l	Surface color and predictability determine contextual modulation of V1 firing
2	and gamma oscillations

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9 Abstract

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10 The integration of direct bottom-up inputs with contextual information is a core feature of neocortical circuits. In area V1, neurons may reduce their firing rates when their receptive field input can be predicted by spatial context. 11 Gamma-synchronized (30-80Hz) firing may provide a complementary signal to rates, reflecting stronger synchroniza-12 tion between neuronal populations receiving mutually predictable inputs. We show that large uniform surfaces, which 13 have high spatial predictability, strongly suppressed firing yet induced prominent gamma synchronization in macaque 14 15 V1, particularly when they were colored. Yet, chromatic mismatches between center and surround, breaking predictability, strongly reduced gamma synchronization while increasing firing rates. Differences between responses to 16 different colors, including strong gamma-responses to red, arose from stimulus adaptation to a full-screen background, 17 suggesting prominent differences in adaptation between M- and L-cone signaling pathways. Thus, synchrony signaled 18 whether RF inputs were predicted from spatial context, while firing rates increased when stimuli were unpredicted 19 20 from context.

21 Keywords: Efficient coding; Predictive Coding; Contextual Modulation; Surround suppression; Gamma oscillations;

22 Synchronization; Color vision

23 Introduction

Visual processing relies on an integration of information over space, and an understanding of spatial relationships. 24 This integration takes place in part in a feedforward manner through convergence of neurons with small receptive 25 fields (RFs) onto neurons with larger RFs in higher areas (DiCarlo et al., 2012; Felleman and C Van Essen, 1991; 26 27 Lamme and Roelfsema, 2000; Serre et al., 2005). However, already in early visual cortex, neuronal responses to sensory inputs into the RFs are strongly modulated by the spatio-temporal context in which they are embedded. For 28 instance, the firing rates of V1 neurons to stimuli in their classical RF (CRF), i.e. the region in space where stimuli 29 have a strong driving effect, can be increased or decreased by stimuli presented in their surround (Angelucci et al., 30 2017; Gilbert, 1992; Rao and Ballard, 1999; Vinje and Gallant, 2000) In terms of anatomy, surround modulation 31 represents a departure from feedforward processing. It is mediated by recurrent lateral and feedback connections, 32 through which a given V1 neuron can be informed about a larger region of space than covered by its CRF (Angelucci 33 et al., 2017; Gilbert, 1992; Lund et al., 2003). One view on surround modulation is that it merely represents a form of 34 normalization, such that neuronal firing rates are essentially scaled by the amount of drive in the surround (Carandini 35 and Heeger, 2011). Additionally, it has been suggested that surround modulation may play an important role in various 36 related functions like contour integration (Liang et al., 2017), perceptual filling-in (Land, 1959; Wachtler et al., 2003; 37 38 Zweig et al., 2015), figure-ground separation (Lamme, 1995), computation of a saliency map (Coen-Cagli et al., 2012; 39 Li, 2002), as well as efficient and predictive coding operations (Rao and Ballard, 1999; Vinje and Gallant, 2000).

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Theories of efficient coding postulate that surround suppression of neuronal firing contributes to remove image 40 redundancies across space from neuronal representations (Barlow, 2001; Coen-Cagli et al., 2012, 2015; Rao and 41 Ballard, 1999; Schwartz and Simoncelli, 2001; Simoncelli and Olshausen, 2001; Vinje and Gallant, 2000; Zhu and 42 Rozell, 2013). Predictive coding theories hold that neuronal responses result from a comparison between predictions 43 from the surround and the inputs into the CRF (Friston, 2005; Rao and Ballard, 1999; Spratling, 2010). Most studies 44 on surround modulation have focused on the modulation of neuronal firing rates. However, if the modulation of 45 46 neuronal firing rates arises from specific relationships between stimuli across space, then it might also have important consequences for temporal correlations among neuronal responses (Singer and Gray, 1995). 47

Recent work has extended the frameworks of efficient and predictive coding beyond firing rate modulations to in-48 clude neuronal synchronization (Bastos et al., 2012; Chalk et al., 2016; Jadi and Sejnowski, 2014; Vinck and Bosman, 49 2016). Neuronal synchronization plays a functional role for the encoding and transmission of information, as well 50 as for synaptic plasticity, and may therefore play an important role in contextual integration processes (Abeles, 1982; 51 Akam and Kullmann, 2010, 2014; Azouz and Gray, 2000; Ballard and Jehee, 2011; Ballard and Zhang, 2018; Bernan-52 der et al., 1994; Börgers and Kopell, 2008; Bressler et al., 1993; Buzsáki, 2006; Buzsáki and Wang, 2012; Cardin 53 et al., 2009; Fries, 2005, 2009; Fries et al., 2007; Havenith et al., 2011; Kempter et al., 1998; Kopell et al., 2000; 54 O'Keefe and Recce, 1993; Palmigiano et al., 2017; Salinas and Sejnowski, 2000, 2001; Sejnowski and Paulsen, 2006; 55 Singer, 1999; Singer and Gray, 1995; Sohal et al., 2009; Varela et al., 2001; Vinck et al., 2010a; Wang, 2010). A 56 distinguishing feature of V1 activity, induced by many stimulus conditions, is synchronization of neuronal activity 57 in the gamma-frequency band (≈30-80 Hz) (Fries, 2009; Gieselmann and Thiele, 2008; Gray et al., 1989; Jia et al., 58 2013b; Ray and Maunsell, 2010; Vinck and Bosman, 2016). A link between contextual modulation processes and V1 59 gamma-band synchronization is suggested by the finding that the amplitude of V1 gamma oscillations increases with 60 stimulus size and therefore surround stimulation (Chalk et al., 2010; Gieselmann and Thiele, 2008; Gray et al., 1990; 61 Jia et al., 2011, 2013b; Perry et al., 2013; Ray and Maunsell, 2011) (for a detailed discussion, see Vinck and Bosman 62 (2016)). There are different views on the way in which gamma oscillations might relate to predictive and efficient 63 coding operations and therefore center-surround relationships (Arnal and Giraud, 2012; Bastos et al., 2012; Chalk 64 et al., 2016; Jadi and Sejnowski, 2014; Korndörfer et al., 2017; Vinck and Bosman, 2016). Bastos et al. (2012) and 65 Arnal and Giraud (2012) hypothesized that gamma-band synchronization subserves the encoding and transmission 66 67 of prediction error signals in the feedforward direction, and that lower frequency bands carry feedback predictions from higher areas (Arnal and Giraud, 2012; Bastos et al., 2012, 2015). Consistent with this hypothesis, bottom-up 68 and top-down Granger-causal influences are strongest in the gamma and alpha/beta (≈10-20 Hz) band, respectively 69 (Bastos et al., 2015; Bosman et al., 2012; Bressler et al., 2006; Michalareas et al., 2016; Richter et al., 2018; van 70 Kerkoerle et al., 2014). According to this hypothesis, a mismatch between center and surround stimuli should lead 71 to an increase in both firing rates and gamma-band synchronization, conveying prediction error signals. In contrast, 72 Vinck and Bosman (2016) recently hypothesized that (1) the amplitude of gamma oscillations in a given column 73 reflects the extent to which classical RF inputs are predictable from the surround, and (2) that gamma-band synchro-74 nization among columns with non-overlapping RFs reflects predictability among their visual inputs. This could in 75 turn provide a mechanism for orchestrating interactions between distributed neuronal columns, and for integrating 76 77 efficiently-encoded signals in higher visual areas (Vinck and Bosman, 2016) (see Discussion). According to this hy-78 pothesis, redundancy between center and surround stimuli should lead to a decrease in firing rates (reflecting efficient coding) yet an increase in gamma-band synchronization. To distinguish between these conflicting views, precise 79 manipulations of center-surround predictability are required. 80

As a starting point to test the interdependence between center-surround relationships, synchronization and firing 81 rates, we considered the case of uniform surfaces and varied their size, center-surround relationships and color. The 82 latter is an important feature for object recognition and visual search, and plays a role in social interactions and 83 foraging (Bichot et al., 2005; Corso et al., 2016; D'Zmura, 1991; Gerald et al., 2007; Santos et al., 2001; Waitt et al., 84 2006). Despite the importance of the color domain in vision, colored stimuli have rarely been studied with respect 85 to gamma synchronization (Brunet et al., 2015; Rols et al., 2001; Shirhatti and Ray, 2018). Furthermore, uniform 86 surfaces are of particular interest because they contain highly redundant information across a relatively large image 87 88 region. The predictability hypothesis (Vinck and Bosman, 2016) suggests that large, uniform surfaces should reliably 89 induce gamma-band synchronization but be accompanied by low neuronal discharge rates. It further suggests that a modulation of center-surround predictability due to a chromatic mismatch (e.g. red center and green surround 90 stimulus) should strongly reduce gamma-band synchronization but increase firing rates. 91

Uniform surfaces are characterized by hue, luminance and saturation, and can be broadly divided into chromatic 92 and achromatic (black and white) surfaces. Although uniform chromatic and achromatic surfaces both have a high 93 degree of predictability at the (physical) image level, there are likely substantial differences in the way these surfaces 94 are processed by area V1. Correspondingly, their predictability on the neuronal level likely differs. There are two 95 different ways through which V1 surface representations may arise (Zweig et al., 2015). First, neurons with RFs at 96 the uniform region of a surface stimulus (e.g. the center) may be directly activated. These may generate redundant 97 98 (predictable) signals locally. Specifically for chromatic surfaces, single-opponent, hue-selective neurons (in LGN or 99 V1) with RFs at the uniform surface region may directly encode color and luminance information. These are neurons with L+/M-, M+/L-, or blue (S) and yellow (L and M) color opponencies (Livingstone et al., 1984; Shapley and 100 Hawken, 2011). Second, surface information may be encoded by neurons with RFs at the edge of the surface, and 101 then propagate towards neurons with RFs at the uniform region of the surface (Land, 1959; Wachtler et al., 2003; 102 Zweig et al., 2015). The relative contributions of these two mechanisms (local vs. edge-derived) remain largely 103 unknown and likely differ between chromatic and achromatic surfaces (Zurawel et al., 2014; Zweig et al., 2015). 104 Zweig et al. (2015) have addressed this question by making voltage-sensitive dye recordings of V1 populations and 105 comparing the responses at the surface's center to the edge (Zweig et al., 2015). Activity patterns for achromatic 106 surfaces were consistent with an edge-derived "fill-in" process (Zweig et al., 2015). However, this was not observed 107 for chromatic surfaces (Zweig et al., 2015), which could be due to the availability of another, surface rather than edge-108 based, information source provided by single-opponent cells. Because contextual interactions likely have a different 109 nature for achromatic than chromatic stimuli, we asked whether there are differences in the contextual modulation of 110 firing activity and gamma-band synchronization between these two classes of stimuli. 111

In this study, we investigated the contextual modulation of V1 firing activity and gamma-band synchronization using chromatic and achromatic surfaces of different sizes, and a center-surround mismatch paradigm. Additionally, we examined differences among color hues, adaptation over time, and the influence of the full-screen background on which surfaces were displayed.

116 **Results**

We recorded multi-unit (MU) activity and local field potentials (LFP) from the primary visual cortex (area V1) 117 in two macaque monkeys, while they performed a fixation task. These recordings were made using a 64 channel 118 chronic microelectrode array in monkey H and a 32-channel semichronic microelectrode array in monkey A (see 119 Methods). Classical receptive fields (RFs, referring to classical RFs unless otherwise mentioned) of the MU activity 120 were estimated using moving bar stimuli (see Methods; monkey H: median RF eccentricity 6.2 deg, range 5.2-7.1 deg, 121 median RF diameter 0.48 deg, range 0.26-1.88 deg; monkey A: median eccentricity 5.4 deg, range 3.2-8.5 deg, median 122 123 RF diameter 0.91 deg, range 0.46-2.3 deg). Compared to a surface stimulus of 6 deg diameter, receptive fields had a median proportional diameter of 0.08 (0.04-0.31, monkey H) or 0.15 (0.08-0.38, monkey A). We first studied LFP and 124 MU responses to the presentation of stationary surface stimuli, namely large uniform disks covering the cluster formed 125 by all RFs (6 deg diameter, flashed on and then maintained on screen; Figures 1A-B; Dataset 1, see Methods). The 126 stimuli did not overlap with the fixation spot. Note that the stimuli were much larger than the RFs of the multi-units, 127 such that they covered a large portion of the multi-units' respective surround regions. 128

Initially, we analyzed differences between chromatic and achromatic surface stimuli (Figures 1 and 2; see Methods). We then considered the specific differences among responses to distinct color hues and achromatic stimuli (Figures 4-7). The LFP power spectra had similar frequency profiles in the two monkeys (i.e. the peaks were well aligned; Figure 1-figure supplement 2), and the MUs showed similar temporal profiles (Figure 1-figure supplement 2). Therefore, we pooled the data from the two animals. Note that statistical parameters are largely described in the figure captions.

135 Characteristics of firing activity and LFP signals in response to uniform surface stimuli

We examined the effect of uniform surface stimuli on LFP power spectra. The presentation of large, chromatic surface stimuli (equiluminant red, green and blue; see Methods) induced prominent, narrow-band gamma oscillations in LFP power spectra (Figure 1C-D). These oscillations were clearly visible in the LFP traces (Figure 1B). In comparison, gamma-band oscillations were significantly weaker for achromatic surface stimuli (black or white,

maximal contrast to background; Figures 1C-D). This finding was highly consistent across sites. For each site and 140 chromatic/achromatic condition, we determined the peak power change in the gamma-frequency range (30-80 Hz) 141 using a polynomial fit (see neuronal and Methods). Gamma peak power changes were stronger for chromatic than 142 achromatic surface stimuli at 97.8% (45 out of 46) of LFP recording sites (Figure 1-figure supplement 2). Note that in 143 the Section Controls for luminance-contrast and cone-contrast, we will describe the results of control experiments in 144 which the chromatic and achromatic stimuli are matched in terms of luminance-contrast and DKL cone-contrast (see 145 146 Methods) to the full-screen background. We find that the difference in gamma-band oscillations between chromatic and achromatic stimuli is not explained by either luminance or cone-contrast to the full-screen background. We also 147 removed 100 ms data epochs after each microsaccade and found that the LFP results on gamma oscillations were 148 qualitatively unchanged (Figure 1-figure supplement 3). 149

To test whether V1 spiking activity was synchronized with the induced LFP gamma oscillations, we computed spike-field phase locking spectra (Pairwise Phase Consistency, Vinck et al. (2010b)) between MU and LFP activity obtained from nearby but separate sites (Figure 1E; see Methods). Spike-field phase-locking spectra for chromatic surface stimuli showed a prominent peak in the gamma-frequency band consistent with the gamma peak in the LFP power spectrum (Figure 1D), whereas phase-locking was significantly weaker for achromatic surface stimuli (Figure 1E). The main point of this analysis is that gamma-synchronization for chromatic stimuli is not merely observed at the level of synaptic currents within V1, but also at the level of V1 output spikes.

