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# Stimulus repetition modulates gamma-band synchronization in primate visual cortex

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**When a sensory stimulus repeats, neuronal firing rate and functional MRI blood oxygen level-dependent responses typically decline, yet perception and behavioral performance either stay constant or improve. An additional aspect of neuronal activity is neuronal synchronization, which can enhance the impact of neurons onto their postsynaptic targets independent of neuronal firing rates. We show that stimulus repetition leads to profound changes of neuronal gamma-band (~40–90 Hz) synchronization. Electroencephalographic recordings in two awake macaque monkeys demonstrated that repeated presentations of a visual grating stimulus resulted in a steady increase of visually induced gamma-band activity in area V1, gamma-band synchronization between areas V1 and V4, and gamma-band activity in area V4. Microelectrode recordings in area V4 of two additional monkeys under the same stimulation conditions allowed a direct comparison of firing rates and gamma-band synchronization strengths for multiunit activity (MUA), as well as for isolated single units, sorted into putative pyramidal cells and putative interneurons. MUA and putative interneurons showed repetition-related decreases in firing rate, yet increases in gamma-band synchronization. Putative pyramidal cells showed no repetition-related firing rate change, but a decrease in gamma-band synchronization for weakly stimulus-driven units and constant gamma-band synchronization for strongly driven units. We propose that the repetition-related changes in gamma-band synchronization maintain the interareal stimulus signaling and sharpen the stimulus representation by gamma-synchronized pyramidal cell spikes.**

adaptation | learning | oscillation | plasticity | priming

**S**timulus repetition typically leads to reduced neuronal firing rates and reduced functional MRI blood oxygen level-dependent signals, whereas behavior that is based on stimulus processing is not affected or is enhanced (1). Different models have been proposed to reconcile these behavioral and neurophysiological findings (1). In a “fatigue model,” neuronal responses are reduced in proportion to their amplitude, leaving relative response patterns unchanged; in a “sharpening model,” neurons that code features irrelevant to identification of a stimulus exhibit repetition suppression, leading to a sparser and sharpened representation of the repeated stimulus; and in a “facilitation model,” stimulus repetition leads to faster stimulus processing, and thereby smaller overall neuronal activity. Gotts and coworkers (2–4) suggested a “synchronization model” in which stimulus repetition leads to reduced firing rates accompanied by increased synchronization. The increased synchronization might explain how less-activated neuronal groups can maintain their impact onto postsynaptic neurons and, ultimately, behavior, while reducing metabolic costs at the same time. The synchronization model has received support from a number of studies in human subjects, using source-localized magnetoencephalography. Ghuman et al. (5) report enhanced frontotemporal 14-Hz synchronization for repeated vs. novel stimuli. Gilbert et al. (3) found that stimulus

repetition leads to enhanced 5- to 15-Hz power in the right fusiform gyrus and enhanced 15- to 35-Hz power in striate and extrastriate cortex. Corresponding data were also reported for multisite microelectrodes recordings in striate and parietal cortex of awake cats, where von Stein et al. (6) found that interareal alpha-band synchronization was stronger for repeated compared with novel stimuli. The common finding across these studies is enhanced alpha/beta activity or coupling for repeated stimuli. The alpha coupling reported by von Stein et al. (6) occurs in a behavioral context and has a phase relationship and layer specificity that suggests a top-down-directed interaction. Thus, enhanced alpha/beta activity or coupling for repeated stimuli might reflect enhanced top-down signaling, perhaps related to enhanced predictability of repeated stimuli. However, increased synchronization with stimulus repetition according to the model of Gotts and coworkers (2–4) should also serve the maintenance of feedforward signaling of repeated stimuli in the face of reduced firing rates. Feedforward signaling has been strongly linked to local and interareal gamma-band synchronization (7–9). Local gamma-band synchronization likely enhances the postsynaptic impact of the precisely synchronized output spikes (10). Interareal gamma-band synchronization likely aligns excitability cycles such that inputs arrive when postsynaptic target neurons are receptive (11, 12). However, whether multiple presentations of a stimulus result

## Significance

**When a visual stimulus repeats multiple times, visual cortical neurons show decreasing firing rate responses, yet neither perception nor stimulus-related behavior is compromised. We show that stimulus repetition leads to increased neuronal gamma-band (~40–90 Hz) synchronization within and between early and higher visual areas. The enhanced gamma-band synchronization likely maintains effective stimulus signaling in the face of dwindling firing rates. We also show that synchronization to the gamma rhythm increases for spikes in general and for those of putative interneurons, whereas it decreases for spikes of putative excitatory neurons if they are not strongly stimulus-driven. Thus, inhibitory interneurons might create increasingly precise gamma-band synchronization, and thereby prune the stimulus representation by pyramidal cells to be sparser and more efficient.**

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in enhanced gamma-band synchronization remains unknown (details are provided in *SI Discussion*). We investigated gamma-band synchronization within and between macaque monkey areas V1 and V4 and report that stimulus repetition leads to profound changes in gamma-band synchronization within and between these areas.

