Title: Gamma oscillations in primate primary visual cortex are severely attenuated by small stimulus discontinuities

Running title: Stimulus discontinuities attenuate V1 gamma

Authors

Vinay Shirhatti^{1,2,3}, Poojya Ravishankar^{1,4} and Supratim Ray^{1*}

Affiliations

¹Centre for Neuroscience, Indian Institute of Science, Bangalore, India, 560012

²IISc Mathematics Initiative, Indian Institute of Science, Bangalore, India, 560012

Current address:

³Institute for Systems Research, University of Maryland, College Park, Maryland 20742

⁴Committee on Computational Neuroscience, University of Chicago, Illinois 60637

Telephone +91 80 2293 3437, Facsimile +91 80 2360 3323

Corresponding author and Lead Contact:

*Supratim Ray: sray@iisc.ac.in

Number of Pages: 43

Number of Figures: 8 main figures, 1 supplementary figure (all color)

22 **Summary**

23 Gamma oscillations have been hypothesized to play an important role in feature binding,
 24 based on the observation that continuous long bars induce stronger gamma in the visual
 25 cortex than bars with a small gap. Recently, many studies have shown that natural images,
 26 that have discontinuities in several low-level features, do not induce strong gamma
 27 oscillations, questioning their role in feature binding. However, the effect of different
 28 discontinuities on gamma has not been well studied. To address this, we recorded spikes
 29 and local field potential from two monkeys while they were shown gratings with
 30 discontinuities in space, orientation, phase or contrast. Gamma, but not spiking activity,
 31 drastically reduced with small discontinuities in all cases, suggesting that gamma could be
 32 a resonant phenomenon. An excitatory-inhibitory population model with stimulus-tuned
 33 recurrent inputs showed such resonant properties. Therefore, gamma could be a signature
 34 of excitation-inhibition balance, which gets disrupted due to discontinuities.

35

36 **Keywords:** Gamma, LFP, V1, Gratings, Discontinuities

37 **Introduction**

38 Gamma oscillations (~30-80 Hz) are strongly induced in the primary visual cortex (area
39 V1) by stimuli such as gratings, bars or colors (Bartoli et al., 2020). One influential
40 hypothesis posits that gamma oscillations play a role in visual perceptual grouping or
41 feature binding, based on the finding that continuous bars induce stronger gamma
42 synchronization between neurons whose receptive fields (RFs) contain parts of the bar as
43 compared to discontinuous bars, even when the discontinuity is outside their RFs (Castelo-
44 Branco et al., 1998; Engel et al., 1991; Gray et al., 1989; Gray and Prisco, 1997). However,
45 in the case of natural images, studies have reported disparate observations regarding the
46 consistency of gamma oscillations (Bartoli et al., 2019; Brunet et al., 2013; Hermes et al.,
47 2014), casting doubts on a causal role for them in feature binding in a natural setting.
48 Because such natural stimuli might occur as discontinuities along many feature dimensions
49 across the RF of neurons, it is important to study how different types of structural
50 irregularities affect firing responses and gamma oscillations. A recent study explored
51 discontinuities in chromatic content and showed that stimulus discontinuities can reduce
52 gamma synchronization between responsive neurons (Peter et al., 2019). However, the
53 effect of discontinuities along other feature dimensions, such as orientation, phase and
54 contrast, on gamma oscillations and firing rates remain largely unknown.

55

56 In addition, it is unclear how gamma oscillations depend on the size of the discontinuity.
57 Recently, Hermes and colleagues proposed an image-computable model of gamma
58 oscillations, in which the amplitude of gamma depends on the variability across orientation
59 channels (Hermes et al., 2019). In such models, reduction in gamma is expected to be

60 graded and proportional to the size of the discontinuity. However, other studies have
 61 suggested that gamma could be a resonant phenomenon arising due to a tight interplay of
 62 excitatory and inhibitory (E-I) signals in a neuronal network (Atallah and Scanziani, 2009;
 63 Brunel and Wang, 2003; Buzsáki and Wang, 2012; Jia et al., 2013; Moca et al., 2014; Veit
 64 et al., 2017) Indeed, the V1 RF structure has an excitatory center region flanked by
 65 suppressive near-surround and far-surround regions, and involves interactions between
 66 feedforward geniculocortical signals, lateral intracortical signals from horizontal
 67 connections and feedback signals from higher areas (Angelucci et al., 2017). Stimulus
 68 discontinuities could potentially modulate the interactions between these diverse neuronal
 69 sub-populations and alter the levels of E-I in this network, which may result in a drastic
 70 reduction in gamma even with a small discontinuity.

71

72 To address these questions, we recorded spikes and local field potential (LFP) from area
 73 V1 of passively fixating alert monkeys using microelectrode arrays, while they were
 74 shown sinusoidal luminance gratings with or without discontinuities that varied along one
 75 of four dimensions: space, orientation, phase and contrast. Further, the magnitude of
 76 discontinuity for each dimension was parametrically varied. We compared how gamma
 77 oscillations and firing rates changed with the magnitude of such discontinuities. Finally,
 78 we built an E-I network based on Wilson-Cowan model operating in an inhibition
 79 stabilized mode (Jadi and Sejnowski, 2014; Tsodyks et al., 1997; Wilson and Cowan,
 80 1972) and added stimulus dependent local recurrent inputs to model discontinuities. This
 81 simple model could mimic crucial aspect of our observations.

82

83 **Results**

84 We implanted a microelectrode array in area V1 of two monkeys and estimated the RFs of
 85 the recorded sites by flashing small sinusoidal luminance gratings on locations forming a
 86 dense rectangular grid on the approximate aggregate RF for all the sites ((Dubey and Ray,
 87 2019, 2016); see Methods for details). We have previously shown that large gratings
 88 induce two distinct gamma oscillations in V1, termed slow (20-35 Hz) and fast (35-70 Hz)
 89 gamma (Murty et al., 2018). Here, we presented large static gratings (radii of 9.6° and 6.4°
 90 for the two monkeys) at a spatial frequency of 4 cycles/degree (cpd), 100% contrast
 91 (except in the contrast discontinuities experiment), at an orientation that induced strong
 92 fast gamma oscillations (although for Monkey 2, these induced moderately strong slow
 93 gamma as well), and introduced discontinuities of different types. Therefore, the following
 94 results are focused on the fast gamma band, and ‘gamma’ refers to this band. Unless
 95 otherwise stated, for the discontinuous gratings, the radius of the inner grating was fixed at
 96 0.3° and 0.2° for Monkeys 1 and 2 respectively, which was close to the average RF sizes
 97 (mean $\pm$ s.e.m. for Monkey 1: $0.28^\circ \pm 0.009^\circ$, Monkey 2: $0.17^\circ \pm 0.0065^\circ$). Thus, the
 98 discontinuity across experiments occurred approximately in the visual space corresponding
 99 to a transition between the center and surround. In each session, stimuli were centered on
 100 the RF center of one of the recorded sites.

101

102 ***Annular cut discontinuity disrupts gamma***

103 We first tested the effect of a discontinuity in space by introducing an annular cut in the
 104 gratings, whose width could take one of the following 5 values: 0° (no discontinuity),

105 0.025°, 0.05°, 0.1°, and 0.2° (Figure 1A, topmost row). The trial averaged time frequency
 106 (TF) difference spectra for an example site from a session in Monkey 1 shows a drastic
 107 reduction in gamma power by ~58% with an introduction of the smallest tested
 108 discontinuity of 0.025° (Figure 1A, second row). This effect was qualitatively consistent in
 109 the population across multiple sessions in both monkeys (Figure 1A, rows 3 and 4) and
 110 was also evident in the average change in power plot (computed between a stimulus period
 111 of 250-750 ms and compared against a baseline period of -500 to 0 ms, where 0 ms
 112 represents stimulus onset) for different stimuli (Figure 1B). Here, we also observed a
 113 second peak at ~80-100 Hz in Monkey 1, which was simply a harmonic of the fast gamma.
 114 In comparison, the spiking activity showed only a modest increase across different
 115 conditions (Figure 1C) as the surround suppression reduced with increasing annular cut
 116 width.

117

118 To directly compare the relative effects of annular discontinuity on gamma power and
 119 spiking activity at the population level, we first selected units which had a mean firing rate
 120 of at least 1 spike/sec during the stimulus epoch for at least one of the stimulus conditions,
 121 normalized both gamma power and firing rates by dividing by the maximum value across
 122 the five stimulus conditions, and computed the mean across sites (Figure 1D). While the
 123 mean normalized gamma power decreased significantly for each discontinuity level (as
 124 indicated by red asterisks in Figure 1D) in both monkeys, the increase in firing rate was
 125 less salient, only reaching significance for the comparison between no discontinuity and
 126 the smallest discontinuity in Monkey 1. Slopes of regression of change in mean normalized
 127 gamma power with increasing annulus width were -3.22 ± 0.08 units/° (mean $\pm$ s.e.m. units

per degree of visual angle) and -2.27 ± 0.09 units/ $^{\circ}$ for the two monkeys, both significantly negative (Monkey 1: $p = 0.12 \times 10^{-5}$, Wilcoxon signed rank (WSR) test, Monkey 2: $p = 0.11 \times 10^{-6}$), whereas similar regression slopes with normalized firing rates were 1.52 ± 0.25 units/ $^{\circ}$ for Monkey 1 ($p = 0.3 \times 10^{-4}$, WSR test) and 0.26 ± 0.23 units/ $^{\circ}$ for Monkey 2 ($p = 0.41$). Importantly, the magnitude of slope was significantly greater for gamma power than for firing rates across individual sites (Figure 1E, $p = 0.12 \times 10^{-4}$ and 0.77×10^{-5} for Monkey 1 and 2 respectively, WSR test), implying that the mean rate of change in normalized gamma with annulus width was significantly greater than that for normalized firing rates. These results indicate that overall gamma was more sensitive to the annular discontinuity than firing rate.