Next, using the same stimulus paradigm, we examined the way in which the presentation of uniform surface stimuli 157 affected MU firing activity. The presentation of chromatic and achromatic surface stimuli induced short-latency onset 158 transients of similar magnitude (Figure 1F). However, we observed a stronger decrease in MU firing activity over time 159 during continuous stimulus presentation for chromatic than achromatic surface stimuli, starting around 200 ms after 160 the stimulus onset (Figure 1F). Strikingly, for chromatic surface stimuli, MU firing activity fell below baseline levels 161 (Figure 1F). Note that in Figure 4D, we show that the decrease in MU firing below baseline only occurred for a subset 162 of colors. The reduction in MU firing rates (0.3-1.3 s period) for chromatic as compared to achromatic surface stimuli 163 was observed for 92% of recording sites. Control analyses in which data epochs after microsaccades were removed 164 indicate that the late decrease in MU firing was not due to microsaccades (Figure 1-figure supplement 3). 165

These findings demonstrate that large, uniform, chromatic surface stimuli induce low firing activity yet highly gamma-synchronous V1 responses, whereas achromatic surface stimuli induce much weaker gamma-band synchronization but relatively more vigorous firing activity (for further interpretation of this finding, see Discussion).

169 Dependence of firing activity and LFP signals on stimulus size

The results shown in Figure 1 are consistent with the predictability hypothesis (Vinck and Bosman, 2016) out-170 lined in the Introduction. Yet, they do not demonstrate directly that the enhancement in gamma-band synchronization 171 172 observed for large uniform colored surfaces is due to contextual surround modulation, because we did not manipulate the surround input. Furthermore, it remains unclear whether the observed differences between chromatic and achro-173 matic surfaces can be explained by a difference in contextual surround modulation or other factors like stimulus drive. 174 To address these questions directly, we used a paradigm that varied the stimulus size across trials (Figure 2A; see 175 Methods). We selected one site (or a few nearby sites with RF centers within 0.5 deg of the target site) per session and 176 centered the stimulus on the multi-unit's RF, which was previously mapped with moving bars. In each trial a stimulus 177 of a particular size (0.5, 1, 2 or 6 deg diameter) was presented for 600 ms (Figures 2A-B). 178

We first examined how the characteristics of LFP power spectra depended on stimulus size. Analysis of LFP power 179 spectra revealed a strong dependence of gamma power on stimulus size for chromatic stimuli, and by comparison a 180 much weaker dependence for achromatic stimuli (Figure 2B). To quantify this size dependence, we determined the 181 gamma peak power between 30-80 Hz (as described for Figure 1). For chromatic stimuli, increases in stimulus size 182 resulted in increases in induced gamma peak power as soon as the stimulus also covered the surround (i.e. from 183 2 deg onwards, Figure 2B). By contrast, for achromatic stimuli, a gamma peak in the 30-80 Hz band emerged from 184 2 deg stimulus size onwards and showed no further increase with stimulus size. Given the relatively broad increase in 185 >100 Hz LFP power seen in Figure 2B, we also determined gamma peak power and peak frequency in a wider range 186 (30-150 Hz). This analysis revealed LFP power peaks >100 Hz for the sizes below 2 deg, and again the strong size 187 dependence for chromatic compared to achromatic stimuli (Figure 2-figure supplement 1A; also see Figure 2-figure 188

189 supplement 1B for an analysis per animal).

We further investigated the way in which MU firing was modulated by surround stimulation. We observed that 190 for both achromatic and chromatic stimuli, MU firing activity was highest for 0.5-1 deg stimulus sizes (Figure 2C). 191 This was consistent with the estimates obtained from RF mapping and the fact that we centered the presented stimuli 192 on the MUs' estimated RFs. For small stimuli (0.5-1 deg), only the initial transient in MU firing activity showed a 193 difference between chromatic and achromatic conditions, with slightly higher firing activity for achromatic than chro-194 matic stimuli (Figure 2C). In contrast, the presentation of a 2 or 6 deg stimulus, increasingly covering the surround, 195 196 induced strong suppression of MU firing activity as compared to the 0.5 deg stimulus (Figure 2C, rightmost panel). This surround suppression was stronger for chromatic than achromatic stimuli (Figure 2C). 197

Furthermore, we analyzed responses during a later period in the trial, when the small stimulus had been presented for 600 ms, and a large (6 deg) surface stimulus of the same color was added for another 600 ms period (Figure 2-figure supplement 1C). We found that this addition of the surround stimulus alone induced a rapid suppression of MU firing activity, which was significantly more pronounced for chromatic than achromatic stimuli (Figure 2-figure supplement 1C).

These findings suggest that the relatively strong decrease in firing over time observed for large, chromatic surfaces (Figure 1) is at least partially explained by surround suppression. They furthermore indicate that for the small RF stimuli, there are no substantial differences on average between chromatic and achromatic surfaces in terms of MU and LFP responses. Yet, we find a prominent difference in the way chromatic and achromatic stimuli are affected by surround stimulation.

208 Modulation of firing activity and LFP signals by center-surround predictability

A potential explanation for the results shown in Figure 1-2 may be the center-surround predictability hypothesis 209 outlined in the Introduction (Vinck and Bosman, 2016). Yet, the employed paradigm used stimuli of different sizes, 210 211 which may have recruited different neuronal circuits and may also have changed stimulus salience. We therefore used an additional stimulus paradigm in which surround influences were modified, while stimulus size was held constant. 212 Specifically, we created three sets of equally sized stimuli. In one set, the surround was fully predictive of the RF 213 stimulation, because it used a uniform surface (called "uniform" stimulus). In the second set (called "blob mismatch"), 214 the surround was not predictive of the RF stimulation, because the surround stimulus and the 1 deg RF stimulus had 215 216 different colors (which were physically equiluminant). In the third set (called "annulus mismatch"), the surround had the same color as the RF stimulation, but the two were separated by an annulus ring of a different, physically 217 equiluminant color. This annulus ring had 0.25 deg thickness and an inner diameter of 1 deg. 218

We found that compared to the uniform surfaces, stimuli with a chromatic (blob or annulus) mismatch had higher MU firing activity (Figure 3C). This held true both for the initial transient period and the subsequent sustained response period (Figure 3C). At the same time, we observed a marked decrease in the amplitude of LFP gamma oscillations for the chromatic mismatch compared to the uniform surface stimuli (Figures 3B-C). This result was consistent across animals (Figure 3-figure supplement 1A).

We further investigated whether this pattern of changes was specific to the sites having RFs near the center stimu-224 lus. To this end, we examined sites with RFs on the outer uniform regions of the stimulus (with RF centers 1.5-2 deg 225 226 from the stimulus center; Figure 3D). For these sites the MU firing responses did not differ significantly between con-227 ditions during the initial transient period (Figure 3D). During the later sustained response phase, however, MU firing activity was reduced for the chromatic mismatch stimuli compared to the uniform surface stimulus (Figure 3D). Note 228 that whenever the RF center covered a large uniform surface region, either in the uniform stimulus condition or when 229 it covered the surround region of the mismatch stimuli, sustained firing levels were below baseline. This confirmed 230 the respective finding reported in Figure 1. 231

These results suggest that a mismatch between stimuli at the RF center and the surround can dramatically change 232 the surround influence on responses to the center. We wondered whether the surround influence on gamma oscillations 233 originates from the uniform surface region or rather from the edge of the surface. To this end, we analyzed sessions in 234 which we compared two sets of trials: First, trials with a full surface stimulus centered on a site's RF ("RF-on-center" 235 condition; Figure 3-figure supplement 1B). Second, trials with a full surface stimulus positioned such that its edge 236 237 fell into the RF center, i.e. with the surface shifted by 3 deg horizontally ("RF-on-edge" condition; Figure 3-figure 238 supplement 1B). We found that the amplitude of gamma oscillations was significantly higher at the center ("RF-oncenter") than at the edge of the surface stimulus ("RF-on-edge"), whereas the opposite was observed for MU firing 239 activity (Figure 3-figure supplement 1B). In one session (monkey H), we also showed disk stimuli that had their edge 240

blurred with a Gaussian (2.5 deg size, 1 deg standard deviation). There were clear gamma-responses also in this case
(Figure 3-figure supplement 1C).

Together, these results indicate that for colored surfaces the amplitude of gamma-band oscillations is commensurate with the "chromatic" predictability among visual inputs in space, and that gamma-band oscillations are not a mere consequence of input drive to a larger cortical region. Furthermore, these results suggest that gamma strength can be dissociated from stimulus salience, because the chromatic mismatch condition provided a highly salient stimulus in the RF, but resulted in weaker gamma.

248 Differences in firing activity and LFP signals between color hues

The results above show prominent differences between chromatic and achromatic surfaces in terms of gamma-249 band synchronization. The respective analyses pooled different chromatic conditions (equiluminant red, green and 250 blue) together. However, there may exist further differences in gamma-band synchronization within the chromatic 251 conditions, i.e. between different hues. To investigate this we used two types of stimulus sets, which were presented 252 in separate sessions. In the first stimulus set (Figure 4A) we presented each surface color at its maximum possible 253 luminance level (given the limits of the employed monitor), and sampled from the entire spectrum of hues available 254 with the monitor (see Methods). In the second stimulus set, we presented surface stimuli with different color hues at 255 equated luminance levels (Figures 4B-C). 256

Using the first stimulus set, we found that gamma-band LFP oscillations were reliably induced across the entire 257 spectrum of hues (Figure 4A, Figure 4-figure supplement 1, see also Supplementary Table 1 for all luminance and 258 CIE values). In addition, we found that gamma-band synchronization was reliably induced by surfaces with "extra-259 spectral" colors, i.e. colors resulting from a mixture of blue and red primaries (Figure 4A), as well as brownish hues. 260 We further replicated our finding that gamma oscillations were relatively weak for both black and white surface stimuli 261 as compared to all colored surfaces (Figure 4A). In one monkey (A), we found that gamma-band activity was stronger 262 for black than for white stimuli, consistent with previous results showing stronger firing rate responses to black than 263 white stimuli (Xing et al., 2010; Yeh et al., 2009). However a trend in the opposite direction was observed for monkey 264 H (Figure 4-figure supplement 2). 265

For the first stimulus set (Figure 4A), the different colors were presented at their maximum possible luminance 266 267 levels, which might confound the effects of hue and luminance. We therefore used a second stimulus set in which we presented surface stimuli with different color hues at three levels of equal physical luminance, i.e. different color 268 values (Figures 4B-C). For all three hues, gamma amplitudes were greater for the highest compared to the lowest 269 luminance condition (P<0.05, bootstrap test, see Methods; Figures 4B-C). The dependence of gamma amplitude on 270 stimulus luminance was greater for green than for red or blue surface stimuli (difference between high versus low, 271 Figures 4B-C). Gamma oscillations had a higher amplitude for red than for blue or green surface stimuli across all 272 three luminance conditions (Figures 4B-C), whereas gamma amplitude was higher for blue than green surface stimuli 273 for low and intermediate luminance conditions (Figures 4(B-C)). Another difference between the hues was that the 274 gamma peak had a significantly lower frequency for green compared to red or blue surface stimuli (P < 0.05, bootstrap 275 test; Figures 4B-C and Figure 4-figure supplement 2). The results of these analyses were consistent across both 276 277 monkeys (Figure 4-figure supplement 2).

Given the relationships between MU firing activity and LFP gamma-band oscillations shown in Figures 1-3, we asked how these differences in LFP gamma oscillations were related to changes in firing activity. During the initial transient, MU firing activity was higher for red and blue rather than for green surface stimuli, with slightly stronger responses for red than blue surface stimuli (Figure 4D). Yet, we found that the post-transient decrease in MU firing activity over time was particularly pronounced for red and particularly weak for green stimuli (Figure 4D). In agreement with the data shown in Figure 1, we observed that MU firing activity fell below baseline levels for red and blue surface stimuli (Figure 4D).

Together, these results indicate that surfaces of all color hues tend to induce gamma-band oscillations with a higher amplitude compared to achromatic surfaces, and that the amplitude of gamma oscillations is relatively high for red surfaces.