## Results

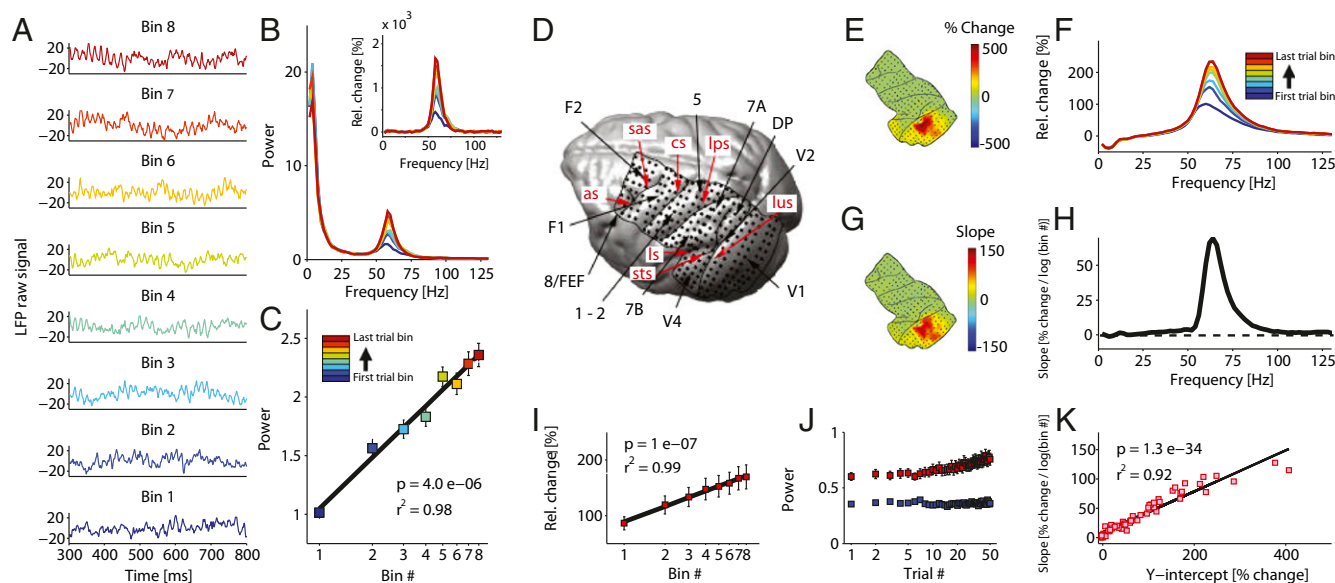
We investigated repetition-related changes in gamma-band synchronization in two datasets, each containing data from two awake macaque monkeys (details of stimulus, task, and recording are provided in *Methods*). The first dataset was obtained from two monkeys (monkeys E1 and E2) implanted with an electrocorticographic (ECoG) grid covering many superficial areas, including areas V1 and V4. The second dataset was obtained from two monkeys (monkeys M1 and M2) and was recorded with standard tungsten microelectrodes in area V4. For both datasets, monkeys were fixating while one or two eccentric patches of drifting grating were presented and the monkeys monitored either the fixation point or one of the grating patches.

### Stimulus Repetition Leads to Increasing Area V1 Gamma-Band Activity.

We sorted trials according to trial number into eight equally sized and nonoverlapping trial bins. For each trial bin, Fig. 1*A* shows a representative raw local field potential (LFP) trace. Traces are from one recording site in area V1 from one recording session in monkey E1. Fig. 1*B* shows the trial bin averages of the absolute and baseline-normalized power spectra and demonstrates that repeated presentations resulted in increasing gamma-band responses. Fig. 1*C* shows the gamma power as a function of trial bin

number. Visually induced gamma-band (52–74 Hz) power was highly correlated to the logarithm of the trial bin number ( $r^2 = 0.98$ ,  $P = 4.0 \times 10^{-6}$ ). Fig. S1 shows the same analysis as in Fig. 1*B* (*Inset*), but averaged over all sites with significant visually driven gamma-band activity and averaged over three sessions. During these recording sessions, the monkey reported color changes of the fixation point, and the peripheral grating stimulus, which induced gamma-band activity, was behaviorally irrelevant. This suggests that the repetition-related gamma increase did not depend on attention being directed to the gamma-inducing stimulus. Gamma-band activity in these sessions was particularly strong because a full-field grating was used (13).