138

To test whether our results depended on the location of the discontinuity, we performed the same experiment but with the discontinuity appearing at one of the following 4 radii from the center of the stimulus: 0.15° , 0.3° , 0.6° and 1.2° in Monkey 1 and 0.1° , 0.2° , 0.4° and 0.8° in Monkey 2. For each case, the width of the cut could take one of the same 5 values as in the annular cut experiment. Figure 2A and 2B show the normalized gamma power and firing rates for the two monkeys (see Supplementary Figure 1 for more details). Gamma was more severely disrupted by a discontinuity that occurred closer to the center (Figure 2A, Supplementary Figure 1A-1B). This was reflected in the magnitude of the regression slope between normalized gamma power and annulus width, which decreased for farther cut locations (Figure 2C). On the other hand, increases in firing rate were more modest (Figure 2B, Supplementary Figure 1C), with regression slopes significantly smaller than the corresponding slopes for gamma for smaller cut radii (as indicated in Figure 2C).

151

152 *Effect of orientation discontinuity*

153 To evaluate the effect of orientation discontinuity we varied the relative orientation of the
 154 inner and outer parts of the static grating stimulus (Figure 3A). Average TF difference
 155 spectra across trials of the different stimuli, for an example site from a session in Monkey
 156 1, show that gamma oscillations were strongest for matched orientations, and their strength
 157 reduced drastically even with the smallest mismatch of 10° on both sides (by $\sim 72\%$ for a
 158 difference of -10° between outer and inner orientation ($(O-I)^\circ$), and by $\sim 69\%$ for $(O-I)^\circ =$
 159 10°). As the orientation difference systematically increased between the inner and outer
 160 gratings, there was a drastic reduction in the strength of gamma power across the
 161 population in both monkeys as evidenced in the average TF spectra (Figure 3A, rows 3 and
 162 4) and change in power (Figure 3B). On the other hand, spiking activity increased as the
 163 mismatch between inner and outer orientation increased (normalized firing rates, Figure
 164 3C). This is consistent with previous studies of cross orientation suppression where lateral
 165 inhibition from the surround has been shown to be the strongest when the center and
 166 surround orientation are matched and weakens with increase in orientation differences
 167 (Blakemore and Tobin, 1972; Knierim and van Essen, 1992; Sillito et al., 1995).

168

169 For a subset of strongly firing units, we compared the dependence on orientation
 170 discontinuity of the normalized gamma power to normalized spiking activity (Figure 3D),
 171 similar to the analysis in Figure 1D. For the smallest orientation discontinuity that we
 172 presented, normalized gamma power reduced significantly for both sides by $\sim 48\%$ (for $(O-$

173 $I)^{\circ} = -10^{\circ}$, $p = 0.96 \times 10^{-6}$, WSR test) and ~52% (for $(O-I)^{\circ} = 10^{\circ}$, $p = 0.80 \times 10^{-6}$) in
174 Monkey 1 and ~12% (for $(O-I)^{\circ} = -10^{\circ}$, $p = 0.67 \times 10^{-7}$) and ~15% (for $(O-I)^{\circ} = 10^{\circ}$, $p =$
175 0.13×10^{-8}) in Monkey 2, whereas firing rates remained mostly unchanged (Figure 3D,
176 WSR test, $p = 0.06$ and $p = 0.29$ for the two sides in Monkey 1; similarly $p = 0.64$ and $p =$
177 0.43 in Monkey 2). To further compare the rate of change in gamma and firing rates due to
178 orientation discontinuity, we computed the slope of regression of their normalized values
179 with discontinuity on both sides over the range where mean values varied clearly ($(O-I)^{\circ} =$
180 0° to $\pm 20^{\circ}$ in Monkey 1, and $(O-I)^{\circ} = 0^{\circ}$ to $\pm 30^{\circ}$ in Monkey 2). Across sites the slopes
181 were significantly negative for gamma ($p = 0.88 \times 10^{-6}$ and 0.80×10^{-6} on the two sides in
182 Monkey 1, and 0.75×10^{-10} and 0.89×10^{-10} in Monkey 2, WSR test), and significantly
183 positive for firing rates ($p = 0.16 \times 10^{-4}$ and 0.54×10^{-4} in Monkey 1, $p = 0.64 \times 10^{-4}$ and
184 0.48×10^{-2} in Monkey 2, WSR test). However, the magnitude of the mean slope (averaged
185 across both sides) was larger for gamma than for firing rates consistently across individual
186 sites in both the monkeys (Figure 3E, $p = 0.42 \times 10^{-5}$ in Monkey 1, and 0.66×10^{-8} in
187 Monkey 2, WSR test). Interestingly, the mean firing responses changed significantly
188 between conditions of 10° to 20° orientation differences between the inner and outer
189 gratings, after which they again remained comparable for increasing orientation differences
190 in both the monkeys (Figure 3D). Gamma, on the other hand, was sensitive to orientation
191 differences across a larger range and this effect was more consistent across the recorded
192 sites.

193

194 *Effect of phase discontinuity*

Next, we introduced increasing levels of spatial phase difference between the inner and outer gratings. Gamma dropped drastically with the smallest phase difference of 60° on both sides (both $(O-I)\phi^\circ = 60^\circ$ and 300° imply a phase difference of 60° from two sides of the spatial cycle) as seen in the average TF difference spectra for an example site in Monkey 1 (Figure 4A, row 2, gamma reduced by $\sim 57\%$ for $(O-I)\phi^\circ = 60^\circ$ and $\sim 52\%$ for $(O-I)\phi^\circ = 300^\circ$) and for the population in both the monkeys (Figure 4A, 3rd and 4th row). Across the population, the matched condition showed the strongest gamma oscillations and the strength of gamma reduced progressively as the phase disparity increased from both sides of the spatial cycle until 180° , at which the center and surround were in perfect anti-phase, showing that gamma changed in accordance with the magnitude of discontinuity (Figure 4A, 4B). Firing rates remained mostly unchanged with the smallest discontinuities and showed a small increase with bigger discontinuities (Figure 4C, 4D).

207

The stimulus period mean normalized gamma power (Figure 4D, similar to Figure 1D and 3D) reduced significantly by $\sim 44\%$ with the smallest phase differences on both sides in Monkey 1 ($p = 0.40 \times 10^{-17}$ for $(O-I)\phi^\circ = 60^\circ$ and 0.18×10^{-14} for $(O-I)\phi^\circ = 300^\circ$, t-test) and by $\sim 17\%$ ($(O-I)\phi^\circ = 60^\circ$, $p = 0.23 \times 10^{-13}$) and $\sim 18\%$ ($(O-I)\phi^\circ = 300^\circ$, $p = 0.61 \times 10^{-17}$) in Monkey 2. The corresponding change in normalized firing rates was not significant in Monkey 1 ($p = 0.36$ and 0.48 , t-test) and increased significantly only for $(O-I)\phi^\circ = 300^\circ$ in Monkey 2 ($p = 0.57 \times 10^{-3}$; $p = 0.26$ for $(O-I)\phi^\circ = 60^\circ$). To compare the dependence of gamma and firing rates on phase discontinuity at each site, we computed the slope of regression of their normalized values with phase discontinuities from 0° to 180° from both

sides of the spatial cycle. Slopes were significantly negative for normalized gamma ($p = 0.8 \times 10^{-6}$ for both sides in Monkey 1; $p = 0.87 \times 10^{-13}$ and 0.20×10^{-12} for Monkey 2, WSR test) and significantly positive for firing rates ($p = 0.58 \times 10^{-4}$ and 0.10×10^{-2} in Monkey 1; $p = 0.62 \times 10^{-3}$ and 0.12×10^{-3} in Monkey 2) on both sides in both monkeys. The magnitude of slope was significantly larger for gamma than for firing rates across individual sites (Figure 4E, $p = 0.20 \times 10^{-4}$ in Monkey 1; $p = 0.33 \times 10^{-5}$ in Monkey 2). Thus, change in gamma power was more sensitive to phase discontinuities for a much broader range compared to firing rate (Figure 4D) and showed a higher sensitivity consistently across sites (Figure 4E). The most significant changes in firing responses were observed for bigger mismatches in phases of 120° or 240° between the center and surround region. They did not increase further for larger mismatches in both monkeys (Figure 4D, black line). Thus, there is a critical sub-range of maximum sensitivity of firing rates to phase differences, similar to the orientation discontinuity effects.