288 Controls for luminance-contrast and cone-contrast

In the analyses above, we observed a strong difference in gamma-band power between chromatic and achromatic surfaces. We performed several control analyses and experiments to investigate whether this observed difference was

explained by differences in DKL cone contrast or luminance contrast between chromatic and achromatic surfaces. A 291 linear regression of gamma peak height against absolute Michelson luminance contrast (luminance stimulus - lumi-292 nance baseline / (luminance stimulus + luminance baseline)) across the surface stimuli shown in Figure 4B showed no 293 significant relationship (r=-0.44,p=0.16, F-test, Figure 4-figure supplement 2; note that the relationship, if any, was 294 negative). In an additional control experiment, we directly matched the luminance (and thereby luminance-contrast) 295 of the achromatic and chromatic stimuli across 5 brightness values, including the full-screen background brightness 296 297 and two steps of positive and negative contrast. We found that achromatic gamma-responses were much weaker than chromatic gamma-responses regardless of overall luminance level, also under these matched conditions (Figure 4-298 figure supplement 3A). We additionally used this experiment as a control for the effect of pupil size (see Methods) on 299 gamma-band amplitudes (Figure 4-figure supplement 3B). Note that gamma responses for achromatic stimuli were 300 weak regardless of the degree of pupil change. 301

In another experiment, which is part of the data shown in Figure 6, we matched cone-contrasts between chromatic 302 and achromatic stimuli. Specifically, we compared gamma-responses to a colored surface on an achromatic full-screen 303 background with gamma responses to a corresponding achromatic surface on a chromatic full-screen background of 304 the same respective color (e.g. red on a gray background versus gray on a red background). These comparisons keep 305 the changes in cone-activation relative to the background the same. Note that this does not mean that the cone-contrasts 306 are matched in the DKL space, because this space contains an additional normalization step, which incorporates the 307 extent to which the full-screen background itself activates the different cones. Nevertheless, although only the non-308 normalized changes in cone-contrasts are matched, it can be seen that e.g. the white stimuli have very strong DKL 309 cone-contrast to the chromatic full-screen backgrounds along the L-M and S-(L+M) axes (Figure 6-figure supplement 310 1). This cone-contrast for white surfaces on chromatic backgrounds exceeds that of chromatic stimuli on the white 311 background (Figure 6-figure supplement 1). Our analyses reveal that for each tested color (except for red on a black 312 313 surface), gamma was much stronger for chromatic than achromatic surfaces of matched cone contrast (Figure 6F). Together, these data indicate that the difference in gamma-band response between chromatic and achromatic surfaces 314 was not due to luminance- or DKL cone-contrast relative to the full-screen background. ' 315

In the previous section, colored stimuli were either presented at maximum brightness or presented at the same 316 physical luminance. We performed additional experiments in which colored surfaces were matched in terms of DKL 317 318 space coordinates in units of Weber cone contrast (see Methods, Figure 4-figure supplement 4). These coordinates were the L-M (red-green opponency), S-(L+M) (blue-yellow opponency) and L+M (luminance) cone-contrasts rel-319 ative to the gray full-screen background. In the first experiment (Figure 4-figure supplement 4A), we selected three 320 luminance steps (L+M cone-contrast was -0.25, 0, or +0.25). For each luminance step, we then took an equal step in 321 the positive and negative L-M direction. This step was taken as the maximum possible step for which the magnitudes 322 were equal in both directions. Similarly, we took a step of equal magnitude in the positive or negative S-(L+M) direc-323 tion. In the second experiment (Figure 4-figure supplement 4B), we sampled from 8 different angles in the DKL plane 324 at an equiluminant level to the gray background. Note that this yields stimuli that are highly desaturated as compared 325 to the stimuli shown in Figure 4. 326

327 The data from these control experiments show that gamma-band responses were stronger for reddish than greenish 328 hues. This is consistent with the results shown in Figure 4A (see Figure 4-figure supplement 1D). Achromatic stimuli 329 did not induce detectable gamma-band response peaks, neither in the positive or negative luminance-contrast (L+M) step, consistent with the findings of Figure 1-2 and 4. Furthermore, these data suggest that increasing S-(L+M) cone-330 contrast (blue-yellow opponency) independent (or in absence of) L-M cone-contrast also boosts gamma oscillations 331 (Figure 4-figure supplement 4B). These results further support the notion that gamma-band oscillations for uniform 332 surfaces are mediated by color-opponency signals. They further indicate that hue (i.e. the angle in the DKL-plane) 333 itself is a determinant of gamma-band oscillation strength, and that the dependence on hue is not explained by the 334 magnitude of cone-contrasts. This is also consistent with the finding that the magnitudes of the DKL cone-contrasts 335 for the chromatic surface stimuli shown in Figure 4A are not significantly correlated with gamma-band power (Figure 336 4-figure supplement 1C). Note that this lack of a correlation might be due to the use of stimuli with largely very high 337 brightness and cone contrasts, such that the effects of hue differences dominate. 338

339 Temporal evolution of gamma-band responses

The observed differences in gamma oscillations between the color hues (Figure 4) might reflect a static and context-independent property of visual cortex to respond differently to distinct hues. Yet, the continuous presentation of a uniform surface stimulus for the duration of an entire trial likely induces substantial adaptation at many

levels of the nervous system. We thus wondered whether different hues might adapt at different rates. To address this,

we examined the temporal evolution of LFP power spectra over a longer time period, i.e. up to 3 s after stimulus onset. Time-frequency representations showed that qualitative differences between hues and between luminance levels

tended to be relatively stable over time (Figure 5A). However, we found that the amplitude of gamma-oscillations de-

³⁴⁷ creased more rapidly over time for green than for blue or red surface stimuli (Figures 5A-B). This result held also for

both animals individually (monkey H/A red change over time $-0.07\pm0.05/-0.12\pm0.04$, green $-0.51\pm0.06/-0.36\pm0.04$,

blue $-0.23\pm0.05/-0.10\pm0.04$). The main effect of decrease with time, as well as stronger decreases for green compared

to both red and blue, were signicant in both animals individually (all P < 0.05 corrected for multiple comparisons).

This suggests that there may be differences in the time course and strength of adaptation between color hues, specifically stronger adaptation for green surface stimuli.

353 Dependence on full-screen background hue

One potential source of adaptation, other than the surface stimulus of a given trial, is the color composition of 354 the continuously presented background. In the experiments described above, all surface stimuli were displayed on a 355 gray full-screen background (FSB). Gamma-band responses to achromatic and chromatic surface stimuli may have 356 been affected by the use of this gray FSB, given that the FSB itself may induce adaptation at many levels of the 357 nervous system. We therefore asked how gamma-band responses to surface stimuli depend on the color of the FSB. 358 To answer this question, we performed experiments in which we used different FSBs in separate, adjacent sessions 359 (gray, white, black, blue, green, yellow and red) (Figure 6A and Figure 6-figure supplement 1; see Methods). The 360 FSB was continuously presented during the entire session, i.e. remained on both during the pre-stimulus period, 361 post-stimulus period and the period during which the surface stimuli were displayed (Figure 6A). In Figure 6, we 362 analyze LFP responses to the presentation of chromatic surface stimuli of different hues, which were presented at the 363 maximum possible luminance level (see Figure 6-figure supplement 2 for equiluminant red, green and blue as well as 364 achromatic surface stimuli). 365

We first examined how the responses to surface stimuli with specific hues (e.g. green) were altered by using an 366 FSB with the same hue (e.g. green), comparing them to the sessions with a gray FSB (Figure 6B). Surprisingly, we 367 found that when the FSB had the same hue as the surface stimulus, there was a nearly complete abolishment of gamma 368 oscillations for blue, green and yellow stimuli (Figure 6B and Figure 6-figure supplement 2). This was observed both 369 when the surface stimulus had the same luminance as the background (Figure 6) and when the surface stimulus had 370 a lower luminance (Figure 6-figure supplement 2). Interestingly, red stimuli could still induce detectable gamma 371 oscillations when presented on a red FSB, although the gamma amplitude was strongly reduced compared to the gray 372 FSB condition (Figure 6B and Figure 6-figure supplement 2). 373

The reduction in gamma-band oscillations for the same-hue FSB condition may have been an effect of stimulus 374 size, because the background is effectively a very large surface. Alternatively, it may have been an effect of stimulus 375 history. To investigate these possibilities, we analyzed the post-stimulus period immediately following the offset of a 376 gray surface stimulus that was displayed on a colored FSB. We found that the reappearance of the FSB after the offset 377 378 of the colored surface induced prominent gamma-band oscillations (Figure 6-figure supplement 3). This indicates 379 that the decrease in gamma-band oscillations with the same hue FSB condition was not due to the large size of the background color stimulation, but that it was due to the continuous presence of the same-hue background. This is also 380 consistent with a previous report showing strong gamma with full-screen color stimuli that change color across trials 381 (Shirhatti and Ray, 2018), and with the positive relation between gamma and stimulus size shown in Figure 2C. 382

Next, we considered interactions between distinct hues. We wondered whether gamma oscillations can not only be 383 reduced by same-hue FSBs, but also enhanced by FSB hues that are different from the stimulus hue, in particular when 384 FSB and stimulus assume opponent colors. The organization of color vision around color-opponency axes, namely 385 the red-green and the blue-yellow axes, is a key principle found both at the neurophysiological and psychophysical 386 level (Livingstone et al., 1984; Solomon and Lennie, 2007; Tailby et al., 2008a; Wachtler et al., 2003). These color 387 opponencies are thought to result from the computation of differences among signals deriving from L and M cones 388 389 (red-green), and S cones versus L and M cones (blue-yellow). We found that for all surface hues, gamma oscillations 390 were amplified when stimuli and FSBs were of opponent color hues (Figure 6C). This suggests that gamma oscillations are dependent on opponency signals along the red-green and the blue-yellow axes (Figure 6C). Given the strong 391 dependence of gamma-band oscillations on the FSB, we asked whether the use of a gray FSB may have induced 392

differences in gamma-band amplitude among distinct hues. To examine this possibility, we used a black FSB, which 393 should induce minimal adaptation for all cones. Quite surprisingly, the difference among red, green and blue hues 394 that we had observed with a gray FSB could not be replicated when we presented the stimuli on a black FSB (Figure 395 6D). Compared to the gray FSB condition, gamma-band amplitudes were significantly lower for red and blue surface 396 stimuli and significantly higher for yellow and green surface stimuli (Figure 6D). As a consequence, for the black FSB 397 condition, gamma-band power was no longer highest in response to red stimuli, but showed a different dependence 398 399 on hue (Figure 6D; Figure 6-figure supplement 2). Specifically, gamma-band power was higher for green and yellow than red and blue surface stimuli (Figure 6D). The resulting pattern could not be explained by luminance contrast 400 differences, because contrast increased for all hues on the black compared to the gray FSB, whereas gamma increased 401 for some hues and decreased for others (Figure 6D). 402

In Figure 6B-C, we compared stimulus responses in the same-hue and opponent-hue background conditions with 403 stimulus responses in the gray background condition. However, because of the evidence that the gray FSB may not 404 have affected all stimulus hues equally, we also directly compared the same-hue and opponent-hue FSB conditions 405 with the black FSB condition. This analysis revealed a marked difference between red and the other hues (Figure 6E). 406 First, when an FSB of the same hue as the stimulus was compared to a black FSB, gamma was almost abolished for 407 blue, green and yellow, but not for red stimuli. Second, when an FSB of the opponent hue was compared to a black 408 FSB, gamma was enhanced for all colors, but particularly strongly for red (Figure 6E). The full matrix of gamma 409 responses for different FSB conditions in Figure 6-figure supplement 2 shows that for all non-red chromatic FSBs, 410 gamma oscillations were strongly amplified for red surface stimuli. 411

We also analyzed the gamma-responses to achromatic stimuli on colored backgrounds, and asked in particular whether responses of achromatic stimuli on colored surfaces were as strong as responses of colored stimuli on achro-

414 matic surfaces (Figure 6F). Achromatic responses on colored backgrounds were substantially weaker than the reverse

415 (see Section Controls for luminance-contrast and cone-contrast). These data demonstrate that gamma oscillations de-

⁴¹⁶ pend strongly on the FSB, in a way that follows the color-opponency axes. Furthermore, a commonly used "default"

417 of the display, namely gray, introduces adaptation effects that are color-specific.

418 A quantitive model relating hue dependence of gamma-band oscillations to adaptation

To explain how gamma-band responses to surface stimuli depend on the FSB, we constructed a quantitative model 419 by estimating the degree to which each FSB differentially adapts the S-, M- and L-cone pathways. Note that this model 420 is agnostic to the neuronal locus at which adaptation of the distinct cone pathways occurs, e.g. it might occur in the 421 retina, LGN or visual cortex. We hypothesize that gamma-band oscillations for colored surface stimuli are mediated 422 by the activation of single color-opponent cells in a large spatial region by the same color input. The combination of 423 bottom-up drive at each point of the surface and strong surround modulation may then lead to gamma oscillations. 424 425 The result that gamma oscillations are particularly strong in the opponent-hue background condition (Figure 6) further suggests that when this circuit is more strongly activated (leading to stronger input drive as well as stronger surround 426 modulation), gamma oscillations increase. 427

Following this reasoning, we further hypothesized that the dependence of gamma-band oscillations on the FSB can be explained by adaptation of specific cone pathways (see Discussion for further argumentation). As an example, a green FSB should lead to stronger adaptation of the M-cone compared to the L-cone pathway. This should increase the degree to which single-opponent cells with L+/M- color-opponencies are activated by red surface stimuli, which may in turn increase the amplitude of gamma-band oscillations.

To capture this intuition in a quantitative manner, we constructed a model in which we aimed to predict the 433 difference in gamma-band amplitudes between red and green surface stimuli (for blue and yellow surface stimuli see 434 further below). The variable to be predicted was the red-green gamma ratio, defined as $\gamma_{ratio} = \log_{10}(\gamma_{red}/\gamma_{green})$, 435 where γ_{red} and γ_{green} are the respective gamma-amplitudes for red and green surface stimuli. This γ_{ratio} was computed 436 separately for all the different FSBs. We estimated the degree to which each FSB adapts the M- and L-cones, using 437 the known response curves of the three cones as a function of wavelength from macaque monkeys (Hárosi, 1987) (see 438 Methods, Figure 7A). We then measured the physical wavelength spectrum for each FSB as realized on our monitor. 439 We multiplied the FSB spectra of the different color primaries with the response functions of each cone and summed 440 over wavelengths. This yielded for each FSB stimulus two parameter values, M_{adapt} and L_{adapt} . We then fitted a 441

442 multiple regression model predicting γ_{ratio} from M_{adapt} and L_{adapt} plus a constant regression intercept (Figure 7B).

For this model, we used response data for both green and red surfaces presented at maximum possible luminance, as well as equiluminant red and green surfaces, across the different FSBs.

