation. A.** Time-course of population
809 response for gratings for small (20° diameter) and large (90°) patches of drifting grating.
810 Responses were normalized to the mean response across all patch sizes (most of which are not
811 shown) before averaging ($n = 98$). Dashed horizontal line shows the maintained rate in
812 absence of patterned visual stimulus, normalized in the same way. Error bars are omitted for
813 clarity. **B.** Size-tuning for early (0-0.5 s) and late (1.5-2 s) response, normalized in the same
814 way as (A).. Error bars are ± 1 SEM across neurons that passed criteria for inclusion (early: n
815 = 92; late: $n = 80$). **C.** Comparison of suppression index for early and late response ($n = 73$).
816 Dashed line shows the unity line. Points falling below the line indicate neurons in which
817 suppression was stronger in the early response than in the late response.

818

819 **Figure 4. Tuning of surround suppression in SC of awake mouse. A,B.** Response of an
820 example neuron. **A.** Tuning of spiking activity evoked by a large patch of drifting grating (45°
821 diameter) of varying orientation/direction. Dashed horizontal line shows the maintained rate
822 in absence of patterned visual stimulus. **B.** Tuning of suppression induced by an annular
823 grating of varying orientation/direction. Responses are shown for presentation of a 15° patch

824 of drifting grating (upper dashed line, 'Centre alone') of direction 180° , the same stimulus
825 when abutted by an annular grating of outer diameter 80° ('Centre+surround'), and two of the
826 annular gratings presented in absence of the centre grating ('Surround alone'). The lower
827 dashed horizontal line shows the maintained rate in absence of patterned visual stimulus. A
828 suppression index, SI, can be calculated for each annulus direction as the proportional
829 reduction in response from the 'Centre alone' stimulus to the relevant 'Centre+surround'
830 stimulus. Error bars in (A,B) are ± 1 SEM over trials. **C.** Comparison of tuning for spiking
831 activity (abscissa) and suppression (ordinate). Each unit contributes two points: the open
832 symbols indicate a global measure of direction tuning (Equation (5)) and the filled symbols
833 indicate a similar measure of orientation tuning. **D, E.** Population averages. **D.** Population
834 average spiking activity evoked by a large grating, after aligning each neuron to its preferred
835 direction, subtracting the maintained rate, and then normalizing by the mean response across
836 all stimuli. **E.** Average suppression index, obtained as in (B), after aligning each neuron to the
837 direction of the central grating patch. Dashed horizontal line shows an SI of zero. Error bars
838 in (D,E) are ± 1 SEM over neurons. **F.** Distribution of preferred orientation of suppression,
839 relative to the orientation of the centre grating, in units in which the preferred orientation
840 could be defined (orientation tuning index greater than 0.1). A relative orientation of zero
841 indicates neurons in which the most suppressive stimulus was the same orientation as the
842 centre; a relative orientation of 90° indicates neurons in which the most suppressive stimulus
843 was orthogonal to the central stimulus. Schematics in panels A,D,E are not to scale.

844

845 **Figure 5. Impact of adaptation on tuning of spiking activity and surround suppression.**

846 **A-D.** Responses in early (first 0.5s) time points. **A.** Population average tuning of spiking
847 activity evoked by a large grating. Conventions as in Fig 4D. **B.** Population average tuning of
848 suppression induced by annular grating. Conventions as in Fig 4E. **C.** Comparison of
849 suppression index for annular gratings that match the direction of the central grating

850 ('parallel', abscissa), or are tilted by 45° (ordinate). Suppression index for the latter was
851 averaged across both possible directions of tilt. Dashed lines are the unity line. **D.** Distribution
852 of the difference in suppression for the two annular gratings. Positive indices indicate more
853 suppression by a parallel annulus than a tilted annulus. **E-H.** Same A-D, but for late (last 0.5s)
854 time points. Schematics in panels A–C are not to scale.

855

856 **Figure 6. Adaptation's effects magnify flexible surround suppression. A-D.** Responses in
857 early (first 0.5s) time points. **A.** Spiking activity of an example neuron during presentation of
858 a central stimulus either presented alone (C1,C2), or abutting an annulus of varying direction.
859 Two measurements were made, first with a central grating near the preferred direction of
860 spiking activity (C1) and then with a central grating tilted by 45° (C2). Error bars are ± 1 SEM
861 over trials. **B.** Population average tuning of suppression for each of two central gratings
862 (C1,C2). Conventions as in Fig 4E. **C.** Comparison of suppression induced by pairs of stimuli.
863 The abscissa shows the suppression induced by an annular grating (S1) that matched the
864 direction of the central grating C1. The ordinate shows the suppression induced by an annular
865 grating (S2) that matched the central grating C2. Points below the unity line (dashed line)
866 indicate stronger suppression for S1 than S2. Filled circles show measurements obtained with
867 C1: these generally lie below the unity line, indicating that when C1 is used, S1 is more
868 effective than S2. Open circles show measurements obtained for C2: measurements are
869 generally above the unity line, indicating that S2 is more effective than S1. This is the pattern
870 of results expected if suppression is stronger when the stimuli over the centre and surround
871 are matched. **D.** Distribution of the difference in suppression for each of the centre gratings,
872 C1 (lower) and C2 (upper). Positive indices indicate more suppression by S1 than S2. **E-H.**
873 Same as A-D but for late (last 0.5s) time points. Example neuron in E is the same as that in A.
874 Schematics above A,E are not to scale.

875

876 **Figure 7. Descriptive model for interaction of spatial and temporal gain controls in SCs.**

877 **A.** Standard model of receptive fields early in the visual pathway. The classical receptive field
878 ('CRF') filters the visual image, and its output is subject to a spatial gain control ('Surround')
879 before driving spiking output. The surround is comprised of units with receptive fields similar
880 to that of the CRF. **B.** Adaptation's effects reduce the response of the neuron under study, and
881 the responses of neurons that contribute to the spatial gain control. **C.** Addition of a second,
882 less adaptable, component to the spatial gain control allows for preservation of suppression
883 when the features of the image over the CRF matches that over the surround.