230

231 *Effect of contrast discontinuity*

Increasing the contrast of a visual stimulus has been shown to increase the spiking responses as well as the strength (Henrie and Shapley, 2005) and frequency of gamma oscillations in V1 (Jia et al., 2013; Ray and Maunsell, 2010). Likewise, increasing the stimulus size, which is expected to increase surround suppression, also increases gamma power but reduces the peak frequency (Gieselmann and Thiele, 2008; Jia et al., 2013; Ray and Maunsell, 2011). We studied how a discontinuity in the contrast profile across the inner and outer regions of the grating affects gamma oscillations, by varying their contrast independently over five different values (25 combinations). In Figure 5A, the inner and

240 outer contrasts were matched along the diagonal, and contrast discontinuity progressively
 241 increased away from this diagonal. If gamma depended mainly on the overall input
 242 strength, it should increase with an increase in contrast of either the inner or outer segment
 243 of the stimulus. In such a scenario gamma should increase from the left to the right column
 244 (Figure 5A, as outer contrast increases) and from the top to the bottom row (as inner
 245 contrast increases). Instead, gamma was strongest for the contrast matched stimuli along
 246 the diagonal compared to stimuli away from the diagonal (Figure 5A). This is also clear in
 247 Figure 5B, where each plot represents the change in power for a fixed inner contrast and
 248 varying levels of outer contrast, and in the comparison of the mean level of normalized
 249 gamma for all stimulus conditions, averaged across all center sites across sessions (Figure
 250 6A). To quantify this effect, we compared the gamma power for each contrast matched
 251 stimulus and its neighboring mismatched stimuli, obtained by either decreasing or
 252 increasing the contrast of either the inner or outer grating only (Figure 6A, bar plots).
 253 Gamma rhythm was negligible for contrast matched stimuli at low contrasts (below 25% in
 254 our stimulus set) and therefore power in this band simply followed the change in overall
 255 stimulus drive due to discontinuities at low contrasts. However, at higher contrasts (50%
 256 and above), any change in contrast of either the center or surround (decrease or increase)
 257 from the matched case caused a significant reduction in gamma power. This effect was
 258 especially stark when the contrast matched stimulus at 50% or 75% (in Monkey 2) was
 259 changed.

260

261 The spiking activity, on the other hand, showed a more direct dependence on the contrast,
 262 generally increasing with an increase in inner contrast or reduction in outer contrast

(Figure 5C, 6B), and decreasing with a decrease in inner contrast. With an increase in outer contrast, the firing rates occasionally increased, especially at low-level center contrasts (0%, 25%) in Monkey 2, although this increase was smaller than the increase due to center contrast (Figure 5C, 6B). Such an effect of surround contrast is not unexpected, since at low contrasts surround has been shown to be facilitatory (Ichida et al., 2007; Polat et al., 1998). At mid and high contrast discontinuities, firing rates mostly remained unchanged.

269

We compared the effect of contrast discontinuity on gamma and firing rates at each site by plotting the magnitude of change in their normalized values from the continuous case with strongest gamma rhythm (50% in Monkey 1 and 75% in Monkey 2) to the four immediate discontinuity cases i.e. when either the inner or outer contrast changed by one step (Figure 6C). In both the monkeys, the change in gamma was significantly greater than for firing rates in almost all cases ($p = 0.56 \times 10^{-5}$, 0.56×10^{-5} , 0.56×10^{-5} and 0.79×10^{-5} in Monkey 1 for inner contrast decrease and increase, and outer contrast decrease and increase respectively; $p = 0.18 \times 10^{-2}$, 0.11×10^{-3} , 0.14×10^{-5} and 0.78×10^{-1} in Monkey, WSR test). Thus, gamma was more sensitive to contrast discontinuities than firing rates.

279

280 *A resonant model of gamma oscillations*

To understand the resonant properties of gamma oscillations, we used a previously well-studied lumped neuronal model, consisting of an excitatory (E) and an inhibitory (I) neuronal population that can generate oscillations ((Jadi and Sejnowski, 2014), equation 1, refer ‘Model details’ in Methods). To model discontinuities in this framework, we included

285 additional lateral recurrent (LR) inputs (equation 2-3), which were further dependent on
 286 the overall excitatory and inhibitory activity of the population (Figure 7). This effectively
 287 changed the weights of the network model (see Methods for details). In this framework,
 288 loss of recurrent inputs due to a discontinuity could be modeled as a reduction in some of
 289 the weights.

290

291 Figure 8A shows the mean firing rates of the E population (first column), I population
 292 (second), peak gamma power (third) and peak gamma frequency (fourth), as a function of
 293 the external inputs given to the E and I populations (denoted by iE and iI). Here, increasing
 294 the size of the stimulus increases iI (vertical progression in these plots), while increasing
 295 the contrast of the stimulus increases both iE and iI (diagonal progression in the plots). Jadi
 296 and Sejnowski showed that in a regime in which the responses of I population is strongly
 297 superlinear while E population is sublinear (as indicated by white lines; for details see
 298 (Jadi and Sejnowski, 2014)), increasing stimulus contrast increases gamma peak frequency
 299 and increasing stimulus size decreases gamma peak frequency and increases its magnitude,
 300 as observed in real data (Gieselmann and Thiele, 2008; Henrie and Shapley, 2005; Jia et
 301 al., 2013; Ray and Maunsell, 2011, 2010).

302

303 Here we show that small perturbations in the model operating within this regime, which
 304 only lead to small changes in the steady-state firing rates of the E and I populations, can
 305 severely attenuate gamma oscillations. We modeled the discontinuity as a drop in the
 306 excitatory synaptic weights for E (w_{EE}) by 10% (Figure 8B) and 20% (Figure 8C). Even a

10% drop in *wee* caused oscillations to weaken considerably (8B, 8D), and they were almost abolished with a 20% reduction (8C-D). Importantly, the mean E or I response remained almost unchanged. To study the properties of this dynamical system, we plotted the excitatory and inhibitory nullclines and found that reduction in *wee* led to a minor flattening of the excitatory nullcline (Figure 8E). While this led to only a minor change in the fixed point (mean E and I responses), the oscillatory power (limit cycle) reduced drastically. Jadi and Sejnowski (2014) had shown that by varying the external inputs (which cause a translation of the E and I nullclines), the dynamical system can transition from a stable operating regime to an oscillatory one through a transition known as a supercritical Andronov-Hopf bifurcation, in which both the power and frequency of the oscillations critically depend on the weights and time constants (exact dependence is derived in Jadi and Sejnowski, 2014 and is therefore not replicated here). Such a finely balanced system near the bifurcation point could be brought back to a stable regime by a slight reduction of the excitatory weights, leading to the loss of oscillations. Modifications in other weights (such as *wii*, *wei* or *wie*), which caused similar changes in the slopes of the E and I nullclines, also led to changes in the oscillatory properties and the expanse of the valid regime where the model behaved as expected. Reduction in weights mostly led to shrinking of this valid regime, and concomitant changes in weights produced even stronger effects. Overall, these results demonstrate a resonance like behavior of the oscillations, similar to the experimental observations, whereby small perturbations (here modelled by a small change in *wee*) that do not change the steady state firing rates by much can nonetheless cause huge changes in the magnitude of the oscillations.

329 **Discussion**

330 Strong gamma oscillations in V1 LFP are known to be induced by optimized grating
 331 stimuli. When the center and surround of V1 RF were stimulated by gratings of different
 332 orientations, phases or contrasts, or when there was a grey annular cut between these
 333 regions, strength of gamma oscillations was severely reduced. Importantly, gamma
 334 oscillations were more sensitive to these discontinuities compared to the spiking activity.
 335 Furthermore, this sensitivity of gamma to the discontinuity was dependent on the location
 336 of discontinuity with respect to the center-surround structure of the V1 RF. We
 337 demonstrate that an E-I neuronal network model can exhibit such a behavior when there
 338 are small changes in overall weights in the network due to such discontinuities.

339

340 ***Gamma and visual irregularities***

341 Gamma oscillations induced by large gratings have been shown to be stronger and
 342 coherent over larger spatial extents than those induced by small gratings, but are adversely
 343 affected by addition of noise (Jia et al., 2013, 2011; Zhou et al., 2008), or superimposition
 344 of cross orientation gratings to form plaids (Lima et al., 2010). While addition of noise or
 345 an orthogonal orientation component modifies both the center and surround properties, our
 346 manipulations mostly change the stimulus outside the classical RF, bringing out the strong
 347 influence of this extra-classical modulation on gamma oscillations. This modulation can be
 348 both inhibitory and excitatory, and is mostly mediated through inputs from lateral
 349 intracortical connections, feedback from higher areas, and feedforward inputs (Angelucci
 350 et al., 2017, 2002; Nassi et al., 2013; Nurminen et al., 2018; Ozeki et al., 2004). In a

351 similar context, a study in mouse V1 (Veit et al., 2017) showed that orthogonal orientation
352 in the extra-classical surround reduces the power of a ‘context-dependent gamma’ rhythm.

353

354 Across all the discontinuity types an additional contrast component introduced by the sharp
355 stimulus transition across the discontinuity edge may contribute to the excitation of
356 heterogeneous groups of neurons preferring other orientations and spatial frequency in V1,
357 thereby adding to the E-I imbalance. In this context, the orientation and phase
358 discontinuities have been shown previously to cause an effect called brightness induction
359 or enhancement (Biederlack et al., 2006; Huang et al., 2002; Sillito and Jones, 1996),
360 under which the center appears perceptually brighter due to the orientation contrast or
361 phase contrast. A previous study (Biederlack et al., 2006) reported that the firing rates for
362 the units responding to the center grating increased only with orientation discontinuity but
363 not with phase discontinuity. We found that firing rates increased for both the stimulus
364 variations, as well as for the annular cut case, which has been shown to not cause any
365 brightness enhancement, although the change was not as pronounced as the change in
366 gamma power, especially for the smallest discontinuities we used. In general, however, it
367 has been shown that gamma and spiking activity may not necessarily show a definite
368 relationship across stimulus variations (Jia et al., 2013).