The regression analysis reveals that γ_{ratio} can be highly accurately predicted by the way in which each FSB adapts 445 the L and the M cones (Figure 7B; $R^2=0.91$, P < 0.05, F-Test). The regression coefficients for M_{adapt} and L_{adapt} were 446 positive and negative, respectively. This indicates that adaptation of the M-cone increases γ_{ratio} , whereas adaptation of 447 the L-cone decreases γ_{ratio} (Figure 7B). We also found that the γ_{ratio} could not be significantly predicted when using 448 S_{adapt} and L_{adapt} as predictors (P=0.23), consistent with the idea that the neuronal mechanisms underlying the red-449 green opponency are dependent on the M versus L cone contrast. The regression intercept of the model (on the γ_{ratio} 450 axis) was not significantly different from zero. This indicates that green and red tend to generate gamma oscillations 451 of similar amplitude when the FSB does not adapt the cones, consistent with the findings shown for the black FSB 452 (Figure 6). Strikingly, we found that the M_{adapt} coefficient had an absolute magnitude approximately twice as large as 453 the Ladapt coefficient (Figure 7B). This suggests that uniform surfaces tend to adapt the M-cone pathway more strongly 454 than the L-cone pathway, or that adaptation of the M-cone pathway has a stronger effect on gamma-band oscillations 455 than adaptation of the L-cone pathway. 456

The model further explains some non-trivial findings that would have been unexpected if FSBs had affected the 457 M- and L-cone pathway in a similar way: We observed that the yellow FSB strongly amplified γ_{ratio} (Figure 7B). 458 Given its wavelength spectrum, the yellow FSB is expected to adapt the L-cones more strongly than the M-cones, 459 which would predict a reduced γ_{ratio} , i.e. red responses being weaker than green responses. By contrast, we found 460 that γ_{ratio} was enhanced. The models explain this by the fact that the stronger L-cone than M-cone activation by 461 the yellow background is more than compensated by the much greater M_{adapt} than L_{adapt} coefficient. Similarly, the 462 γ_{ratio} increased for a gray compared to a black FSBs, even though gray FSBs should in principle adapt the M- and 463 L-cone pathways to a similar degree (Figure 6). This was again compensated by the much greater M_{adap} than L_{adap} 464 coefficient. 465

We performed a similar analysis for the yellow-blue (L+M - S) opponency axis, aiming to predict the gamma ratio 466 of blue over yellow (Figure 7C). We first fitted a model with the S, L and the M cone parameters, and γ_{ratio} was now 467 defined as $\gamma_{ratio} = \log_{10}(\gamma_{blue}/\gamma_{yellow})$. This regression model explained a large degree of variance ($R^2 = 0.99$), with al-468 most equal magnitude of S (negative, -1.23) and L (positive, 1.24) coefficients, but a much smaller and non-significant 469 470 coefficient for the M cone (-0.29). The finding that the model fit included a highly positive L-cone coefficient and non-significant (and negative) M-cone coefficient seems prima facie to contradict the canonical idea that the percep-471 tual blue-yellow opponency axis is mediated by an S versus (L+M) opponency. However, neurophysiological data has 472 shown that the main opponency for LGN cells on the yellow-blue axis is the L versus S cone (Tailby et al., 2008b). 473 We further simplified our model using two predictive parameters, equating the blue axis to the S cone and the yellow 474 axis to the L cone (Figure 7C). Again, we found a highly predictive relationship with negative weight for the S cone 475 and a positive weight for the L cone (Figure 7C), with only a small and non-significant difference in the magnitude of 476 the adaptation coefficients. The results were qualitatively highly similar between animals and individually significant 477 (Figure 7- figure supplement 1). These findings indicate that gamma oscillations are mediated not only by opponency 478 signals along the red-green axis, but also along the blue-yellow axes, consistent with the data shown in Figure 4-figure 479 480 supplement 4. Note that the results of the model shown in Figure 7 were qualitatively highly similar between animals 481 and individually significant (Figure 7- figure supplement 1).

482 Discussion

483 Summary

We investigated the way in which V1 responses to chromatic and achromatic surfaces are modulated by spatial and temporal context. We report the following main findings:

(1) Compared to achromatic surfaces, chromatic surfaces induced strong synchronization of neuronal activity in
 the gamma-frequency band (Figures 1 and 2). This finding held true for color hues across the entire wavelength
 spectrum (Figure 4).

(2) Whereas chromatic and achromatic surfaces induced an initial MU firing transient of similar magnitude (Figure
 1 and 2), we found relatively weaker firing responses to chromatic surfaces in the sustained stimulation period, which
 was evident from a stronger decrease in firing over time related to an increase in surround suppression (Figures 1 and
 2).

(3) Compared to uniform chromatic surfaces, composite stimuli with a chromatic mismatch between the stimulus
covering the RF center and the surrounding surface evoked high firing activity, yet induced a very prominent reduction
in the amplitude of gamma band oscillations (Figure 3). This supports the hypothesis of Vinck and Bosman (2016)
outlined in the Introduction, namely that gamma-band synchronization reflects the degree to which inputs into the
CRF can be predicted from the surround.

(4) Stimulus-induced gamma-band oscillations were also strongly modulated by the larger spatio-temporal con-498 text: We found that their amplitude depended strongly on the full-screen background (FSB) on which the surfaces 499 were displayed (Figures 4-7). We concluded that the dependence of gamma-band synchronization on the FSB was 500 explained by two key factors: First, color opponency along one of the two main color-opponency axes (red versus 501 green and yellow versus blue). Second, a comparatively stronger adapting influence of FSBs on the M-cone pathway, 502 which leads to comparatively stronger gamma oscillations for red surfaces for many (but not all) FSBs (Figures 6-7). 503 This is consistent with our finding that the decrease in gamma-band amplitude within a trial is particularly strong for 504 green surface stimuli (Figure 5). 505

506 Differences between chromatic and achromatic surfaces

We asked whether there are differences in V1 gamma-band synchronization and firing responses between chro-507 matic and achromatic stimuli. A previous voltage-sensitive dye imaging study has shown differences in V1 responses 508 to chromatic compared to achromatic surfaces (Zweig et al., 2015). For achromatic surfaces, V1 response charac-509 teristics were indicative of a fill-in process, in which surface information emanates from the surface's edge. This 510 was not the case for chromatic surfaces (Zweig et al., 2015), which suggests that the V1 representation of surface 511 color may largely depend on single-opponent LGN inputs to V1 and responses of V1 neurons with RFs within the 512 uniform surface (Livingstone et al., 1984; Shapley and Hawken, 2011; Zweig et al., 2015). Indeed, the data shown in 513 514 Figures 6-7 suggests that V1 gamma oscillations are mediated by color-opponency signals. It has been shown that a subset of neurons with chromatic opponencies in LGN and V1 exhibit elevated firing as compared to baseline for 515 large chromatic surfaces, and carry information about the surfaces hue (Ts'o and Gilbert, 1988). These cells can be 516 subdivided into Type I, Type II and modified Type II responses. These color-selective neurons would not be active 517 for a large achromatic stimulus (Ts'o and Gilbert, 1988), indicating that there may be stronger LGN and/or layer 4 518 519 cortical drive for chromatic than achromatic stimuli. However, a subset of V1 neurons also fire to temporal luminance changes for black and white surfaces (Xing et al., 2010), and neurons might also be activated for achromatic surfaces 520 by fill-in processes from the surround (Zweig et al., 2015). This means that chromatic and achromatic stimuli may 521 differ in input drive, and perhaps other aspects of processing (Zweig et al., 2015). Several human imaging studies 522 have shown stronger fMRI signals in response to chromatic stimuli (for review, see Schluppeck and Engel (2002), 523 Shapley and Hawken (2011)). Because the fMRI signal correlates not only with spiking activity, but also with gamma 524 responses (Ekstrom (2010); Logothetis and Wandell (2004); Maier et al. (2008); Nir et al. (2007); Scheeringa et al. 525 (2016); Thomsen et al. (2004); Viswanathan and Freeman (2007), for visual gamma in particular Bartolo et al. (2011); 526 Niessing et al. (2005)), it remains unclear how these fMRI findings are related to the present findings. 527

In the present study, we observed that chromatic surfaces exhibited much stronger gamma-band synchronization 528 yet more suppressed firing than achromatic surfaces. This finding is consistent with the idea that V1 representations 529 530 of surface color depend on the direct activation of neurons with RFs in the uniform region of the surface. It further supports the hypothesis that gamma-band synchronization arises from the predictability of visual inputs across space 531 (Vinck and Bosman, 2016). Together, these data suggest that one could think of color, like stimulus orientation, as 532 a "feature", with predictive value for stimulus features in color space. If the features at the center stimulus are cor-533 rectly predicted by the surround (context), this results in strong gamma-band synchronization. On the other hand, 534 predictability of stimulus luminance by itself in the absence of color information, as in the case of a large uniform 535 white stimulus, may not be processed as a stimulus feature. Luminance by itself, in the absence of color information, 536 may not be sufficient for inducing strong gamma-band synchronization. In contrast, prominent gamma-band synchro-537 nization can be generated in response to achromatic stimuli when they have structural features (orientation, frequency, 538 phase) that are highly predictable over space, e.g. bars and gratings (Chalk et al., 2010; Gail, 2000; Gieselmann and 539 540 Thiele, 2008; Gray et al., 1989; Singer, 2018).

541 Overall, our data suggests that both sufficient drive and spatial predictability are the necessary ingredients for the 542 generation of V1 gamma. There are several cases in our manuscript where differences in V1 gamma are dissociated 543 from differences in firing rate. For example, in Figure 3 we show a strong increase in firing rates for the annulus and blob condition as compared to the uniform surface, however gamma oscillations are markedly decreased. In

Figure 3-figure supplement 1B, we show that gamma-band oscillations are stronger at the center than the edge of a

546 chromatic surface stimulus, however firing rates are much stronger at the edge of the chromatic surface stimulus. In 547 V1, most cells with chromatic opponencies are found in the superficial layers, to which our recordings are biased and

in which gamma is thought to be generated (see Discussion section Mechanisms of gamma-band synchronization).

549 Most of these V1 neurons are strongly driven by the presence of chromatic edges and have band-pass rather than

⁵⁵⁰ low-pass spatial characteristics, and the majority of neurons has been classified as double-opponent rather than single-

opponent (Friedman et al., 2003; Johnson et al., 2008; Shapley and Hawken, 2002, 2011). This is consistent with our

finding that firing rates are relatively high at the edge of the chromatic surface stimulus and for the blob and annulus mismatch conditions (Figure 3, Figure 3-figure supplement 1B). As opposed to these cases where high firing rates are

accompanied by weak gamma, we also present cases where stimuli have high spatial predictability, but where gamma

is weak or absent likely due to low drive (Figure 1 achromatic stimuli, Figure 6 chromatic stimuli after prolonged adaptation).

An important question is how to functionally relate the dependence of gamma on both predictability and drive. Notably, even though chromatic and achromatic (uniform) surfaces both have high spatial predictability at the *image level*, they may differ in the degree of predictability at the level of inputs at the *neuronal level*. Before information about an image reaches the cortex, it is processed through various stages. Noise could accumulate through these processing steps, for example due to synaptic release noise, ion channel noise and background synaptic activity. We can sketch two extreme cases as a function of the signal-to-noise ratio, which we call the efficient coding (1) and the inference regime (2) (de Lange et al., 2018; Rao and Ballard, 1999):

(1) In the efficient coding regime where the signal-to-noise ratio is high and the image has predictable relationships
 over space, redundant information should be removed by a subtraction of predictions. The removal of redundant
 information should lead to a sparse code (Rao and Ballard, 1999), accompanied by gamma-synchronization. This
 may be mediated by GABAergic, inhibitory mechanisms (Jadi and Sejnowski, 2014; Vinck et al., 2013b) (see the
 discussion section on mechanisms below).

(2) If the sensory input is relatively weak, as in case of stimulus with low luminance-contrast, the signal-to-569 noise ratio is expected to be low. In such a case, there is less redundancy between center and surround inputs, i.e. 570 571 less predictability. The principle of Bayesian inference tells us that in these kind of conditions, the surround may effectively be used to infer representations at the RF location (de Lange et al., 2018; Rao and Ballard, 1999). In other 572 words, the representation in this case is biased towards the contextual prediction, and is essentially a weighting of 573 the input with the contextual prediction (de Lange et al., 2018; Rao and Ballard, 1999). The weighting of contextual 574 surround information with the input may in this case rely on an increase in local firing driven by excitatory surround 575 influences, and a concurrent decrease in the recruitment of GABAergic interneurons by surround inputs (Jadi and 576 Sejnowski, 2014; Rao and Ballard, 1999). Consistent with these ideas, previous work has shown surround facilitation 577 and an expansion of the classical receptive field under low luminance-contrast condition (Grosof et al., 1993; Kapadia 578 et al., 1999, 1995; Von Der Heydt et al., 1984), and perception is biased towards expectation under low signal-to-579 noise ratio conditions (for a review see de Lange et al. (2018)). Furthermore, it has been shown that gamma-band 580 581 synchronization for grating stimuli increases with luminance-contrast (Hadjipapas et al., 2015; Henrie and Shapley, 582 2005; Ray and Maunsell, 2010; Roberts et al., 2013). For achromatic stimuli, responses at the surface's center derived from local signals may be weak. Responses should therefore be influenced by excitatory contextual influences from 583 neurons with receptive fields on the surface's edge (Zweig et al., 2015). In contrast, the surface representation for 584 chromatic stimuli may largely depend on the direct activation of single-opponent cells with RFs on the uniform region 585 of the surface. In this case, there is high redundancy across space and the efficient coding process dominates, which 586 is accompanied by gamma-synchronization. Future studies are required to carefully characterize the responses of 587 different color-responsive cell types to investigate this hypothesis. The dependence of predictability of inputs on the 588 signal-to-noise ratio may potentially also explain the disappearance of gamma-band synchronization with prolonged 589 visual stimulation (Figure 6, see next subsection). 590

591 Dependence of gamma-band oscillations on hue and full-screen background

We demonstrated a prominent difference in gamma-band synchronization and firing activity between chromatic and achromatic surfaces. However, we also found prominent hue-related differences. These differences could reflect a constant property of the visual system to respond differently to particular hues, or might arise from other contextual processes, such as adaptation to the full-screen background (FSB) on which the surfaces were displayed. When using a gray FSB, we found that gamma oscillations were particularly strong for surface stimuli with red hues. This finding is consistent with previous work that used a gray FSB throughout and showed stronger gamma-band synchronization for red stimuli (Rols et al., 2001; Shirhatti and Ray, 2018). Note that with a gray FSB, gamma oscillations were reliably induced by all surface hues, which is consistent with our findings suggesting that both yellow-blue and redgreen opponencies contribute to the generation of V1 gamma oscillations (Figure 4-figure supplement 4, Figures 6 and 7).