For the following analyses, we will use data from recording sessions during which the monkeys performed a selective visual attention task with grating patches of  $3^\circ$  of visual angle. If not otherwise stated, we use data from the task period when the stimuli were on the screen and attention had been deployed to one of them, and we pool across the two selective attention conditions. Fig. 1*D* depicts the spatial distribution of all ECoG electrodes on the brain of monkey E1, and Fig. 1*E* shows the visually induced gamma-band power change (stimulation vs. baseline, 52–74 Hz) for all ECoG sites. Fig. 1*F* shows the power spectra averaged over the significantly visually driven area V1 sites of monkey E1 for eight nonoverlapping trial bins (62 of a total of 63 sites; details are provided in *Methods*), averaged further across 25 sessions (6,266 trials). Fig. 1*I* shows the average gamma-band power and the corresponding SE across sessions. When the trial bin number was expressed on a logarithmic scale, there was a near-perfect log-linear relation to the gamma increase ( $r^2 = 0.99$ ,  $P = 1 \times 10^{-7}$ ). Next, we investigated the spatial



**Fig. 1.** Stimulus repetition enhances gamma-band activity in visual cortex. (*A*) Raw LFP traces from one representative recording site from area V1 and eight representative trials from one recording session in monkey E1. During this session, monkey E1 performed a color change detection at fixation and the gamma-inducing grating stimulus was behaviorally irrelevant. (*B*) Corresponding absolute and baseline-normalized power spectra. Rel., relative. (*C*) Gamma power as a function of trial bin number on a logarithmic scale. Trials were sorted according to trial number into eight equally sized and nonoverlapping bins, and power was averaged per bin. (*D*) Brain of monkey E1 with ECoG electrodes and major sulci (as, arcuate sulcus; cs, central sulcus; ips, intraparietal sulcus; ls, lateral sulcus; lus, lunate sulcus; sas, spur of the arcuate sulcus; sts, superior temporal sulcus). Black labels point to the covered brain areas. (*E–K*) Data from sessions during which monkey E1 performed a selective attention paradigm. (*E*) Relative change in gamma power during stimulation compared with baseline, averaged over all trials. (*F*) Same as in *B* (*Inset*), but averaged over all visually driven area V1 sites and all sessions in monkey E1. Slopes of regression analyses are shown as in *I*, but separately for each site (*G*) and frequency (*H*). (*I*) Same as in *C*, but averaged over area V1 sites and sessions. (*J*) Trial-wise average of gamma-band power for the first 50 trials. Red squares show power during stimulation, and blue squares show power during baseline. (*K*) Each dot corresponds to a visually driven area V1 site in monkey E1. For each site, the regression analysis was performed separately and the scatter plot shows the respective slopes as a function of the intercepts. The intercept estimates the visually induced gamma-band power before the repetition-related increase occurred. This repetition-independent estimate of the stimulus-induced gamma-power change was predictive of the later repetition-related increase. Dots in *D*, *E*, and *G* show electrode positions, yet power estimates are based on sites (i.e., local derivatives). Absolute power values are shown in arbitrary units (a.u.) in *B*, *C*, and *J*.