369

370 The radial contrast component and the perceptual contrast shift effects as discussed above
371 are studied more directly in the contrast discontinuity experiment. The nature of
372 modulatory inputs from the extra-classical surround region is heavily dependent on the

stimulus contrast (Angelucci et al., 2017; Ichida et al., 2007; Polat et al., 1998; Schwabe et al., 2010). The surround region can be suppressive at high contrast but can provide net excitation at a lower contrast. In general, it has been observed that the size of the excitatory RFs in V1 expand slightly at lower contrasts in comparison to the higher contrasts (Cavanaugh et al., 2002; Sceniak et al., 1999). These contrast dependent effects may play a role in modulating the E-I signals in different ways at different contrasts in our stimulus set, leading to slight differences in the effect of discontinuities at different contrasts (Figure 6). The effect of discontinuities is qualitatively similar even when they progressively remove areas of spatial contrast, as in annular discontinuities, modifying the overall stimulated cortical volume itself. While our results pertain to grating stimuli, gamma oscillations have been observed to be reduced by a mismatched surround or annulus for uniform surfaces as well (Peter et al., 2019). These findings suggest that any visual structural modification that changes the critical level and nature of E-I drive in the network can potentially affect gamma.

387

388 *Animal specific differences*

While all the major results shown here were consistent across monkeys, the magnitude of these effects were in general smaller in Monkey 2 as compared to Monkey 1. One of the factors in this could be that the RFs in Monkey 1 were at a larger visual eccentricity than in Monkey 2. RFs closer to the fovea are known to be smaller, as seen in Monkey 2 here, and the properties of RFs in terms of overall connectivity, gains and center-surround spread and interactions may depend on visual eccentricity. Another notable difference is the presence of a prominent slow gamma rhythm in Monkey 2. The effects of discontinuity on

396 this rhythm were qualitatively similar to fast gamma, although the drop was smaller. In
 397 particular, for annular discontinuities at varying inner radii, slow gamma reduced strongly
 398 even at farther cuts, which is expected if a spatially more widespread network is involved
 399 in its generation (Murty et al., 2018). Moreover, the effect of smallest contrast
 400 discontinuity was most drastic for slow gamma in the mid-contrast range, whereas for fast
 401 gamma it was in the high-contrast range (Figure 5). This effect incidentally follows the
 402 contrast tuning of these two gamma rhythms to large continuous gratings (Murty et al.,
 403 2018).

404

405 *Implications for natural image processing*

406 Selective gamma synchronization of neuronal ensembles responding to an optimized
 407 continuous stimulus may provide stronger or more potent signal for intra and inter-areal
 408 communication in the gamma range of frequencies (Buzsáki and Schomburg, 2015; Fries,
 409 2005). However, some other studies have shown gamma to be dependent more on the
 410 visual context or the spatial properties of the stimulus with respect to the RF and not
 411 necessarily on a unified percept (Dong et al., 2008; Lima et al., 2010; Palanca and
 412 DeAngelis, 2005; Thiele and Stoner, 2003). Given the high sensitivity of gamma to small
 413 stimulus discontinuities that we show, most natural stimuli might not be able to generate
 414 strong gamma oscillations in V1 LFP, as reported by many studies (Bartoli et al., 2019;
 415 Hermes et al., 2019, 2014; Kanth and Ray, 2020; Kayser et al., 2003). Gamma is also
 416 strongly generated by uniform color surfaces (Shirhatti and Ray, 2018), and therefore some
 417 colored natural stimuli may generate strong gamma when favorable uniform color patches
 418 fall on the RF (Bartoli et al., 2019; Brunet et al., 2013; Kanth and Ray, 2020). However,

mismatches in color surfaces in the form of a differently colored blob or annulus can also reduce gamma power (Peter et al., 2019), suggesting that the effect of discontinuities is qualitatively consistent across both achromatic and chromatic pathways, and that most natural stimuli with intricate structural complexities would not generate strong gamma oscillations.

Studies have shown that the responses in V1 for naturalistic stimuli can be explained by the degree of statistical dependence between the stimulus structures falling on the center and surround regions of the V1 RF (Coen-Cagli et al., 2012; Schwartz and Simoncelli, 2001; Simoncelli and Olshausen, 2001). Considering the high sensitivity of gamma to this visual structure, it will be interesting to determine how gamma depends on natural scene statistics. Recently it has been shown that information about images is high in the LFP gamma band (Kanth and Ray, 2020), and orientation variability in images can be used to predict gamma responses (Hermes et al., 2019). It may be argued that gamma in V1 signifies the stimuli more optimized to V1 response properties and as an extension of this, gamma in higher areas might code for larger surfaces or whole objects more relevant to the response properties of those neurons. However, gamma strength may decrease with increasing eccentricity and RF size leading to less prominent oscillations in higher areas (Vinck and Bosman, 2016).

Gamma mechanisms and neural models

Neuronal models with recurrent connections between excitatory and inhibitory populations have been used to model and study oscillations in cortical and sub-cortical networks (Jadi and Sejnowski, 2014; Jia et al., 2013; Kang et al., 2010; Kraynyukova and Tchumatchenko, 2018; Roxin and Compte, 2016; Tsodyks et al., 1997; Wilson and Cowan, 1972). Mechanisms of gamma may be understood better by studying how discontinuities affect the overall network dynamics in such models. Cortical neurons are known to have supralinear input-output response functions such that the net synaptic throughput effectively changes with input strength (Ahmadian et al., 2013; Priebe and Ferster, 2008; Rubin et al., 2015). As the network gets engaged more strongly, as in the case of large gratings, normalization signals dominate and inhibition stabilizes the network activity (Heeger, 1992; Miller, 2016; Ozeki et al., 2009). The tuned nature of these signals can modulate network interactions depending on stimulus properties (Angelucci et al., 2017; Ni et al., 2012; Shushruth et al., 2012). Therefore, discontinuities can modulate the overall network drive, which can effectively modify synaptic gains and the operating regime of the network. Incorporation of the detailed RF structure into the model may further unravel mechanistic properties of these oscillations.

In summary, gamma oscillations in V1 LFP exhibit resonance like behavior which could signify critical E-I balance in the neuronal network. Further investigations with finer variations of stimulus properties across this specialized RF structure may lead to better insights into the dynamics and mechanisms of such oscillations. Studying such oscillations in conjunction with spikes and their sensitivity to the spatiotemporal sensory context may help us understand general principles of cortical sensory processing.

463 MATERIALS AND METHODS

464 Animal preparation and training

465 All experiments were performed as per the guidelines approved by Institutional Animal
 466 Ethics Committee (IAEC) of the Indian Institute of Science and the Committee for the
 467 Purpose of Control and Supervision of Experiments on Animals (CPCSEA). For this study
 468 two adult female monkeys (*Macaca radiata*; 13 years, ~3.3 Kg; 17 years, ~4 Kg) were
 469 used. Animal preparation and training details are the same as described in earlier studies
 470 (Murty et al., 2018; Shirhatti and Ray, 2018). Each monkey was surgically implanted with
 471 a titanium headpost over the anterior/frontal region of the skull under general anesthesia.
 472 Following recovery, the monkey was trained on a passive visual fixation task, and once the
 473 monkey reached a satisfactorily level of training, another surgery was performed under
 474 general anesthesia to insert a microelectrode array (Utah array, 96 active platinum
 475 microelectrodes, 1 mm length, 400 μ m inter-electrode distance, Blackrock Microsystems)
 476 in the primary visual cortex (right hemisphere, centered at ~10-15 mm rostral from the
 477 occipital ridge and ~10-15 mm lateral from the midline; the location varied slightly across
 478 the two monkeys). The receptive fields of the recorded neurons were located at an
 479 eccentricity of between ~3° to ~4.5° in Monkey 1 and between ~1.4° to ~1.8° in Monkey
 480 2, in the lower left quadrant of the visual space with respect to fixation. Considering the
 481 dimensions of the microelectrodes, the recordings are most likely to be around cortical
 482 layer 2/3.

484 Experimental setup and behavior

485 Details of experimental setup, behavior and data recording are as described in previous
 486 studies (Murty et al., 2018; Shirhatti and Ray, 2018). Each monkey viewed a monitor
 487 (BenQ XL2411, LCD, 1280 x 720 resolution, 100 Hz refresh rate, gamma corrected and
 488 calibrated to a mean luminance of 60 cd/m² on the monitor surface using i1Display Pro, x-
 489 rite PANTONE) placed ~50 cm from its eyes, with its head fixed by the headpost in a
 490 custom designed monkey-chair. A Faraday enclosure (constructed using thin copper
 491 sheets, wood and sound isolating material), with a dedicated grounding separate from the
 492 mains supply ground, was used to house the monkey chair and the display and recording
 493 setup during experiments.

494 The monkeys performed a passive visual fixation task, in which they had to maintain
 495 visual fixation at a small dot (0.05° or 0.10° radius) at the center of the screen for the
 496 duration of a trial, which could be either 3.3 or 4.8 s. Each trial began when the monkey
 497 fixated, and following an initial blank grey screen of 1000 ms, 2 to 3 stimuli were shown
 498 for 800 ms each, with an inter-stimulus interval of 700 ms. The monkey was rewarded with
 499 juice for successfully holding its fixation without blinking, within 2° of the fixation spot,
 500 which stayed on throughout this period. Although the fixation window was kept slightly
 501 large, mainly to adjust for occasional small shifts in the head position due to slight
 502 movements of the chair and related apparatus, the monkeys actually maintained fixation
 503 within a much smaller window during the task. The standard deviation of eye position
 504 during a trial across sessions was small on an average for both monkeys (< 0.18° and <
 505 0.16° along the horizontal and vertical axes respectively for Monkey 1; < 0.28° and < 0.29°
 506 for Monkey 2).