602 Importantly, we found that differences in gamma-oscillation strength among hues were highly dependent on the FSB and that with a black background a different dependence on hue emerged. In particular, with a black compared to 603 a gray FSB, gamma oscillations increased in amplitude for green and yellow surface stimuli, but decreased in ampli-604 tude for red and blue surface stimuli. The quantitative model presented in Figure 7 suggests that the M-cone pathway 605 adapts more strongly than the L- and S-cone pathways, even when the adaptation-inducing FSB is supposedly "neu-606 tral" (gray). By extension, background hues during natural vision would play a similar adapting role. An explanation 607 for this phenomenon may be that, in general, uniform surfaces induce stronger or faster adaptation of the M-cone than 608 L- and S-cone pathways, which may have a retinal, thalamic and/or cortical source. This interpretation is consistent 609 with our finding that gamma-band amplitude decreased on a time-scale of seconds more rapidly for green than red or 610 blue surfaces (Figure 5). We observed several other unique response features for green surfaces consistent with the 611 idea of differential M-cone adaptation: First, we found that gamma oscillations were strongly dependent on luminance 612 for green surfaces in particular, which suggests that a stronger luminance is needed to overcome adaptation (Figure 613 4B). Second, we found that gamma oscillations had a significantly lower peak frequency for green than for red or 614 blue surface stimuli (Figure 4B). This suggests a weaker stimulus drive for green than red surface stimuli, because 615 enhancing stimulus drive has been shown to increase the frequency of gamma oscillations (Hadjipapas et al., 2015; 616 Henrie and Shapley, 2005; Jia et al., 2013b; Ray and Maunsell, 2010; Roberts et al., 2013). Third, with a gray FSB, 617 we found that evoked MU transients were weaker for green than for equiluminant red and blue surface stimuli, which 618 is consistent with increased adaptation of the M-cone pathway. Yet, we found that green stimuli exhibited a weaker 619 decrease in firing over time (Figure 4D), and that the decrease in firing over time was particularly pronounced for red 620 stimuli. 621

622 These findings have two important implications: (1) A gray FSB may differentially change neuronal responses to surfaces of different color hues. This may have implications for the design of studies examining differences in neu-623 ronal or behavioral responses between color hues. (2) Differential adaptation to distinct hues may have consequences 624 for color perception in general. Interestingly, at the psychophysical level, it has been shown that psychophysical after-625 effects emerge more rapidly after viewing green than viewing red stimuli (Werner et al., 2000). Differential adaptation 626 of M-cones may reflect important behavioral requirements of primates. The visual environment of primates is domi-627 nated by green and yellowish stimuli like leaves and trees (Mizokami et al., 2003). Detection of fruits with relatively 628 high energy in red hues may be an important behavioral task for many primates (Melin et al., 2017). Trichomacy pro-629 vides behavioral advantages for such detection (Melin et al., 2017), which may be aided by fast adaptation of M-cone 630 derived signals. 631

632 Differential effects of spatial and temporal context on gamma-band synchronization

This study reports two main findings: When the RF stimulus is part of a larger uniform surface, the spatial context 633 allows a prediction of RF content, and gamma oscillations are enhanced. Yet, when the RF stimulus is part of a 634 longer uniform stimulation period, the temporal context allows a prediction of RF content, and gamma oscillations 635 are reduced. This suggests that the two effects are brought about by different mechanisms. When RF content is 636 spatially predictable, enhanced gamma oscillations are accompanied by reduced firing rates. This pattern of results 637 is highly suggestive of enhanced inhibition (Vinck and Bosman, 2016), and is in line with the prominent role of 638 inhibition in the generation of gamma (see Mechanisms of gamma-band synchronization further below). By contrast, 639 when the RF content is temporally predictable, the pattern of results is more suggestive of an adaptation mechanism 640 leading to a progressive reduction in gamma strength. This part of our results is in line with previous reports from 641 642 crossmodal and auditory studies (Arnal et al., 2011; Todorovic et al., 2011), which found enhanced gamma oscillations 643 for unexpected stimuli. These findings are consistent with an earlier hypothesis, which stated that gamma oscillations should be enhanced for stimuli that generate prediction errors (Bastos et al., 2012). Note that the effects of both spatial 644 and temporal predictability do not necessarily rely on top-down feedback. 645

The relationship of V1 gamma-band synchronization to temporal context may be more complex than suggested 646 by this general conceptual notion, however: Previous studies have shown that when continuous stimulus motion 647 has a large degree of jitter/randomness, either in case of entire video frames or in case of bar stimuli, V1-gamma-648 band synchronization tends to be weak, whereas V1 gamma-band synchronization tends to be strong in cases where 649 stimulus motion is predictable (Kayser et al., 2003; Kruse and Eckhorn, 1996; Vinck and Bosman, 2016). Thus, 650 the notion that V1 gamma-band synchronization increases when stimuli are unexpected or salient given the temporal 651 652 context might apply only to discrete stimulus onsets and not generalize to cases where there is continuous stimulus motion. Furthermore, stimulus repetition can lead to a monotonic increase in V1 gamma-band synchronization over 653 trials (Brunet et al., 2014). This increase of V1 gamma-band synchronization with stimulus repetition may reflect a 654 slower learning process in which spatial center-surround interactions are modified by experience (Vinck and Bosman, 655 2016). 656

657 Mechanisms of gamma-band synchronization

The results discussed above revealed several principles underlying the stimulus dependence of gamma synchro-658 nization. Yet, it remains unclear what precise neuronal mechanisms account for the emergence of V1 gamma synchro-659 nization, and its dependence on center-surround predictability. Previous work indicates that in primate and cat V1, 660 gamma-band oscillations are generated cortically, specifically in the superficial layers of the cortex as well as layer 661 4B (Bastos et al., 2014; Buffalo et al., 2011; Herculano-Houzel et al., 1999; Livingstone, 1996; Xing et al., 2012). 662 Furthermore, they have not been detected in the LGN of awake primates (Bastos et al., 2014). Together with the 663 results presented in this paper, this indicates that the emergence of gamma oscillations in superficial layers depends 664 on the integration of bottom-up inputs from the LGN and layer 4 with contextual information mediated through lateral 665 and top-down feedback. Notably, superficial layers exhibit strong lateral connectivity and are densely innervated by 666 top-down feedback (Barone et al., 2000; Lund et al., 1993; Markov et al., 2014). Within the cortex, the interaction 667 between inhibitory and excitatory neurons likely plays a critical role (Bartos et al., 2007; Buzsáki and Wang, 2012; 668 Cardin et al., 2009; Hasenstaub et al., 2005; Jadi and Sejnowski, 2014; Kopell et al., 2000; Perrenoud et al., 2016; 669 Sohal et al., 2009; Tiesinga and Sejnowski, 2009; Veit et al., 2017; Vinck et al., 2013a; Whittington et al., 1995; Wom-670 elsdorf et al., 2014). Specialized electrophysiological sub-classes of pyramidal neurons like chattering (fast-rhythmic 671 bursting) cells, which have resonant properties in the gamma-frequency band, could also be a critical component of 672 gamma rhythmogenesis (Cardin et al., 2005; Gray and McCormick, 1996; Nowak et al., 2003). Tangential, excita-673 tory connections linking preferentially columns with similar feature preferences (e.g. color or orientation) may play 674 a crucial role in synchronizing neuronal assemblies coding for related features (Gray et al., 1989; Korndörfer et al., 675 2017; Vinck and Bosman, 2016). A stimulus with high spatial predictability is likely to simultaneously activate a large 676 number of preferentially coupled columns. This could then give rise to enhanced cooperativity among these columns 677 678 and boost gamma synchronization by the recruitment of local excitatory and inhibitory neurons. In addition, feedback from higher visual areas could be critical, considering that the spatial spread of tangential connections is somewhat 679 limited and covers a smaller surround region than cortical feedback (Angelucci et al., 2017). 680

681 Functions of gamma-band synchronization

We finish with a discussion of the functional implications of the present findings. Early theories of gamma syn-682 chronization proposed that it may contribute to solving the "binding problem" (Singer, 1999; Singer and Gray, 1995). 683 This refers to the problem that the visual system segments images into segregated objects, which raises the problem 684 that the local features comprising the object must at some processing stage be bound together. It was proposed that 685 the activity of distributed neurons can be dynamically grouped together through synchrony according to perceptual 686 Gestalt principles (Engel et al., 1992; Milner, 1974; Singer, 1999, 2018; Singer and Gray, 1995; Von Der Malsburg, 687 1994). Notably, functions that have been linked to surround modulation, such as contour integration (Liang et al., 688 2017), perceptual filling-in (Land, 1959; Wachtler et al., 2003; Zweig et al., 2015), and figure-ground segregation 689 (Lamme, 1995), may contribute to perceptual grouping and underlie some of the Gestalt principles. Later work em-690 phasized that gamma synchronization can flexibly regulate communication between neuronal populations (Akam and 691 Kullmann, 2010; Colgin et al., 2009; Fries, 2005; Jia et al., 2013a; Knoblich et al., 2010; Palmigiano et al., 2017; 692 Salinas and Sejnowski, 2001). For example, the communication-through-coherence hypothesis states that communi-693 cation between neuronal populations can be flexibly modulated by selective coherence according to cognitive demands 694

(Fries, 2005, 2015). Recent studies have shown that neuronal groups in distant visual areas show gamma-band coherence primarily when they processes an attended stimulus and that the level of coherence predicts behavioral benefits
of attention (Bosman et al., 2012; Buschman and Miller, 2007; Gregoriou et al., 2009; Grothe et al., 2012; Rohenkohl
et al., 2018).

In the context of efficient and predictive coding and the relationship of V1 gamma with spatial predictability, V1 gamma synchronization may play two functional roles (Vinck and Bosman, 2016), which remain to be tested:

 Gamma synchronization may be a mechanism to increase the effective synaptic gain of V1 neurons on postsynaptic targets (e.g. V2) (Bernander et al., 1991; Fries, 2005; König et al., 1996; Salinas and Sejnowski, 2000, 2001;
 Softky, 1994) when a stimulus is efficiently encoded. This may ensure reliable transmission of V1 outputs even when firing is sparse, which is especially important in the presence of noise within or competing inputs to the receiving area.
 Gamma synchronization could play an important role in coordinating the interactions between distributed V1
 columns receiving related, and thereby redundant, visual inputs. The outputs of these columns need to be synaptically

⁷⁰⁷ integrated, for which gamma synchronization could be a mechanism (Fries, 2005; König et al., 1996)

In sum, the present work provides evidence that visual cortex shows sparse and gamma-synchronized responses when surround stimulation predicts RF center stimulation. In contrast, firing rates are high when the surround does not predict the center. These effects are particularly pronounced in case of chromatic, compared to achromatic surfaces. A second key insight is that the FSB on which surfaces are displayed strongly modulates gamma synchronization, in a way that suggests that uniform surfaces lead to stronger adaptation of the M-cone compared to L-cone pathways. This not only explains differences in gamma-band oscillations between surfaces of different hues, but may also have important behavioral and perceptual consequences, which needs to be explored in future work.

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727 Methods

All procedures complied with the German and European regulations for the protection of animals and were approved by the regional authority (Regierungspräsidium Darmstadt).

730 Surgical procedures

Two male adult macaque monkeys (Macaca mulatta) were used in this study (age 9-10 years, 15-17 kg). All 731 surgeries for implantations were performed under general anesthesia and were followed by analgesic treatment post-732 operatively. A head post was implanted in both monkeys to allow for head fixation. In monkey H, we implanted 733 CerePort ("Utah") arrays with 64 microelectrodes (inter-electrode distance 400 μ m, tip radius 3-5 μ m, impedances 734 70-800 kOhm at 1000 kHz, half of them with a length of 1 mm and half with a length of 0.6 mm, Blackrock Mi-735 crosystems). One such array was implanted into area V1, another one in V4, both in the left hemisphere. The V4 736 array is not considered here. For array implantation, a large trepanation covering both areas was performed, the dura 737 was cut open and reflected, arrays were inserted using a pneumatic device (Blackrock Microsystems), and both dura 738 and bone were surgically closed. A reference wire was inserted under the dura towards parietal cortex. In monkey A, 739 we implanted a semi-chronic microelectrode array Microdrive into area V1 of the left hemisphere (SC32-1, Gray 740

Matter Research, containing 32 independently movable Alpha Omega glass insulated Tungsten electrodes with an 741 impedance range of 0.5-2 MegaOhm and an inter-electrode distance of 1.5 mm). The microdrive chamber was used 742 as the reference during recordings. The precise layers/depths that were recorded from could not be identified based 743 on histological verification, which is the current gold-standard, because the animals are still alive. However, based on 744 the observation that all sites in monkey H and the vast majority of sites in monkey A do not show the typical inversion 745 of the event-related potential as is found in the deep layers (Li et al., 2015), we estimate that our recordings mainly 746 sample activity from layers 2-4. Sites in monkey A and monkey H behaved qualitatively in a consistent manner across 747 748 depths, such that all recording sites were pooled.

749 Behavioral task

Both monkeys were trained on a fixation task. Monkeys were seated in a custom-made primate chair in a darkened 750 booth. The two animals were positioned 83 (monkey H) or 64 cm (monkey A) in front of a 22 inch 120 Hz LCD 751 monitor (Samsung 2233RZ, (Ghodrati et al., 2015; Wang, 2011). Both monkeys self-initiated trials by fixating on a 752 small fixation spot, which was presented at the screen center. Monkey H performed a pure fixation task. For monkey H, 753 the fixation spot was a Gaussian with a white center, tapering smoothly into the background. For recordings with white 754 background, the fixation spot color was changed to red. Note that the pattern of results for gray and white FSBs was 755 very similar despite this difference (Figure 6-figure supplement 2), and that receptive fields were not covering the 756 fovea. The task of monkey A was to report a change in the fixation spot from red to green or blue (randomly) with 757 758 a lever release. The change in the fixation spot occurred only after the stimulus period and an additional 700 ms of background stimulation, during which the animal maintained fixation. For the recordings with colored backgrounds 759 in monkey A, fixation colors were changed to remain visible, with a magenta fixation spot during the baseline and 760 stimulus period. For both animals, trials during which the eye position deviated from the fixation spot by more than 761 0.8-1.5 visual deg radius were aborted. Correctly performed trials were rewarded with diluted fruit juice delivered 762 with a solenoid valve system. 763

764 Recordings

Data acquisition was performed using Tucker Davis Technologies (TDT) systems. Data were filtered between 0.35 and 7500 Hz (3 dB filter cutoffs) and digitized at 24.4140625 kHz (TDT PZ2 preamplifier). Stimulus onsets were recorded with a custom-made photodiode. Eye movements and pupil size were recorded at 1000 Hz using an Eyelink 1000 system (Eyelink Inc.) with infrared illumination. Eye signals were calibrated before each recording session using a standardized fixation task. Behavioral control and stimulus presentation was done using in house custom software running in Matlab, including ARCADE (Dowdall et al., 2018).

771 Visual stimulation paradigms during recordings

For all paradigms, stimuli were circular, did not have overlap with the fixation spot, and typically spanned a region from ca. 3-9 deg of eccentricity (monkey H) or 2.5-8.5 deg (monkey A, maximum: 1.6-9.6 deg for *Dataset 4*) in the lower right visual quadrant, matching RF locations. Trials always started with a baseline that lasted 0.5-0.6 s (monkey H) or 0.5-0.8 s (monkey A), and during which only the FSB and the fixation spot was shown. We used the following stimulus paradigms:

Dataset 1: For Figure 1, 4B and 5, we presented large uniform stimuli of 6 deg visual angle diameter on a gray FSB. For the chromatic condition, we used stimuli that were either green, red, or blue, at three different luminance levels (which are shown in Figure 4). For Figure 1, only the chromatic conditions with the highest available luminance level were used, approximately corresponding to the maximum possible luminance level for the blue primary. For the achromatic condition, we used either black (minimum luminance) or white (maximum luminance) stimuli.