and spectral specificity of the gamma increase. Fig. 1G color-codes the slope of regression lines that were obtained as shown in Fig. 1I, but separately for all ECoG sites. The topography of slopes (Fig. 1G) was very similar to the topography of visually induced gamma (Fig. 1E). This suggests that the increase was specifically related to visually induced activity rather than to drifts in the overall state of the brain or in the recording system. However, Fig. 1E shows the visually induced gamma-band activity averaged across all trials (i.e., including later trials in which the visually induced gamma-band activity was already affected by the repetition-related gamma increase). To avoid any circularity and to demonstrate the fine-grained dependence of the repetition-related gamma increase over trials on the visually induced gamma increase within trials, we performed the following analysis. For each of the sites showing clear visually induced gamma, we performed a separate regression analysis and extrapolated the regression line to the y-axis intercept for bin number zero, so as to use this intercept as an estimate of the visually induced gamma before any repetition-related increase occurred. We then investigated whether this intercept value predicted the repetition-related regression slope, by calculating a regression between the two parameters. Fig. 1K demonstrates a strong correlation ( $r^2 = 0.92$ ,  $P = 1.3 \times 10^{-34}$ ), confirming that the repetition-related increase was systematically related to the strength of visually induced gamma-band activity. To investigate the spectral specificity of the increase, Fig. 1H shows the slopes for the visually driven sites, now as a function of frequency. The slope spectrum demonstrates that the repetition-related increase was specific for the gamma-frequency band, with a spectral shape very similar to the stimulus-induced gamma-power enhancements.

To test whether there was any stimulus-induced gamma-band power in the first few trials of a session, we averaged gamma-band power across sessions separately for each of the first 50 trials (Fig. 1J; red squares indicate absolute power during visual stimulation, and blue squares indicate absolute power during prestimulus baseline). This revealed that gamma-band activity was induced already by the very first stimulus presentation of a given session. This analysis also demonstrated that the increase was present for the absolute gamma-band power during visual stimulation ( $P = 2.8 \times 10^{-20}$  for monkey E1 and  $P = 3.5 \times 10^{-11}$  for monkey E2) and not for the absolute gamma-band power during prestimulus baseline ( $P = 0.98$  for monkey E1 and  $P = 0.11$  for monkey E2). This illustrates that the repetition effect on visually induced gamma power was not due to decreases in prestimulus, but rather to increases in poststimulus gamma-band power. Fig. S2 shows the same analysis for monkey E2, demonstrating a remarkable consistency across the two animals. In monkey E2, 39 area V1 sites were significantly stimulus-driven (of a total of 40 sites), nine recording sessions had been obtained (3,511 trials), and the gamma-frequency band extended from 68 to 82 Hz.

The fact that gamma increased with stimulus repetition both when the stimulus was a large unattended grating and when it was a smaller attended grating suggested that the effect did not depend on attention. We performed an additional analysis in this regard by analyzing the period when visual stimuli were already on the screen but no attentional cue had been given yet. Consistent with the other results, this showed the repetition-related gamma increase (Fig. S3). We also considered that the repetition-related increase was modulated by switches in stimulus features or in the allocation of attention. The respective analyses (Fig. S4) revealed only that the repetition-related increase was slightly larger for repetitions that involved a change in stimulus color, an effect that might be related to predictive coding (14).

**Stimulus Repetition Leads to Increasing Area V1–V4 Gamma Coherence and Area V4 Gamma Activity.** Gamma power in one area might contribute to communication with connected areas through interareal coherence (7, 8, 11, 12, 15, 16). Therefore, we tested

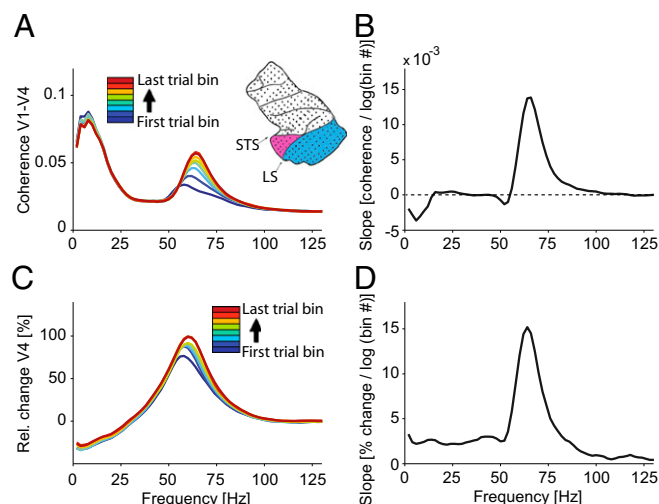
whether the increase was also present for the coherence between area V1 and area V4. All analyses were done after bipolar derivation, thereby excluding a common reference, which can otherwise lead to artifactual coherence estimates. Fig. 2A (Inset) shows the anatomical definition of area V1 (pink) and area V4 (blue) in monkey E1 (Methods). Fig. 2A shows the interareal coherence for the eight trial bins averaged over all sessions in this monkey, revealing that interareal coherence also increased monotonically with trial number (62 significantly stimulus-driven area V1 sites of a total of 63 sites and 16 significantly stimulus-driven area V4 sites of a total of 17 sites, 992 interareal site pairs, and 6,266 trials). We performed the same regression analysis as for power, and we plot the resulting slope spectrum in Fig. 2B. The dominant result was a coherence increase in the gamma-frequency band. In addition, there was a smaller decrease in a theta-frequency band.