507

508 **Data recording**

509 A 128-channel Cerebus Neural Signal Processor (Blackrock Microsystems) was used to
 510 record raw signals on 96 channels. To obtain the LFPs, these raw signals were filtered
 511 online between 0.3 Hz (Butterworth filter, 1st order, analog) and 500 Hz (Butterworth
 512 filter, 4th order, digital), sampled at 2 KHz and digitized at 16-bit resolution. To extract
 513 multiunit spikes, the raw signals were filtered online separately between 250 Hz
 514 (Butterworth filter, 4th order, digital) and 7.5 KHz (Butterworth filter, 3rd order, analog)
 515 and the filtered signal was subjected to a threshold (amplitude threshold of ~5 standard
 516 deviations of the signal). No further offline filtering of the LFP signals or offline spike
 517 sorting was done.

518 An ETL-200 Primate Eye Tracking System (ISCAN Incorporated) was used to record eye
 519 position data in terms of horizontal and vertical co-ordinates/position and pupil diameter,
 520 at a sampling rate of 200 Hz during the task. A custom software running on MAC OS
 521 monitored the eye signals, and controlled the progression of task and trials, stimulus
 522 generation and pseudorandom stimulus presentation.

523

524 **Electrode selection and data analysis**

525 For each monkey, a receptive field mapping experiment was run regularly across multiple
 526 sessions across days to verify the stability of RFs and assess the suitability of electrodes for
 527 data analyses. In this experiment, small sinusoidal gratings (radius of 0.3° and 0.2° for
 528 Monkey 1 and 2 respectively; static, full contrast, spatial frequency of 4 cycles per degree
 529 (cpd), at four orientations of 0°, 45°, 90° and 135° in both monkeys) were flashed for 200

ms at equally spaced (9 x 9) locations within a rectangular grid on the visual space that approximately covered the aggregate RF of the entire microelectrode array. A two-dimensional Gaussian fitted to the spatial profile of the maximum drop in the LFP (during 40-100ms after stimulus onset for both monkeys; baseline corrected) induced by stimuli presented at the various locations yielded the RF estimate for each electrode (Dubey and Ray, 2016). Electrodes with consistent stimulus induced changes in LFP and reliable estimates of RF size across sessions were chosen after subjecting their mean distribution across sessions to an arbitrary threshold based on inspection. Since we primarily analyzed and characterized LFP responses, an LFP based measure was used, although estimates based on spiking activity were similar (Dubey and Ray, 2019, 2016). Electrodes which showed noisy or inconsistent signals; or a high degree of crosstalk across sessions; or impedances outside the range 250 K Ω to 2500 K Ω , were discarded from analyses. This procedure yielded an overall 65 and 39 usable electrodes for Monkey 1 and 2 respectively, which were considered for all further analyses. Out of these, the electrodes that showed high impedance during certain sessions were not considered for analysis for that session. The resultant set of electrodes were considered while choosing the center sites/electrodes (explained ahead) during any session. The final number of electrodes used for analysis of data from different sessions are stated in the figures or in the related text descriptions.

For each session the sites whose RFs were sufficiently close to the stimulus center (within a range of 0.2° and 0.15° for monkeys 1 and 2 respectively; a smaller range was chosen for Monkey 2 since the RFs were less eccentric and smaller than in Monkey 1) were selected as the ‘center’ sites for analyses. For the annular cut discontinuity experiment with different cut locations, this range was 0.15° and 0.1° for monkeys 1 and 2 respectively,

corresponding to the nearest cut location. All analyses were done for such sites and the mean was taken across sites across sessions.

Every experiment was repeated over several sessions, each yielding data from a few sites whose RFs were close to the center of the stimulus. After rejection of electrical artifacts or noisy data (average rejection rate: 1.57 % in Monkey 1, 2.07 % in Monkey 2; procedure summarized in (Murty et al., 2018)), the number of sessions, number of center electrodes, and the mean number of repeats across sessions, for the two monkeys respectively, were as follows - Annular cut discontinuity experiment (Figure 1): 13 sessions, 60 electrodes (out of which 44 were unique, since some electrodes were repeated across sessions), 11.02 repeats for Monkey 1 and 8 sessions, 53 (32 unique) electrodes, 15.16 repeats for Monkey 2; Annular cut discontinuity experiment with different cut locations (Figure 2, Supplementary Figure 1): 13 sessions, 33 (25 unique) electrodes, 11.93 repeats for Monkey 1 and 7 sessions, 21 (17 unique) electrodes, 15.23 repeats for Monkey 2; Orientation discontinuity experiment (Figure 3): 11 sessions, 57 electrodes (43 unique) and 12.32 repeats for Monkey 1 and 9 sessions, 74 electrodes (32 unique) with 14.55 repeats for Monkey 2 ; Phase discontinuity experiment (Figure 4): 12 sessions, 62 (44 unique) electrodes, 12.42 repeats for Monkey 1 and 13 sessions, 124 (37 unique) electrodes, 16.09 repeats for Monkey 2; Contrast discontinuity experiment (Figure 5-6): 9 sessions, 48 (42 unique) electrodes, 11.95 repeats for Monkey 1 and 6 sessions, 48 (27 unique) electrodes, 14.72 repeats for Monkey 2. All these data analyses were performed using custom written codes in MATLAB, MathWorks.

Spectral Analyses

Spectral analyses were performed using the Multitaper method, implemented using functions in the 'Chronux toolbox'(Mitra and Bokil, 2008) (<http://chronux.org/>, developed for MATLAB). To obtain the time-frequency difference spectrum, the power spectrum was first calculated using a single taper with a sliding window of 0.25s yielding a 4 Hz frequency resolution. The logarithm of the mean power spectrum across repeats was computed for each electrode. Then the mean power at each frequency in the mean spectrum during the spontaneous period (0.5 to 0 s before stimulus onset) was calculated and subtracted from the entire spectrum, followed by multiplication by 10 to get the difference spectrum in decibel.

Power spectral density (PSD) were computed using a single taper between 0.25-0.75 seconds after stimulus onset and compared to the PSD during spontaneous period (0.5 to 0 seconds). The change in power was calculated by subtracting the logarithm of power during stimulus period and spontaneous activity and multiplying by 10 to yield units in decibels. In Figure 8, PSD was similarly calculated using a single taper for the signal between 1s to 2s.

Power in any frequency band is calculated as the sum of PSD at all frequencies in that band. Normalized gamma power was calculated for each electrode by first calculating the mean gamma power for each condition and then dividing these by their maximum value across conditions for that electrode. The change due to the smallest discontinuity was computed by subtraction of the normalized gamma power for the continuous stimulus from that for the smallest discontinuity stimulus. In the case of orientation and phase discontinuities an average of values for the smallest discontinuities on either side was considered.

Large gratings that substantially extend into the surround region of the RF can induce two distinct gamma rhythms (slow and fast), whose strength and peak frequency can vary with the grating orientation (Murty et al., 2018). Since the stimuli in this study were optimized to generate strong fast gamma rhythms, analyses and results are focused on this band. Therefore, across all figures and results ‘gamma’ refers to fast gamma unless stated otherwise. For all static grating stimuli at 100 % contrast (Figure 1 to Figure 4), fast gamma band was chosen as per inspection of PSD as: [35 65] Hz in Monkey 1, and [45 75] Hz in Monkey 2. The same bands were chosen in the contrast discontinuity experiment, for stimuli in which at least one of the inner or the outer grating was at 100 % contrast. For others, in which both inner and outer grating were at a contrast lower than 100 %, the bands were shifted lower by 5 Hz, since gamma rhythm is known to shift lower in frequency with decreasing contrast, and as also observed in the corresponding PSD.

Analyses of spiking units

The center units which showed clear spikes and had an average firing rate of at least 1 spike/second for at least one of the stimulus conditions were chosen for analyses of firing responses. The firing rates for each unit were normalized by dividing by the maximum firing rate for that unit across time and conditions to obtain the mean normalized firing rate for each condition. For comparison of normalized gamma power and normalized firing rate these same spiking units were considered. The mean normalized value of gamma power and firing rate for each condition were calculated by averaging these quantities across the chosen units.

620 **Model details**

621 The model consists of two interconnected neuronal populations representing a local
622 recurrent network in an orientation column of V1, with external inputs to the network
623 arising from stimulation and lateral or feedback signals. If E and I are considered as the
624 response variables representing the mean response of the two neuronal populations, then
625 the equations governing the dynamics of E and I are given by,

$$626 \quad \tau_x \frac{dX}{dt} = -X + f_x(I_x) \dots\dots\dots (1)$$

627 Where x can be E or I. τ_x is the corresponding time constant of the variable build up, and f_x
628 is the function transforming the total synaptic input, I_x , to the resultant spiking response.

629

$$630 \quad I_e = W_{ee}E - W_{ei}I + iLR_e + iE \dots\dots\dots (2)$$

$$631 \quad I_i = W_{ie}E - W_{ii}I + iLR_i + iI \dots\dots\dots (3)$$

632 f_x is considered to be a sigmoid function as described in (Jadi and Sejnowski, 2014).

$$633 \quad f_x(I_x) = (1/(1+\exp(-m_x*(I_x - \theta_x)))) - (1/(1+\exp(m_x*\theta_x))) \dots\dots\dots (4)$$

634

635 The external inputs arising from the center (inner) and surround (outer) stimuli are iE and
636 iI for E and I respectively. These equations are similar to the model used by Jadi and
637 Sejnowski (Jadi and Sejnowski, 2014), except there were no separate lateral inputs (iLR_e
638 and iLR_i) in their model. We added iLR_e and iLR_i as the effective intracortical inputs from
639 similar nearby local recurrent input networks through interconnections in the orientation
640 hypercolumn (Angelucci et al., 2017; Shushruth et al., 2012). W_{xy} implies the synaptic gain
641 from input y to the receptor x . Considering that all nearby local recurrent networks differ

only in their orientation tuning, iLR_x is effectively a weighted function of the E and I activity, for the sake of this simplified single column model design. Therefore equations 2 and 3 can be rewritten as follows.

$$I_e = W_{ee}E - W_{ei}I + W_{eELR}E - W_{eILR}I + iE \dots \dots \dots (5)$$

$$I_i = W_{ie}E - W_{ii}I + W_{iELR}E - W_{iILR}I + iI \dots \dots \dots (6)$$

W_{xELR} and W_{xILR} denote the gain function for the excitatory and inhibitory inputs respectively from the other local recurrent networks in the hypercolumn. Note that in a multi-column architecture these inputs (iLR_x) can be derived from the actual outputs of the nearby columns. Equations (5) and (6) can be written as follows.

$$I_e = (W_{ee} + W_{eELR})E - (W_{ei} + W_{eILR})I + iE \dots \dots \dots (7)$$

$$I_i = (W_{ie} + W_{iELR})E - (W_{ii} + W_{iILR})I + iI \dots \dots \dots (8)$$

In this model discontinuities can effectively decrease W_{xELR} and/or W_{xILR} , and thereby the overall network gains, pushing the network into a different regime of operation.