The background was of an intermediate gray value that allowed for good eye tracking quality (see Table S1 for all luminance, RGB and CIE values). Stimulus duration was 3.3 s. This dataset included 3 sessions from monkey H and 2 sessions from monkey A. There were 20 ± 0 (H) and 20 ± 0 (A) trials in each session for each of the 11 conditions (2 color hues * 3 luminance levels + black and white). *Dataset 2*: For Figure 2, i.e. the size tuning paradigm, we presented a smaller (either 0.5, 1, or 2 deg) stimulus and a larger (6 deg) surface stimulus in the same trial sequentially, with each stimulus presented for only 0.6 s. In each trial, either the smaller ("small-first") or largest ("large-first") surface was presented first. In addition, we used an "edge" condition in which the selected multi-unit's RF was centered around the vertical edge of the 6 deg stimulus, again followed or preceded by the standard full condition
(Figure 3-figure supplement 1). The colors used were red, blue and green (at the same luminance intensities shown
in Figure 1), black and white, and in case of monkey H, also orange, cyan and magenta hues. This dataset included 5
sessions from monkey H and 4 sessions from monkey A. There were 12.78±4.3 (H, 64 conditions) and 12.86±5.4 (A,
40 conditions) trials in each session for each of the conditions (4 stimulus sizes * 2 presentation orders * 8/5 colors
(H/A)).

Dataset 3: For Figure 3, we used only red, green and blue hues (with the same luminances as the maximum 795 luminant red, green and blue used in Dataset 1, Figure 1). We presented three stimulus conditions: The uniform 796 surface, the "annulus" and the "blob" condition (Figure 3). Stimuli in annulus or blob conditions were of the same 797 size as the uniform surface, but the center 1 deg of the surface was either surrounded by a thin (0.25 deg) annulus 798 of one of the other, equiluminant, hues, or filled completely with one of the other hues (Figure 3). For each surface 799 of a given hue, there were therefore two "annulus" and "blob" conditions with the two remaining colors (Figure 3). 800 In the analysis, we averaged over all the color combinations for a given condition, and compared the three main 801 conditions. For monkey H, we additionally recorded two sessions with maximally luminant instead of equiluminant 802 hues. Note that this generated strong luminance contrast changes between the colors, but yielded qualitatively similar 803 results. This indicates that the observed effects do not depend on equiluminance, a condition that may occur rarely 804 in nature. Because results were qualitatively similar, we pooled these sessions with the remaining 5 sessions of this 805 animal. We used stimulus presentation times of 1.3-3.3 s. The first 1.3 s were analyzed, as in Figure 1. This dataset 806 included 7 sessions from monkey H and 1 session from monkey A. There were 15.88±0.21 (H) and 18.87±0.34 (A) 807 trials in each session for each of the 15 conditions (3 uniform conditions + 3 color hues * 2 color hues for mismatch 808 * 2 (annulus vs blob mismatch)). Dataset 4: For Figure 4A, we recorded "rainbow" sessions in which surfaces 809 (again 6 deg diameter size) of different colors were presented at the maximum possible luminance. We sampled the 810 visible light spectrum linearly in 15 steps of equal size in terms of wavelength, with the MATLAB (MathWorks, Inc.) 811 internal function spectrumRGB.m. Note that the monitor cannot produce line spectra, but can only approximate the 812 corresponding hues through mixing of RGB channels (see e.g. Figure 7A for a yellow hue). We additionally included 813 brown and pink (extra-spectral) hues (see Table S1 and Figure Figure 4-figure supplement 1) and achromatic stimuli. 814 For the analyses shown in Figure 4B, we used Dataset 1. This dataset included 3 sessions from monkey H and 2 815 816 sessions from monkey A. There were 12.1 ± 6.9 (H) and 20 ± 0 (A) trials in each session for each of the 22 conditions. Dataset 5: For Figures 6 and 7, we used FSBs of various hues. The backgrounds used were red, green, blue and yellow 817 at maximum possible luminance, as well as black, white and gray, presented at the same luminance intensities as in 818 the other datasets. Surface stimuli of 6 (monkey H) or 8 (monkey A) deg diameter in size were used. The size was 819 slightly increased for monkey A to place the edge of the surface stimulus further from the most peripheral RFs. The 820 hues used for the surface were identical to the ones used for the FSBs. In addition, we presented chromatic surfaces 821 with reduced values, namely red, green and blue with the same luminance levels as in Figure 1, and a brown surface. 822 All possible combinations of surface and FSB hues were shown. All other presentation parameters were kept as for 823 Dataset 1. 824

For all stimulus paradigms for monkey A, and in Dataset 5 for monkey H, there was a post-stimulus period of 825 826 0.7 s (0.5 s in monkey H) after the offset of the stimulus, during which the monkeys was required to maintain fixation. For monkey A, the fixation color would change after this period and the monkey had to respond to this change with 827 the release of a lever, whereupon the fixation spot was removed. Presentation of different stimulus conditions was 828 in a pseudo-random order. Typically, 15-20 correctly performed repetitions per condition and session were collected 829 (see also Figure captions for trial numbers). This dataset included 16 sessions from monkey H and 9 sessions from 830 monkey A (1-2 per FSB). There were 17.89±0.17 (H) and 19.00±0.08 (A) trials in each session for each of the 11 831 conditions. 832

833 DKL Color Space

In order to calibrate the monitor outputs, the luminance of the RGB monitor primaries were measured with Konica Minolta CS-100A chroma meter and look-up tables were generated. Monitors were gamma-corrected to linearize the dependence of luminance on RGB values.

The Derrington-Krauskopf-Lennie (DKL) Color Space was introduced as a color-opponent modulation space (Derrington et al., 1984; Krauskopf et al., 1982). DKL color space is based on a cone-contrast representation, where cone activation to a color stimulus is quantified as the relative change of the cone activations with respect to the back-

ground color (Brainard, 1996). Weber cone-contrasts are computed in three steps: 1) The change in cone-activation

relative to the full-screen background is computed, 2) This change in cone-activation is normalized (divisively) by the extent to which the background differentially activates the different cones (Brainard, 1996). These cone contrasts are

then transformed into 3 primary axes of the DKL space, which correspond to the mechanisms of L+M (luminance),

LM (red-green opponency), and S-(L + M) (blue-yellow opponency). Along the L-M axis, maximum L/M cone con-

trasts were 9.60% and 14.81% respectively, along the S-(L+M) axis S cone contrast was 79.35%. These values were

found to be similar to previous studies (De Valois et al., 2000; Hansen and Gegenfurtner, 2013)

847 Data analysis

Preprocessing. Data were analysed in MATLAB using the FieldTrip toolbox (Oostenveld et al., 2011). Only 848 correctly performed trials were analyzed. LFPs were derived from the broadband signal using MATLAB's deci-849 mate.m function, by low-pass filtering with a cutoff frequency of 24414.0625/24/2 Hz (FIR Filter with order 30) and 850 downsampling to 24414.0625/24 Hz. Line noise was removed using two-pass 4th order Butterworth bandstop filters 851 between 49.9-50.1, 99.7-100.3 and 149.5-150.5 Hz. LFPs had a unipolar reference scheme described in Recordings. 852 Explorative analyses with local bipolar derivations, obtained by subtracting the signals from immediately neighboring 853 electrodes from each other, yielded comparable results (data not shown). MU signals were derived from the broad-854 band signal through bandpass filtering between 300 and 6000 Hz (4th order butterworth), rectification, and applying 855 low-pass filtering and downsampling the same way as for the LFPs. For the calculation of rate modulations, this MU 856 signal was smoothed with a Gaussian kernel with an SD of 20 ms. Qualitatively similar results were obtained using 857 thresholded multi-unit data. We used this MU signal for all analyses in the main text, as in previous studies by other 858 labs (Legatt et al., 1980; Schmid et al., 2013; Self et al., 2013; Xing et al., 2012). 859

Receptive field estimation. Receptive fields were mapped with moving bar stimuli (spanning the entire monitor). 860 Moving bars (width 0.1 deg, speed 10/17 deg/s) were presented in 8 orientations for monkey H and 8-16 orientations 861 for monkey A, each for 10-20 repetitions. Mapping sessions were intermittent for monkey H and typically daily for 862 monkey A, to confirm stability of the recordings. MU responses were projected onto the stimulus screen, after shift-863 correction by the response latency that maximized the back-projected response. MU responses were then fitted by a 864 865 Gaussian function. This Gaussian was used to extract the 10th percentile and the 90th percentile, and this was done separately for each movement direction. Across the 16 directions, this yielded 32 data points, which were fit with 866 an ellipse. This ellipse was defined as that MU's RF. The RF size is defined as the diameter based on (area of the 867 ellipse/pi)*2. 868

Electrode selection. We included all electrodes for analysis that met the following criteria: (1) the MU showed a response to RF stimulation that was at least two SDs above stimulation outside the RF. (2) The MU response during the response period (0.05-0.15 s) of at least one condition of the respective dataset was at least 2 SD above the corresponding baseline (-0.1-0 s). In case of Figures 2-3, it was additionally required that the RF center of the MU was within 0.5 deg of the stimulus center. In the remaining figures, it was required that the RF center was within the surface stimulus.

Estimation of LFP power spectra. For Figures 1, 3-4 and 6-7, the baseline period was the last 500 ms before stimulus onset, and each stimulation period yielded two non-overlapping epochs of 500 ms (0.3-1.3 s period). For Figure 2, due to the short presentation times, we used epochs of 300 ms (300-600 ms after the onset of the stimulus, and for baseline 300 ms before stimulus onset). LFP epochs were multiplied with discrete prolate spheroidal sequences (multi-tapers for ± 5 Hz smoothing), Fourier transformed and squared to obtain LFP power spectral densities (for a recent discussion on spectral estimation see Pesaran et al. (2018)). For Figure 5, we used windows of 0.3 s length, slid over the data in steps of 50 ms. Data were multiplied with a Hann taper before Fourier transformation.

Normalization of LFP power spectra. To show LFP power changes, we computed relative power spectra by dividing single-trial power spectra from the stimulation period by the average power spectra across conditions and trials from the baseline. This was shown as a fold-change in all figures showing relative changes except for Figure 5 TFRs, where for visualization purposes, we transformed this into dB units.

To investigate absolute LFP power (without reference to the baseline), we normalized power spectra per electrode by the total power above 25 Hz in the baseline condition. This normalization reduced variance or scaling in the LFP power spectra across sessions and animals before averaging. By normalizing both the baseline and the stimulus period by the same normalization factor, we could still examine changes in raw LFP power across conditions, for each frequency bin separately. This would not have been possible if we had normalized the LFP power spectrum in a given condition by the total power across frequencies in the same condition. These power spectra were averaged across the selected channels (except for single-channel analyses as in Figure 1-figure supplement 2).

Quantification of LFP gamma-band amplitude. Quantification of the differences in gamma-band amplitude between conditions is in general a difficult problem because changes in firing rate can cause broad-band shifts in the LFP power spectrum, and because spikes can "bleed-in" at higher LFP frequencies (Buzsáki et al., 2012; Miller et al., 2009; Pesaran et al., 2018; Ray and Maunsell, 2011). We developed an algorithm to extract gamma-band amplitude in order to address these problems (see neuronal for an illustration). We present two versions of this algorithm that are used for separate figures, and are based on constructing a polynomial fit of the LFP spectrum which was detrended in two separate ways. The first algorithm had the following structure:

- Power spectra were log-transformed and the frequency axis was also sampled in log-spaced units to avoid overfitting of high-frequency datapoints. All subsequent polynomial fits were performed on the 20-140 Hz range.
- 902 2. We used the change in stimulus-induced LFP power versus the common baseline (see above), expressed as 903 $\Delta P = \log(P_{stim}) - \log(P_{base})$
- 3. To determine the polynomial order, we used a cross validation procedure to prevent overfitting. A random half of the trials was used for the fitting and deemed the "training set". The remaining trials were the "test set". Polynomials of order 1-20 were fit to ΔP as a function of frequency for the "training set", minimizing the mean squared error. We then computed the mean squared error using the same polynomial fit on the "test set" for each of the 20 orders. This procedure was then repeated for multiple (50) iterations, with a random half of the trials selected for each iteration, and for each iteration, the best-performing order was retained.
- 4. A polynomial with the median of the best-performing orders was then fit to the complete set of trials.
- 5. On the polynomial fit, local maxima and minima in the 30-80 Hz range were identified. The peak gamma frequency was the location of the maximum. The band-width of gamma was estimated as twice the distance between the frequency of the maximum (F_{max}) and the frequency of the first local minimum to the left of the maximum (F_{min}), i.e. $b = 2F_{max} - F_{min}$ (neuronal). The gamma amplitude was then assessed from the difference between the value of the polynomial fit at the maximum and the average of the polynomial fit at F_{min} and $F_{max} + F_{min}$ (neuronal).
- 6. This difference was taken in log-space (because the power spectra were originally log-transformed) and then
 transformed to a fold-change.