Equations (7) and (8) can be summarized as follows.

$$I_e = wee.E - wei.I + iE \dots \dots \dots (9)$$

$$I_i = wie.E - wii.I + iI \dots \dots \dots (10)$$

$$wee = (W_{ee} + W_{eELR}), wei = (W_{ei} + W_{eILR}), wie = (W_{ie} + W_{iELR}), wii = (W_{ii} + W_{iILR}) \dots \dots \dots (11)$$

665

666 The default values of parameters, adapted from (Jadi and Sejnowski, 2014), are as follows.

667 $w_{ee} = 16$, $w_{ei} = 26$, $w_{ie} = 20$, $w_{ii} = 1$, $m_E = 1$, $m_I = 1$, $\theta_E = 5$, $\theta_I = 20$, $\tau_E = 20$, $\tau_I = 10$.

668 These parametric values have been shown to generate gamma oscillations in the network

669 whose properties (peak power and frequency) agree with experimental observations under

670 certain regimes of the network operation, and the network behaves as an inhibition

671 stabilized network (ISN) (Jadi and Sejnowski, 2014; Ozeki et al., 2009). In Figure 8, only

672 W_{eELR} is considered to be reduced by a discontinuity such that $(W_{ee} + W_{eELR})$, i.e. w_{ee} ,

673 effectively decreases by 10% and 20%, and the network moves drastically to a regime with

674 weak oscillations under new weights. To determine the regime where increase in iI caused

675 an increase in the magnitude of oscillation and decrease in its peak frequency, we followed

676 the conditions derived in (Jadi and Sejnowski, 2014) (Appendix B, equation 6, 7, 12, 13

677 and 14) and the procedure described therein.

678

679 **References**

- 680 Ahmadian, Y., Rubin, D.B., Miller, K.D., 2013. Analysis of the Stabilized Supralinear Network.
681 Neural Comput. 25, 1994–2037. https://doi.org/10.1162/NECO_a_00472
682
- 683 Angelucci, A., Bijanzadeh, M., Nurminen, L., Federer, F., Merlin, S., Bressloff, P.C., 2017.
684 Circuits and Mechanisms for Surround Modulation in Visual Cortex. Annu. Rev. Neurosci.
685 40, 425–451. <https://doi.org/10.1146/annurev-neuro-072116-031418>
686
- 687 Angelucci, A., Levitt, J.B., Walton, E.J.S., Hupé, J.-M., Bullier, J., Lund, J.S., 2002. Circuits for
688 Local and Global Signal Integration in Primary Visual Cortex. J. Neurosci. 22, 8633–8646.
689 <https://doi.org/10.1523/JNEUROSCI.22-19-08633.2002>
690
- 691 Atallah, B.V., Scanziani, M., 2009. Instantaneous Modulation of Gamma Oscillation Frequency by
692 Balancing Excitation with Inhibition. Neuron 62, 566–577.
693 <https://doi.org/10.1016/j.neuron.2009.04.027>
694
- 695 Bartoli, E., Bosking, W., Chen, Y., Li, Y., Sheth, S.A., Beauchamp, M.S., Yoshor, D., Foster, B.L.,
696 2019. Functionally Distinct Gamma Range Activity Revealed by Stimulus Tuning in
697 Human Visual Cortex. Curr. Biol. 29, 3345–3358.e7.
698 <https://doi.org/10.1016/j.cub.2019.08.004>
699
- 700 Bartoli, E., Bosking, W., Foster, B.L., 2020. Seeing Visual Gamma Oscillations in a New Light.
701 Trends Cogn. Sci. 24, 501–503. <https://doi.org/10.1016/j.tics.2020.03.009>
702
- 703 Biederlack, J., Castelo-Branco, M., Neuenschwander, S., Wheeler, D.W., Singer, W., Nikolić, D.,
704 2006. Brightness Induction: Rate Enhancement and Neuronal Synchronization as
705 Complementary Codes. Neuron 52, 1073–1083.
706 <https://doi.org/10.1016/j.neuron.2006.11.012>
707
- 708 Blakemore, C., Tobin, E.A., 1972. Lateral inhibition between orientation detectors in the cat's
709 visual cortex. Exp. Brain Res. 15, 439–440. <https://doi.org/10.1007/BF00234129>
710
- 711 Brunel, N., Wang, X.-J., 2003. What Determines the Frequency of Fast Network Oscillations With
712 Irregular Neural Discharges? I. Synaptic Dynamics and Excitation-Inhibition Balance. J.
713 Neurophysiol. 90, 415–430. <https://doi.org/10.1152/jn.01095.2002>
714
- 715 Brunet, N., Bosman, C.A., Roberts, M., Oostenveld, R., Womelsdorf, T., Weerd, P.D., Fries, P.,
716 2013. Visual Cortical Gamma-Band Activity During Free Viewing of Natural Images.
717 Cereb. Cortex bht280. <https://doi.org/10.1093/cercor/bht280>
718
- 719 Buzsáki, G., Schomburg, E.W., 2015. What does gamma coherence tell us about inter-regional
720 neural communication? Nat. Neurosci. 18, 484–489. <https://doi.org/10.1038/nn.3952>

721

722 Buzsáki, G., Wang, X.-J., 2012. Mechanisms of Gamma Oscillations. *Annu. Rev. Neurosci.* 35,
723 203–225. <https://doi.org/10.1146/annurev-neuro-062111-150444>
724

725 Castelo-Branco, M., Neuenschwander, S., Singer, W., 1998. Synchronization of Visual Responses
726 between the Cortex, Lateral Geniculate Nucleus, and Retina in the Anesthetized Cat. *J.*
727 *Neurosci.* 18, 6395–6410.
728

729 Cavanaugh, J.R., Bair, W., Movshon, J.A., 2002. Nature and Interaction of Signals From the
730 Receptive Field Center and Surround in Macaque V1 Neurons. *J. Neurophysiol.* 88, 2530–
731 2546. <https://doi.org/10.1152/jn.00692.2001>
732

733 Coen-Cagli, R., Dayan, P., Schwartz, O., 2012. Cortical Surround Interactions and Perceptual
734 Salience via Natural Scene Statistics. *PLOS Comput. Biol.* 8, e1002405.
735 <https://doi.org/10.1371/journal.pcbi.1002405>
736

737 Dong, Y., Mihalas, S., Qiu, F., Heydt, R. von der, Niebur, E., 2008. Synchrony and the binding
738 problem in macaque visual cortex. *J. Vis.* 8. <https://doi.org/10.1167/8.7.30>
739

740 Dubey, A., Ray, S., 2019. Cortical Electrocorticogram (ECoG) Is a Local Signal. *J. Neurosci.* 39,
741 4299–4311. <https://doi.org/10.1523/JNEUROSCI.2917-18.2019>
742

743 Dubey, A., Ray, S., 2016. Spatial spread of local field potential is band-pass in the primary visual
744 cortex. *J. Neurophysiol.* 116, 1986–1999. <https://doi.org/10.1152/jn.00443.2016>
745

746 Engel, A.K., König, P., Kreiter, A.K., Singer, W., 1991. Interhemispheric synchronization of
747 oscillatory neuronal responses in cat visual cortex. *Science* 252, 1177–1179.
748

749 Fries, P., 2005. A mechanism for cognitive dynamics: neuronal communication through neuronal
750 coherence. *Trends Cogn. Sci.* 9, 474–480. <https://doi.org/10.1016/j.tics.2005.08.011>
751

752 Gieselmann, M.A., Thiele, A., 2008. Comparison of spatial integration and surround suppression
753 characteristics in spiking activity and the local field potential in macaque V1. *Eur. J.*
754 *Neurosci.* 28, 447–459. <https://doi.org/10.1111/j.1460-9568.2008.06358.x>
755

756 Gray, C., König, P., Engel, A., Singer, W., 1989. Oscillatory responses in cat visual cortex exhibit
757 inter-columnar synchronization which reflects global stimulus properties. *Nature* 338, 334–
758 337. <https://doi.org/10.1038/338334a0>
759

760 Gray, C.M., Prisco, G.V.D., 1997. Stimulus-Dependent Neuronal Oscillations and Local
761 Synchronization in Striate Cortex of the Alert Cat. *J. Neurosci.* 17, 3239–3253.
762

763 Heeger, D.J., 1992. Normalization of cell responses in cat striate cortex. *Vis. Neurosci.* 9, 181–197.
764

765 Henrie, J.A., Shapley, R., 2005. LFP Power Spectra in V1 Cortex: The Graded Effect of Stimulus
766 Contrast. *J. Neurophysiol.* 94, 479–490. <https://doi.org/10.1152/jn.00919.2004>
767

768 Hermes, D., Miller, K.J., Wandell, B.A., Winawer, J., 2014. Stimulus Dependence of Gamma
769 Oscillations in Human Visual Cortex. *Cereb. Cortex* bhu091.
770 <https://doi.org/10.1093/cercor/bhu091>
771

772 Hermes, D., Petridou, N., Kay, K.N., Winawer, J., 2019. An image-computable model for the
773 stimulus selectivity of gamma oscillations. *eLife* 8, e47035.
774 <https://doi.org/10.7554/eLife.47035>
775

776 Huang, X., MacEvoy, S.P., Paradiso, M.A., 2002. Perception of Brightness and Brightness
777 Illusions in the Macaque Monkey. *J. Neurosci.* 22, 9618–9625.
778

779 Ichida, J.M., Schwabe, L., Bressloff, P.C., Angelucci, A., 2007. Response Facilitation From the
780 “Suppressive” Receptive Field Surround of Macaque V1 Neurons. *J. Neurophysiol.* 98,
781 2168–2181. <https://doi.org/10.1152/jn.00298.2007>
782

783 Jadi, M.P., Sejnowski, T.J., 2014. Regulating Cortical Oscillations in an Inhibition-Stabilized
784 Network. *Proc. IEEE* 102, 830–842. <https://doi.org/10.1109/JPROC.2014.2313113>
785

786 Jia, X., Smith, M.A., Kohn, A., 2011. Stimulus Selectivity and Spatial Coherence of Gamma
787 Components of the Local Field Potential. *J. Neurosci.* 31, 9390–9403.
788 <https://doi.org/10.1523/JNEUROSCI.0645-11.2011>
789

790 Jia, X., Xing, D., Kohn, A., 2013. No Consistent Relationship between Gamma Power and Peak
791 Frequency in Macaque Primary Visual Cortex. *J. Neurosci.* 33, 17–25.
792 <https://doi.org/10.1523/JNEUROSCI.1687-12.2013>
793

794 Kang, K., Shelley, M., Henrie, J.A., Shapley, R., 2010. LFP spectral peaks in V1 cortex: network
795 resonance and cortico-cortical feedback. *J. Comput. Neurosci.* 29, 495–507.
796 <https://doi.org/10.1007/s10827-009-0190-2>
797

798 Kanth, S.T., Ray, S., 2020. Electrocorticogram (ECoG) Is Highly Informative in Primate Visual
799 Cortex. *J. Neurosci.* 40, 2430–2444. <https://doi.org/10.1523/JNEUROSCI.1368-19.2020>
800

801 Kayser, C., Salazar, R.F., König, P., 2003. Responses to Natural Scenes in Cat V1. *J.*
802 *Neurophysiol.* 90, 1910–1920. <https://doi.org/10.1152/jn.00195.2003>
803

- 804 Knierim, J.J., van Essen, D.C., 1992. Neuronal responses to static texture patterns in area V1 of the
805 alert macaque monkey. *J. Neurophysiol.* 67, 961–980.
806
- 807 Kraynyukova, N., Tchumatchenko, T., 2018. Stabilized supralinear network can give rise to
808 bistable, oscillatory, and persistent activity. *Proc. Natl. Acad. Sci.* 115, 3464–3469.
809 <https://doi.org/10.1073/pnas.1700080115>
810
- 811 Lima, B., Singer, W., Chen, N.-H., Neuenschwander, S., 2010. Synchronization Dynamics in
812 Response to Plaid Stimuli in Monkey V1. *Cereb. Cortex N. Y. NY* 20, 1556–1573.
813 <https://doi.org/10.1093/cercor/bhp218>
814
- 815 Miller, K.D., 2016. Canonical computations of cerebral cortex. *Curr. Opin. Neurobiol.*,
816 *Neurobiology of cognitive behavior* 37, 75–84. <https://doi.org/10.1016/j.conb.2016.01.008>
817
- 818 Mitra, P., Bokil, H., 2008. Observed brain dynamics. Oxford University Press, Oxford; New
819 York.
820
- 821 Moca, V.V., Nikolić, D., Singer, W., Mureşan, R.C., 2014. Membrane Resonance Enables Stable
822 and Robust Gamma Oscillations. *Cereb. Cortex* 24, 119–142.
823 <https://doi.org/10.1093/cercor/bhs293>
824
- 825 Murty, D.V.P.S., Shirhatti, V., Ravishankar, P., Ray, S., 2018. Large visual stimuli induce two
826 distinct gamma oscillations in primate visual cortex. *J. Neurosci.* 2270–17.
827 <https://doi.org/10.1523/JNEUROSCI.2270-17.2017>
828
- 829 Nassi, J.J., Lomber, S.G., Born, R.T., 2013. Corticocortical Feedback Contributes to Surround
830 Suppression in V1 of the Alert Primate. *J. Neurosci.* 33, 8504–8517.
831 <https://doi.org/10.1523/JNEUROSCI.5124-12.2013>
832
- 833 Ni, A.M., Ray, S., Maunsell, J.H.R., 2012. Tuned Normalization Explains the Size of Attention
834 Modulations. *Neuron* 73, 803–813. <https://doi.org/10.1016/j.neuron.2012.01.006>
835
- 836 Nurminen, L., Merlin, S., Bijanzadeh, M., Federer, F., Angelucci, A., 2018. Top-down feedback
837 controls spatial summation and response amplitude in primate visual cortex. *Nat. Commun.*
838 9, 1–13. <https://doi.org/10.1038/s41467-018-04500-5>
839
- 840 Ozeki, H., Finn, I.M., Schaffer, E.S., Miller, K.D., Ferster, D., 2009. Inhibitory Stabilization of the
841 Cortical Network Underlies Visual Surround Suppression. *Neuron* 62, 578–592.
842 <https://doi.org/10.1016/j.neuron.2009.03.028>
843
- 844 Ozeki, H., Sadakane, O., Akasaki, T., Naito, T., Shimegi, S., Sato, H., 2004. Relationship between
845 Excitation and Inhibition Underlying Size Tuning and Contextual Response Modulation in

846 the Cat Primary Visual Cortex. *J. Neurosci.* 24, 1428–1438.
847 <https://doi.org/10.1523/JNEUROSCI.3852-03.2004>
848

849 Palanca, B.J.A., DeAngelis, G.C., 2005. Does Neuronal Synchrony Underlie Visual Feature
850 Grouping? *Neuron* 46, 333–346. <https://doi.org/10.1016/j.neuron.2005.03.002>
851

852 Peter, A., Uran, C., Klon-Lipok, J., Roese, R., van Stijn, S., Barnes, W., Dowdall, J.R., Singer, W.,
853 Fries, P., Vinck, M., 2019. Surface color and predictability determine contextual
854 modulation of V1 firing and gamma oscillations. *eLife* 8, e42101.
855 <https://doi.org/10.7554/eLife.42101>
856

857 Polat, U., Mizobe, K., Pettet, M.W., Kasamatsu, T., Norcia, A.M., 1998. Collinear stimuli regulate
858 visual responses depending on cell's contrast threshold. *Nature* 391, 580–584.
859 <https://doi.org/10.1038/35372>
860

861 Priebe, N.J., Ferster, D., 2008. Inhibition, Spike Threshold, and Stimulus Selectivity in Primary
862 Visual Cortex. *Neuron* 57, 482–497. <https://doi.org/10.1016/j.neuron.2008.02.005>
863

864 Ray, S., Maunsell, J.H.R., 2011. Different Origins of Gamma Rhythm and High-Gamma Activity
865 in Macaque Visual Cortex. *PLOS Biol* 9, e1000610.
866 <https://doi.org/10.1371/journal.pbio.1000610>
867

868 Ray, S., Maunsell, J.H.R., 2010. Differences in gamma frequencies across visual cortex restrict
869 their possible use in computation. *Neuron* 67, 885–896.
870 <https://doi.org/10.1016/j.neuron.2010.08.004>
871

872 Roxin, A., Compte, A., 2016. Oscillations in the bistable regime of neuronal networks. *Phys. Rev.*
873 *E* 94, 012410. <https://doi.org/10.1103/PhysRevE.94.012410>
874

875 Rubin, D.B., Van Hooser, S.D., Miller, K.D., 2015. The Stabilized Supralinear Network: A
876 Unifying Circuit Motif Underlying Multi-Input Integration in Sensory Cortex. *Neuron* 85,
877 402–417. <https://doi.org/10.1016/j.neuron.2014.12.026>
878

879 Sceniak, M.P., Ringach, D.L., Hawken, M.J., Shapley, R., 1999. Contrast's effect on spatial
880 summation by macaque V1 neurons. *Nat. Neurosci.* 2, 733–739.
881 <https://doi.org/10.1038/11197>
882

883 Schwabe, L., Ichida, J.M., Shushruth, S., Mangapathy, P., Angelucci, A., 2010. Contrast-
884 dependence of surround suppression in Macaque V1: Experimental testing of a recurrent
885 network model. *NeuroImage* 52, 777–792.
886 <https://doi.org/10.1016/j.neuroimage.2010.01.032>
887