If firing rate changes relative to baseline (or between conditions) were very strong, e.g. with small stimuli, this 919 fitting procedure occasionally ran into problems, because relative LFP power spectra showed broad increases that were 920 likely due to non-rhythmic processes like spikes or postsynaptic potentials (see Figure 3 for an example of this effect). 921 In addition, in Figure 6 and 7, because we used background stimuli of different hues, a "neutral baseline" like the gray 922 background screen was not always available. In these cases we modified the second step of this algorithm. Instead 923 of computing the change in LFP power relative to baseline, we performed a $1/F^n$ correction on the raw LFP power 924 spectrum. The 1/Fⁿ correction was performed by fitting an exponential to the LFP power spectrum, excluding data 925 points in the typical gamma range of 30-80 Hz. Note that we fitted an exponential function because in many cases, 926 927 bleed-in of spiking energy in the LFP caused a departure from a linearity in the log(power) versus log(frequency) graph (see also Haller et al. (2018); Shirhatti and Ray (2018)). We visually inspected the fits for a large number of 928 spectra and compared this also to a procedure with a mixture of a linear fit and a Gaussian fit to the log(power) versus 929 log(frequency) graph, which had substantially more problems in dealing with spike-bleed at high frequencies, as well 930 as with additional peaks (potentially harmonics) at higher frequencies (e.g. for the red surfaces) (data not shown). 931

Spike-field coherence. For spike-field coherence, we used only electrodes selected by the procedure described 932 above. In addition, for LFP-MUA pairs, we required that the electrodes were direct neighbors in the grid, and in the 933 case of monkey H, given that the microelectrode array had two fixed depths, were of the same depth. Spike-field 934 phase-locking was computed as follows. We estimated the cross-spectral density between LFP and MU signal for 935 each trial separately (cross-spectra) using the same spectral estimation settings as for the LFP power spectrum. This 936 937 yielded one cross-spectrum per trial. We then normalized the cross-spectrum per trial by its absolute values, to obtain 938 the cross-spectral phases (without amplitude information). We used those normalized cross-spectra to compute the Pairwise Phase Consistency (PPC), using FieldTrip (Oostenveld et al., 2011). This measure has the advantage that 939 the bias by trial count, inherent to e.g. the spectral coherence, is avoided (Vinck et al., 2010b). For a given MU site, 940

the PPC values were then averaged across all the combinations with LFPs from the other selected channels. Note that MU-LFP combinations from the same electrode were excluded to avoid artifactual coherence due to bleed-in of spikes into the LFP (Buzsáki et al., 2012; Ray and Maunsell, 2011). Because of the distance between electrodes (at least 400 micrometer), this was not an issue for MU-LFP combinations from different electrodes.

The standard error of the PPC was estimated across sessions. This was different from SE estimation for power and rate, which used the bootstrap (see below). Bootstrap estimates are problematic for PPC because bootstraps contain repetitions of identical trials, which trivially yield high coherence values.

Rate modulation. Rate modulation was computed as $\log_{10} M_{stim}/M_{base}$, where M_{stim} and M_{base} represent the MU firing activity in the stimulus and baseline period, respectively. To quantify surround suppression, we took the differences of these rate modulation indices between small and large stimulus size conditions.

Modulation index of fold-changes To quantify the modulation of LFP gamma-amplitude (expressed as foldchange) between conditions (Figure 5, 6), we computed a modulation index as (A - B)/(A + B), where A and B are the gamma-amplitudes in the two conditions, taken as the fold-change minus 1. Note that the fold-change was extracted using the polynomial fitting procedure described above, and a fold-change of 1 indicated the absence of a gamma peak.

Microsaccade detection and subsequent LFP analysis. For microsaccade detection, we smoothed horizontal and 956 vertical eye signals (rectangular window of ± 5 ms) and differentiated the signals over time points separated by 10 ms to 957 obtain robust eye velocity signals. For monkey H, for whom data from both eyes were available, data were averaged 958 across eyes. We then used the microsaccade detection algorithm described in Engbert and Kliegl (2003) with a 959 velocity threshold of 6^*c , where c is the criterion defined as $c \equiv \text{Median}[v^2] - (\text{Median}[v])^2$. Threshold crossings 960 in either the horizontal or vertical direction were considered as microsaccades. We tested several threshold levels 961 and obtained qualitatively similar results. We then removed data epochs of 100 ms after each microsaccade and 962 recomputed our analyses (based on Lowet et al. (2016); 100 ms is approximately the duration of microsaccade effects 963 in V1). Removing 200 ms after each microsaccade yielded qualitatively similar results but fewer remaining epochs. 964 For the analysis of LFP gamma amplitude, we switched to analyzing epochs of 100 ms using a Hann taper, instead of 965 the 500 ms time bins used before. This is sacrificing some frequency resolution and limiting the results to frequencies 966 >20Hz, in order to obtain a large number of microsaccade-free epochs. Epochs were zero-padded to 1s, effectively 967 968 smoothing the spectra. Note that we show the results for the data including microsaccades with the identical epoch length and taper to allow a fair comparison. 969

Pupil responses. Pupil signals across the two eyes were averaged for monkey H. Pupil size during the comparatively stable period 200ms to stimulus onset was used as a baseline. Pupil size was then computed as percent change from the average response during this time (A-B)/B, where A is the pupil response at each time point and B is the average response during the baseline period. Note that since the Eyelink system gives outputs with arbitrary units, and these were negative during the baseline period, we took the absolute value for the denominator such that pupil size decreases are indicated by negative values.

976 Statistics

Error bars or shaded error regions correspond to \pm one standard error of the mean (SEM). SEM was estimated 977 using a bootstrap procedure, with the exception of spike-field coherence (see above). For the b-th bootstrap out of 978 B = 1000 bootstraps, $b = 1, \dots, B$, the following was done. For each condition in a given session, with a set of N 979 trials \mathcal{T} , we took a random set of N trials from \mathcal{T} with replacement, yielding a new set of trials \mathcal{S}_b . For that sample 980 of N trials S_b , we then computed the statistic of interest. For LFP signals, we then computed the average statistic 981 in a given session over all channels, then averaged over sessions, and then monkeys. The rationale behind averaging 982 across all LFP channels was that these signals are likely highly statistically dependent because of volume conduction 983 among the relatively closely spaced electrodes. For MU signals, we computed the average statistic of interest across 984 sessions per MU site separately, and then averaged across all recording sites. The standard error of the mean was then 985 defined as the standard deviation over the B average statistics, as is common with bootstrapping procedures. 986

We used the bootstrap distributions for inference on fold-change estimates or fold-change modulation indices between conditions, as well as differences in peak gamma frequency. In this case, we computed for each bootstrap the difference between average statistics for two conditions, and then tested whether this distribution was different from zero (with Bonferonni correction for number of comparisons).

For frequency- or time-resolved differences (in absolute and relative LFP power spectra and rate modulation 991 scores), we used multiple-comparison corrected permutation tests: In this case, we shuffled the trials between two 992 conditions per permutation P times, and then constructed a permutation distribution of average absolute differences 993 between conditions. We equalized trial numbers for each comparison, for example between chromatic/achromatic 994 conditions or the different stimulus sizes. We then compared the observed difference between average statistics against 995 this permutation distribution. For multiple-comparison correction, we used the procedure from Korn et al. (2004), 996 which is based on the sorted distribution of absolute differences, with alpha and false discovery rate values of 0.05. 997 998 In this iterative procedure, values in the observed distribution exceeding the 95th percentile of the P maximal values of each permutation distribution (critical value) are deemed significant. Significant values are removed from the 999 observed distribution, and the same positions are removed from all P permutation distributions. Values in the observed 1000 distribution exceeding the critical value based on these permutation distributions are then iteratively collected until no 1001 value in the observed distribution exceeds the critical value. Note that statistical parameters are reported mostly in the 1002 figure captions. 1003

Quantitative model for dependence of gamma-band amplitude on background stimulus 1004

Cone data were extracted from Hárosi (1987) (bleaching difference corrected spectra). Polynomials of order 7 1005 were fit to these curves. The cone response curves were then normalized to the maximum. We measured the spectral 1006 energy of each color as well as black, white and gray (Ocean Optics WaveGo; XWAVE-STS-VIS-RAD). The spectral 1007 1008 energies of the colors were normalized to unit mass. For gray, we added the normalized energies of R, G and B and multiplied with the energy ratio of gray over white. We then convolved the cone response curves with the normalized 1009 1010

spectral energies to determine how strongly each background adapts the three cones. Regression models were then fit as explained in the Results text and caption of Figure 7. SEM for regression coefficients are obtained by the same

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bootstrap procedure as described above. 1012

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Figure 1: Analysis of LFP and multi-unit activity in response to large, uniform surfaces. (A) Illustration of experimental paradigm with large, 6 deg diameter surfaces (*Dataset 1*, see Methods; n = 5 sessions, 60 ± 0 trials per session for chromatic and 40 ± 0 trials per session for achromatic conditions. Trials numbers were euqated by random subselection for statistics.). Trials were self-initiated by fixating on the fixation spot (enlarged for visibility), followed by a baseline period of 0.5-0.8 s with a gray background screen. Surfaces were either chromatic (red, blue, or green) or achromatic (black or white) and presented for 3.3 s, the first 1.3 s of which are analyzed here. Right panel shows the RF locations of analyzed sites in one session. (B) Representative trials of LFP signals for achromatic (and chromatic conditions (having gamma power close to the median of the respective condition). (C) Average LFP power spectra for chromatic (turqoise), achromatic (black) and baseline (gray) conditions. LFP power was estimated using Discrete Fourier Transform of non-overlapping epochs of 500 ms, with multi-tapering spectral estimation (± 5 Hz). LFP spectra for all three conditions were normalized to the summed power (>20 Hz) for the baseline (gray) condition (see Methods). (D) Average change in LFP power, expressed as fold-change, relative to baseline. (E) Average MU-LFP locking, which was estimated using the pairwise phase consistency (PPC, see Methods). (F) Modulation of firing rate relative to baseline, expressed as $log_{10}(stim/base)$. (D-F) Shadings indicate standard errors of the means obtained with bootstrapping (see Methods). Gray bars at bottom of figure indicate significant differences between chromatic and achromatic stimuli, obtained from permutation testing with multiple comparison correction across all frequencies and time points (see Methods).



Figure 2: Dependence of LFP power spectra and MU firing activity on surface size. (A) Illustration of experimental paradigm (*Dataset 2*, see Methods; n = 9 sessions, 59.75±0.09/25.64±0.12 trials chromatic vs achromatic trials per condition in each session). Uniform surfaces of four different sizes were presented on a gray background screen. Fixation spot is enlarged for visibility. Right: Receptive field estimated with bar stimuli for a representative target channel, with the outline (orange dashed line) of the largest size stimulus (see Methods). Note that the activation outside the RF is due to the use of large bar stimuli sweeping over the monitor. (B) LFP power spectra for different sizes and chromatic/achromatic conditions. LFP power spectrum estimated and normalized as in Figure 1C, but now using 300 ms epochs. Right panel shows the gamma-band amplitude as a function of size, estimated using a polynomial fitting procedure between 30-80 Hz (see Methods). The difference between 6 and 0.5 deg stimuli was significantly larger for chromatic than achromatic condition (P<0.05, bootstrap test, see Methods). (C) Modulation of firing rate relative to baseline, expressed as $log_{10}(sim/base)$, for different sizes and chromatic/achromatic conditions. Right panel shows surround suppression, which was defined as the difference in firing rate modulation between the 0.5 degree size and the other sizes.



Figure 3: Dependence of LFP power spectra and firing rates on spatial predictability. (A) Illustration of paradigm (*Dataset 3*, see Methods; n = 8 sessions, 16.26±0.19 trials in each of the 15 conditions per session). We grouped stimuli intro three types. In the "Uniform surface" group of conditions, stimuli of 6 deg diameter were presented with either a red, blue or green hue (R B G, equiluminant). In the second "blob mismatch" group, the central 1 deg of the stimulus had a different (equiluminant) color than the rest of the stimulus. In the third "annulus mismatch" group, we presented an annulus ring (of 0.25 deg) of another color on top of the uniform surface (at equiluminant intensity) around the inner 1 degree from the stimulus center. All combinations of hues and stimulus types were presented, yielding a total of 15 individual conditions. (B) Representative LFP traces (having gamma power close to the median of all trials for the respective condition) for the three stimulus types. (C) Analysis for target channels with RFs at the center of the stimulus. Shown from left to right are: (1) The change in MU firing activity relative to baseline expressed as $log_{10}(stim/base)$. (2) LFP power spectra for the three stimulus conditions and the baseline. LFP power spectrum estimated and normalized as in Figure 1C. (3) The change in LFP power relative to baseline, expressed as a fold-change. (4) The gamma-band amplitude, estimated using a polynomial fitting procedure (see Methods). Gamma-band amplitude was significantly higher for uniform surface than blob and annulus conditions (C), bootstrap test, see Methods). (D) Same as (C), but now for target channels with RFs between 1.5 and 2 deg from the stimulus center, i.e. close to the central region of the larger, uniform region of the stimulus. Gamma-band amplitude did not significantly differ between conditions (bootstrap test, all P>0.08).



Figure 4: Dependence of LFP power spectra and MU firing activity on surface hue and luminance. (A) We presented uniform surfaces of 6 deg at maximum possible luminance levels, sampling from the available spectrum of wavelengths (*Dataset 4*, see Methods; n = 5 sessions, 15.24±0.1 trials per condition in each session). In addition, we presented black and white surfaces. Shown is the change in LFP power relative to the baseline (gray screen), expressed as a fold-change. (B) Three hues (red, green and blue) were presented at three different luminance levels (approximately 2.5, 5 and 10 cd/m², *Dataset 1*, see Methods; n = 5 sessions, 19.8±0.45 trials per condition in each session). Shown are LFP power spectra. LFP power spectrum estimated and normalized as in Figure 1C. (C) Average change in LFP power, expressed as a fold-change, relative to the baseline (gray screen). The dependence of gamma amplitude on stimulus luminance was greater for G than for R or B (difference between high versus low: P<0.05, bootstrap test). Gamma oscillations amplitude R>B or G across all three luminance conditions, and B>G surface stimuli for low and intermediate luminance conditions (P<0.05, bootstrap test). (D) Modulation of firing rate relative to baseline, expressed as $log_{10}(stim/base)$. Horizontal bars at bottom of panel represent significant differences between stimuli at P<0.05 (permutation test, multiple comparison corrected for time bins). (B-D) Color hues were adjusted for better discriminability, panel A of Figure 4-figure supplement 2 shows actual hues.



Figure 5: Within-trial temporal dynamics of LFP power spectra during viewing of uniform surfaces. Time-frequency representations of logtransformed change in LFP power relative to baseline (dB), using *Dataset 1* (n = 5 sessions, 19.8±0.45 trials per condition in each session). Shown are the three (equiluminant) different color hues at three different luminance levels. (B) Change in LFP power relative to 0.3-0.6 s period (third time point), separate for different color hues and luminance levels, shown as fold-change modulation index (see Methods). The first two points correspond to 0.05-0.35 and 0.1-0.4 s and are whitened out because these points are strongly influenced by initial firing transient and associated bleed-in of spiking activity at high frequencies. Right panel shows the modulation of LFP power in early (0.3-0.6 s) versus late (2.7-3.0 s) period, averaged over three luminance levels. The decrease in gamma peak amplitude over time was significantly larger for green than blue and red surfaces (peak amplitude estimated as described in Methods, main effect across luminance levels: P<0.05, bootstrap test), and did not differ between blue and red conditions. This also held true for the modulation of LFP power for the highest luminance condition only (P<0.05, bootstrap test).