- 888 Schwartz, O., Simoncelli, E.P., 2001. Natural signal statistics and sensory gain control. *Nat.*
889 *Neurosci.* 4, 819–825. <https://doi.org/10.1038/90526>
890
- 891 Shirhatti, V., Ray, S., 2018. Long-wavelength (reddish) hues induce unusually large gamma
892 oscillations in the primate primary visual cortex. *Proc. Natl. Acad. Sci.* 115, 4489–4494.
893 <https://doi.org/10.1073/pnas.1717334115>
894
- 895 Shushruth, S., Mangapathy, P., Ichida, J.M., Bressloff, P.C., Schwabe, L., Angelucci, A., 2012.
896 Strong Recurrent Networks Compute the Orientation Tuning of Surround Modulation in
897 the Primate Primary Visual Cortex. *J. Neurosci.* 32, 308–321.
898 <https://doi.org/10.1523/JNEUROSCI.3789-11.2012>
899
- 900 Sillito, A., Jones, H., 1996. Context-dependent interactions and visual processing in V1. *J.*
901 *Physiol.-Paris* 90, 205–209. [https://doi.org/10.1016/S0928-4257\(97\)81424-6](https://doi.org/10.1016/S0928-4257(97)81424-6)
902
- 903 Sillito, A.M., Grieve, K.L., Jones, H.E., Cudeiro, J., Davls, J., 1995. Visual cortical mechanisms
904 detecting focal orientation discontinuities. *Nature* 378, 492–496.
905 <https://doi.org/10.1038/378492a0>
906
- 907 Simoncelli, E.P., Olshausen, B.A., 2001. Natural Image Statistics and Neural Representation.
908 *Annu. Rev. Neurosci.* 24, 1193–1216. <https://doi.org/10.1146/annurev.neuro.24.1.1193>
909
- 910 Thiele, A., Stoner, G., 2003. Neuronal synchrony does not correlate with motion coherence in
911 cortical area MT. *Nat. Lond.* 421, 366–70.
912
- 913 Tsodyks, M.V., Skaggs, W.E., Sejnowski, T.J., McNaughton, B.L., 1997. Paradoxical Effects of
914 External Modulation of Inhibitory Interneurons. *J. Neurosci.* 17, 4382–4388.
915
- 916 Veit, J., Hakim, R., Jadi, M.P., Sejnowski, T.J., Adesnik, H., 2017. Cortical gamma band
917 synchronization through somatostatin interneurons. *Nat. Neurosci.* advance online
918 publication. <https://doi.org/10.1038/nn.4562>
919
- 920 Vinck, M., Bosman, C.A., 2016. More Gamma More Predictions: Gamma-Synchronization as a
921 Key Mechanism for Efficient Integration of Classical Receptive Field Inputs with Surround
922 Predictions. *Front. Syst. Neurosci.* 10. <https://doi.org/10.3389/fnsys.2016.00035>
923
- 924 Wilson, H.R., Cowan, J.D., 1972. Excitatory and Inhibitory Interactions in Localized Populations
925 of Model Neurons. *Biophys. J.* 12, 1–24.
926
- 927 Zhou, Z., Bernard, M.R., Bonds, A.B., 2008. Deconstruction of Spatial Integrity in Visual Stimulus
928 Detected by Modulation of Synchronized Activity in Cat Visual Cortex. *J. Neurosci.* 28,
929 3759–3768. <https://doi.org/10.1523/JNEUROSCI.4481-07.2008>
930
931

932 **Acknowledgements**

933 This work was supported by Wellcome Trust/DBT India Alliance (IA/S/18/2/504003 –
934 Senior Fellowship to S.R and 500145/Z/09/Z – Intermediate fellowship to SR) and DBT-
935 IISc Partnership Programme.

936

937 **Competing financial interests**

938 The authors declare no competing financial interests.

939

FIGURE LEGENDS

Figure 1: Gamma oscillations are reduced by annular discontinuity

A) Top row: grating stimuli with annular cut discontinuity along with the receptive field (magenta) of an example center site in Monkey 1 from an example session. Corresponding cut width is mentioned and color coded for other plots. Trial-averaged TF difference spectra for the example center site in Monkey 1 (2nd row), and for the population (averaged across center electrodes and sessions) in Monkey 1 and 2 (following rows; number of sites, N = 60 and 53 respectively). Gratings were presented between 0 to 0.8 seconds. B) The corresponding mean change in power from baseline ([-0.5 0] s) to stimulus period ([0.25 0.75] s), averaged across these electrodes and sessions. Black lines in A) and B) indicate the gamma ranges (35-65 Hz and 45-75 Hz for the two monkeys). These ranges are chosen to avoid the slow gamma, which is prominent in Monkey 2. C) Mean normalized firing rate (averaged across selected spiking center electrodes and sessions) for different conditions. The firing rate for each electrode is normalized by the maximum for that electrode across time and conditions. D) Normalized gamma power and firing rate during the stimulus period (black lines in (C)); normalized for each selected spiking center electrode in (C) by the maximum across conditions, averaged across these center electrodes across sessions) for different annular discontinuity values. The error bars denote the standard error of mean (s.e.m.); and the asterisks in D) indicate statistical significance (** for $p < 0.01$, * for $p < 0.05$, WSR test) of change in normalized gamma (red) or firing rate (black) between the flanking values of annulus widths. E) Magnitude of slope of regression with annulus width (Δ value/degree of visual angle) of normalized gamma power versus

963 corresponding slopes for normalized firing rate. Each data point represents a selected
964 center electrode. Black data points indicate the mean value across these electrodes.

965

966 **Figure 2: Effect of annular discontinuity at different locations**

967 A) Normalized gamma power and B) Normalized firing rate, for stimuli with annular
968 discontinuity at different inner radii from the center of the stimulus, and as a function of
969 the width of annular discontinuity, averaged across center electrodes, for Monkey 1 (top)
970 and 2 (bottom). C) Magnitude of slope of regression of the values in A and B on annulus
971 width for different inner radii, averaged across the center electrodes. The color-coded lines
972 at the bottom indicate statistical significance ($p < 0.01$, WSR test) of change in
973 corresponding value between the flanking values of annulus widths. The asterisks at the
974 top indicate statistical significance ($p < 0.01$, WSR test) of these values being greater for
975 normalized gamma than for normalized firing rates.

976

977 **Figure 3: Gamma oscillations are reduced by orientation discontinuity**

978 Same format as in Figure 1. For Monkey 2 there are two additional steps of discontinuity
979 on either side (-50° to 50° in steps of 10°).

980

981 **Figure 4: Gamma oscillations are reduced by phase discontinuity**

982 Same format as in Figure 1 and 3. In (D) the values for 0° are repeated on the right side
 983 due to the circular scale of phases and for easy comparison with values for 300° , which is
 984 one of the two smallest discontinuities in this stimulus set.

985

986 **Figure 5: Gamma oscillations are reduced by contrast discontinuity**

987 A) Trial-averaged TF difference spectra for the population, induced by stimuli with
 988 contrast discontinuity (inner and outer contrasts are indicated on the left and top
 989 respectively) and B) the corresponding mean change in power from baseline to stimulus
 990 period. C) Mean normalized firing rate averaged across selected spiking center electrodes
 991 and sessions. Same format as Figure 3A-C. In B-C, every column shows graphs for
 992 varying outer contrast (increasing with brightness of grey), at a fixed inner contrast
 993 (mentioned in (B), and the colored red line represents the stimulus with the corresponding
 994 matched inner-outer contrast).

995

996 **Figure 6: Effect of contrast discontinuity on gamma and firing responses**

997 A) Normalized gamma power and B) Normalized firing rate during the stimulus period for
 998 different outer and inner contrast conditions, for the same electrodes as in Figure 5C, for
 999 Monkey 1 (top) and 2 (bottom). The corresponding effect of change in contrast from a
 1000 continuous stimulus is shown below each. The bar graphs denote the change for a step
 1001 change (decrease or increase) in contrast occurring in either the inner or the outer grating,
 1002 from a continuous stimulus whose contrast is indicated on the x-axis. Asterisks indicate its
 1003 statistical significance (** for $p < 0.01$, * for $p < 0.05$, WSR test). C) Magnitude of change in

normalized gamma power versus normalized firing rates for the four smallest discontinuities from 50% contrast and 75% contrast continuous grating in Monkey 1 and 2 respectively. Larger and bordered data points show the mean across sites.

Figure 7: A resonant model of gamma oscillations

A schematic of the model with an excitatory population (E) and an inhibitory population (I). iE and iI are the external inputs, and $iLRe$ and $iLRi$ are inputs from other nearby local recurrent networks. Wee , Wei , Wie and Wii are the gains of the corresponding connections between the populations.

Figure 8: Effect of stimulus discontinuity in the model

A) Left to right: E and I response, peak power in the gamma range and the corresponding peak frequency, for different values of iE and iI for the default model weights. B) and C) are the corresponding results for modified networks with only wee reduced by 10% and 20% respectively, as excitatory LR inputs to E decrease due to discontinuity (weights indicated in D)). White lines indicate the sublinear E and superlinear I response regime where increase in iI causes gamma amplitude to increase and frequency to decrease (this regime is absent in case 3). Oscillations weaken drastically in the network from case 1 to 2 and 3, even when the mean E and I responses do not change as much. D) E response in the above 3 cases for $iE = 3$, $iI = 7.5$ (marked by the gray circle). E) Phase-plane analysis showing the effect of varying wee on the E and I nullclines. Only the E nullcline shifts in these three cases, while I nullcline (light blue) remains the same.

1026

1027 **Supplementary Figure 1: Effect of annular discontinuity at different locations**

1028 A) Trial-averaged time-frequency difference spectra for the population in Monkey 1 (left
 1029 column) and Monkey 2 (right column), induced by stimuli with annular discontinuity at
 1030 different inner radii (inner radius and annulus width are indicated on the left and top
 1031 respectively) and B) The corresponding mean change in power from baseline to stimulus
 1032 period. C) Mean normalized firing rate averaged across selected spiking center electrodes
 1033 and sessions.