Figure 6: Dependence of LFP power spectra on background stimulus. (A) Illustration of paradigm (*Dataset 5*, see Methods; n = 25 sessions, 18.64±0.11 trials per condition and session). In a given session, a fixed background stimulus was used, and a set of chromatic and achromatic surfaces (6 or 8 deg) were presented in separate trials (see Methods). (B) Average LFP power spectra for the different color conditions during gray background versus same-hue background sessions. We show analyses for blue, green, yellow, and red surfaces, presented at maximum possible luminance. Right: modulation index of LFP gamma-amplitudes (see Methods). Main effect: P<0.05, bootstrap test. R versus G, B or Y, and G versus B: P<0.05, bootstrap test. (C) As B) for comparison of opponent color background and black background condition Main effect: P<0.05. B versus R, G or Y, P<0.05. (D) black background versus gray background. Main effect not significant. All color differences significant (P<0.05, bootstrap test). (E) Modulation of gamma-band amplitude for same-hue vs black background condition (left), as well as opponent-hue vs black background condition (right). Left: P<0.05: R versus G, B or Y; B versus G or Y Right: P<0.05: all combinations except G versus Y. (F) Comparison of gamma-band responses between chromatic surfaces shown on achromatic background and achromatic surfaces shown on the same respective chromatic background (using the data shown in Figure 6-figure) supplement 2).



Figure 7: Quantitative model for dependence of gamma-band amplitude on background stimulus. (A) With a multiple regression model we predicted the ratio of gamma amplitude for red over green surface stimuli. Shown are the LFP gamma power spectra for red (top) and green (bottom) surface stimuli, with a yellow FSB. Normalized cone responses for macaque monkeys are shown on the right, constructed by fitting polynomials to bleaching difference spectra data (Hárosi, 1987). For each full-screen background (FSB) we estimates the extent to which it adapted the three cones (M_{adapt} , L_{adapt} and S_{adapt} ; see Methods), by convolving the spectral energy of the FSB with the normalized cone response curves. For illustration purposes we only show the M- and L-cone response curve. (B) The hues of the data points correspond to the FSB, and the shape indicates whether the red and green surfaces were presented at maximum possible luminance intensity (circle), or whether they were presented at equiluminant intensities (diamond). As predictor variables we used M_{adapt} and L_{adapt} for the different FSBs. The dependent variable was the red/green gamma-ratio, γ_{ratio} . The coefficients indicates the relative influence of the two adaptation parameters on the γ_{ratio} , and the sign indicates whether adaptation of a given cone is increasing or decreasing the red/green gamma-ratio. (C) Similar to (B), but now for blue-yellow. In this case we used S_{adapt} and L_{adapt} and L_{adapt} as prediction parameters. A model using M_{adapt} in addition did not yield a significant coefficient for M_{adapt} .

Supplementary Legends

Fig 1-figure supplement 1

Illustration of fitting procedure. (A) Average LFP power spectra for a large chromatic condition of an example session used in Figure 2. LFP spectra for all conditions were normalized to the summed power (>20 Hz) for the baseline condition (see Methods). (B) Log-transformed, 1/Fⁿ corrected spectra (solid line) and their fit (dashed line). Peak height was determined as the difference between the peak value at location Fmax and a baseline estimate based on the average of the power at location Fmin and Fmin+2*(Fmax-Fmin), the estimate of peak width.

Fig 1-figure supplement 2

Analysis of LFP and multi-unit activity in response to large, uniform surfaces. (A) Average LFP power spectra for chromatic (turquoise), achromatic (black) and baseline (gray) conditions. LFP power was estimated using Discrete Fourier Transform of non-overlapping snippets of 500 ms with a Hanning taper. LFP spectra for all three conditions were normalized to the summed power (>20 Hz) for the baseline (gray) condition (see Methods). (B) Average change in LFP power, expressed as fold-change, relative to baseline. (C) Scatter-plot for all the LFP recordings sites in two monkeys, showing the gamma-band amplitude (expressed as fold change) in chromatic and achromatic conditions. (D) Average LFP power spectra for chromatic (turquoise), achromatic (black) and baseline (gray) conditions for monkey A, using same estimation settings and normalization for power spectral density as in Figure 1 of main text. (E) Average change in LFP power, expressed as fold-change, relative to baseline. (F) Modulation of firing rate relative to baseline, expressed as log₁₀ (stim/base), for monkey A. (G-I) as (D-F), but now for monkey H. (A-I) Shadings and error bars indicate standard errors of the means (see Methods). Gray bars at bottom of figure indicate significance bars, obtained from permutation testing with multiple comparison correction across all frequencies and time points.

Fig 1-figure supplement 3

Control analysis for microsaccades. (A) Average LFP power spectra and rate modulation for chromatic (turquoise), achromatic (black) and baseline conditions, separately for data epochs defined irrespective of microsaccades (top) and epochs excluding 100 ms after each microsaccade. Microsaccade detection was based on the algorithm of Engbert and Kliegl (2003) (see Methods). Analysis was based on same dataset as in Figure 1. Analyses were performed as for Figure 1, except that the Fourier spectra were computed based on 100 ms epochs that were Hann-tapered and zero-padded to 1 s. (B) Modulation of firing rate relative to baseline, expressed as log₁₀ (stim/base), separately for data with microsaccade epochs included (top) and excluded (bottom).

Fig 2-figure supplement 1

Analysis of LFP and multi-unit activity in response to stimuli of varying size. (A) Gamma-band peak amplitude and peak-frequency as a function of size, estimated using a polynomial fitting procedure between 30-150 Hz. A wider range instead of the standard 30-80 Hz range was used here, to also capture peaks >100 Hz, which is far outside the typical range of classical visual gamma range. This activity may reflect spike bleed-through, which is beyond the scope of the present study. (B) Average gamma-band peak height in 30-80 Hz range, shown separately for the two monkeys. This figure panel corresponds to Figure 2B of the main text. The difference between 6 and 0.5 deg stimuli was significantly larger for the chromatic than achromatic condition for both animals (P<0.05, bootstrap test). (C) Each trial contained a sequence of two stimuli, either the small stimulus first for 600 ms, or the large stimulus first for 600 ms (see Methods). Here we show the first type of sequence to illustrate the onset of a surround when the stimulus covering the classical RF is already present. Modulation of firing rate relative to baseline, expressed as log_{10} (stim/base), for different sizes and chromatic/achromatic conditions. Note rapid firing suppression after onset of the large stimulus following the 0.5 deg stimulus, with a significant difference arising already after ≈ 100 ms.

Fig 3-figure supplement 1

Additional analyses and experiments performed in relationship to Figure 3 in the main text. (A) Comparison of gamma-band power between full surface and mismatch conditions, separately for the two monkeys. For both monkeys, gamma-band amplitude was significantly higher for uniform surface than blob and annulus conditions when the RF was at the center of the surface stimulus (P<0.05, bootstrap test, see Methods). (B) Illustration of paradigm (*Dataset*

2). Uniform surfaces were either centered on the unit's RF, or the edge of the surface was centered on the unit's RF. (C) Modulation of firing rate relative to baseline, expressed as \log_{10} (stim/base). (D) Average LFP power spectra, using the same analysis time window and spectral estimation parameters as in Figure 2 of main text, comparing "RF-on-center" and "RF-on-edge" conditions. Dashed gray line corresponds to baseline (gray background screen). Right: Gamma-band amplitude (expressed as fold-change) for the two conditions. Gamma-band amplitude was significantly higher for "RF-on-center" condition (P<0.05, bootstrap test). (E)-(H): Single session (from monkey H) illustrating responses to Gaussian surface stimuli. Stimuli were otherwise the same as *Dataset 1*. Gamma oscillations were not abolished by removal of the sharp stimulus edge. (E) Example Gaussian stimulus that had a blurred edge. (F) Average LFP power spectra for chromatic (turquoise), achromatic (black) and baseline (gray) conditions, computed as in Figure S1. (G) Average change in LFP power, expressed as fold-change, relative to baseline. (H) Modulation of firing rate relative to baseline, expressed as log₁₀ (stim/base), for monkey A.

Fig 4-figure supplement 1

Dependence of gamma LFP power on the surface hue: additional analyses in relation to main Figure 4A. (A) Representation of hues used for Figure 4A in DKL space. (B) LFP power spectra as in Figure 4A, for additional hues. The pure blue, green and red stimuli are shown for reference, followed by red surfaces of decreasing luminance and the brown surface stimuli. See Table S1 for CIE and luminance values. (C) Correlations of gamma-band amplitude (log10 of peak height estimate) with absolute cone contrasts in DKL space were not significant, with trends for negative correlation values. Log-transformed values were used to reduce the effects of outliers on correlations. The pattern was similar across monkeys, with monkey A showing a significant, negative correlation of absolute S-(L+M) value to peak height (p=0.039 corrected for multiple comparisons within but not across animals). (D) Gamma peak height as a function of angle in the DKL plane. Angles were obtained by normalizing the L-M and S-(L+M) axes to the maximum absolute value for each respective axis. The resultant vector length was at an angle of 73.95 deg (where 90 deg is defined as maximum L-M contrast and no S-(L+M) contrast) and significantly clustered (resultant length = 0.33, P<0.001, permutation test). The panel on the right shows the DKL space coordinates of the colors used in the left panel.

Fig 4-figure supplement 2

Dependence of gamma LFP power on the surface hue: further analyses in relation to main Figure 4B. (A) Representation of hues used for Figure 4B in DKL space. (B) Peak frequency estimates (Hz) based on cross-validated fitting procedure (see Methods) for the surface stimuli of Figure 4B. (C) A regression of absolute luminance contrast (Michelson contrast) against gamma peak height (fold-change) showed no significant relationship (p=0.23). Note that since there was relatively little gamma power for achromatic, high-contrast stimuli, if anything there would be a negative relationship between luminance contrast and gamma power, the very opposite of findings about gamma power for achromatic gratings. Also note that for red stimuli, gamma power appears to follow a U-shape with decreasing luminance and increasing contrast (see also Figure 4A). (D) Gamma power (fold change) and peak frequency estimates (Hz) for the surface stimuli of Figure 4B, per animal. For both animals, the brightest stimuli showed stronger gamma-responses than the darkest stimuli. The difference in fold-change gamma amplitude as a function of luminance was greater for green than for red for both animals and significantly greater than blue in monkey A. Moreover, red responses across luminances were stronger than green or blue responses, with the exception of the brightest blue responses in monkey H. (B-D) Color hues were adjusted for better discriminability given the small dot sizes, (A) shows actual hues.

Fig 4-figure supplement 3

Dependence of gamma LFP power on the surface hue: control experiment for luminance-contrast. (A) Single session from monkey H with luminance match between achromatic and chromatic surface stimuli. Each color, including gray, was shown at 5 luminance levels, namely equiluminant to the background grey, or in two steps of 10cd/m² brighter or darker than the background. Blue and red hues at higher luminances were obtained by adding luminance from the green channel to maximal blue or red output, respectively. Note that achromatic responses are weaker than chromatic responses also in this luminance-matched case. (B) Dependence of gamma-band power on pupil responses. Pupil responses represent the maximal percent change from baseline during the stimulus period. The correlation over

all hues was not significant (r=0.38, p=0.1). Note that gamma responses for achromatic stimuli were poor regardless of the degree of pupil change.

Fig 4-figure supplement 4

Gamma-band power for stimuli defined on equiluminant DKL planes, control experiment related to Figure 4 of main text. (A) The DKL-space plots at the top illustrate the employed colors. They were designed to present stimuli with equal cone-contrast in L-M (red-green opponency) and S-(L+M) (blue-yellow opponency) directions, separately for three luminance (L+M) steps of -0.25, 0 and +0.25 relative to the gray background (having RGB values of 175, 175, 175) (N=1 session in Monkey H). These luminance intensities corresponded to 54.7 ± 7.9 cd/m². The spectra and bar plots below show the resulting gamma-band responses. Gamma-band oscillations were stronger for reddish than greenish stimuli and very weak or non-detectable for the blue/yellow and achromatic stimuli. Note however that the blue/yellow components were perceptually very faint at these S-(L+M) values that were matched to the L-M conecontrast values. In (B) we therefore used a normalization of the S-(L+M) axis to the most negative S-(L+M) value obtainable (along the L-M=0 axis). (B) Top: Gamma-band activity for stimuli with equal cone-contrast in positive and negative L-M directions, and equal cone-contrast in positive and negative S-(L+M) directions (N=1 session in monkey H). Stimuli were equiluminant relative to the gray background, which was the same as in (A). Gamma was stronger for reddish than greenish hues. In addition, with a stronger S-(L+M) cone-contrast as compared to panel (A), prominent gamma-band activity was now generated in the absence of a cone-contrast in the L-M direction. This gamma-band activity was stronger in the yellow (positive S-(L+M) values) than the blue direction. Bottom: Same as top, but now for a darker gray background (the same as used for Figure 1 in main text) and darker surface stimuli (of matched luminance to background) (N=1 session in Monkey H).

Fig 6-figure supplement 1

DKL-space representation for Figure 6 (main text) and Figure 6-figure supplement 2.

Fig 6-figure supplement 2

Dependence of gamma LFP power on the combination surface hue and background stimulus. We show here all the condition combinations for *Dataset 5*. Different rows correspond to different stimulus background conditions. The color of the background is indicated by the background stimulus shown on the left. The second row corresponds to a white background. Different columns correspond to different stimulus hue conditions, which are indicated by the color of the lines in each graph. Each graph depicts the average LFP power spectrum, using the same estimation parameters as in Figure 6 of the main text. Bar graphs on the bottom show the gamma peak amplitude (fold-change) for the different surface hues, separate for each background condition.

Fig 6-figure supplement 3

LFP power spectra for the post-stimulus period for the four chromatic background hues (3.5-3.8 s, excluding the initial transient response after stimulus offset at 3.3 s). Clear gamma-band responses were observed for full-screen surfaces after both gray and opponent-hue surface presentation in the stimulus period.

Fig 7-figure supplement 1

Analysis of Figure 7 in main text performed separately for the two monkeys. Top: Red-green opponency. Shown are the adaptation coefficients M_{adapt} and L_{adapt} for the two monkeys separately, and the regression coefficients of the red-green γ_{ratio} as a function of these coefficients. Bottom: Same, but now for blue-yellow opponency.

Supplementary File 1

RGB values, luminances (cd/m^2) and CIE values (*1000) used in this study. Luminances and CIE values were measured with a Konica Minolta CS-100A chromameter, CIE values refer to the 1931 2 degree standard observer. Standard black, white and gray used across datasets are in rows 1-3.



