Enhanced gamma coherence between areas V1 and V4 is expected to result in enhanced gamma power in area V4 (12). Fig. 2C shows LFP power spectra from area V4 of monkey E1 (16 significantly stimulus-driven sites of a total of 17 sites and 6,266 trials), and Fig. 2D shows the corresponding slope spectra, confirming a repetition-related increase in area V4 power in the gamma-frequency band. Fig. S5 shows the repetition-related changes in area V1–V4 coherence and area V4 power for monkey E2, demonstrating that the gamma increase was consistent across the two animals (39 significantly stimulus-driven area V1 sites of a total of 40 sites, 16 significantly stimulus-driven area V4 sites of a total of 17 sites, 624 site pairs, and 3,511 trials).

We considered that the increases in local and long-range gamma-band synchronization could be related to changes in behavior. Therefore, we analyzed behavioral parameters in the same way as power and coherence, by binning trials and performing a regression analysis. This did not reveal any significant effect for response accuracy, for reaction times, or for the rate of microsaccades.

#### Stimulus Repetition Leads to Increases in the Gamma-Peak Frequency.

Recent studies have shown that not only the strength but also the frequency of gamma-band activity can change systematically (e.g., with contrast) (8, 17). Correspondingly, we investigated the gamma

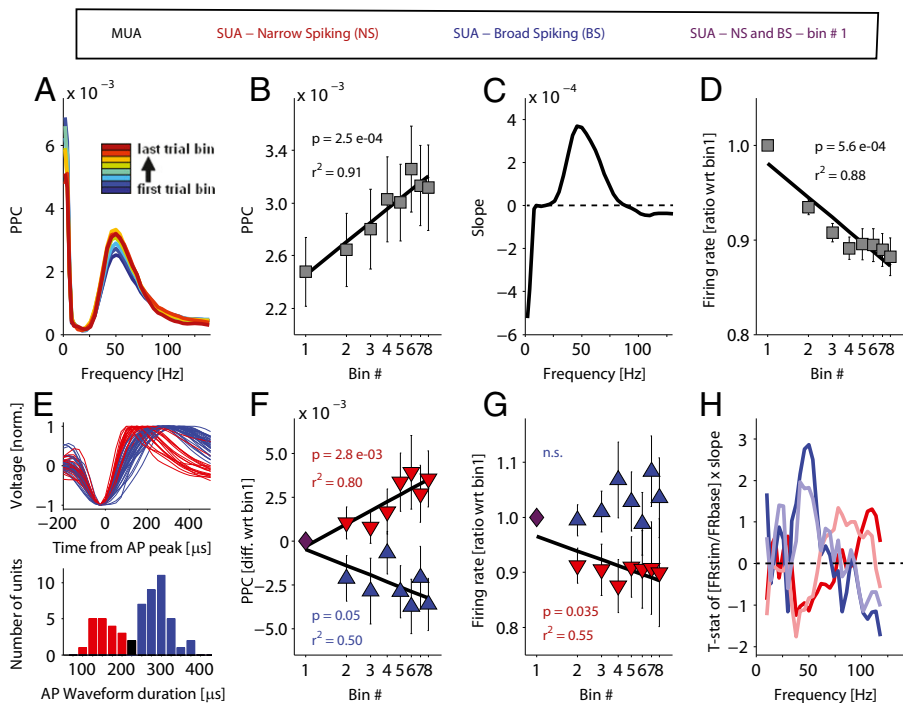


**Fig. 2.** Stimulus repetition enhances gamma-band coherence between areas V1 and V4 and the gamma-band power in area V4. (A) Coherence spectra for monkey E1, averaged over 25 recording sessions and all possible pairs of interareal sites. (Inset) Monkey E1 areas V1 (blue) and V4 (pink). LS, lunate sulcus; STS, superior temporal sulcus. (B) Slope of the regression of coherence vs. log(trial bin number) as a function of frequency. (C and D) Same as in A and B, but for V4 power.





**Fig. 4.** Effect of stimulus repetition on the gamma-band spike-LFP synchronization. (A) PPC of multiunit spikes with regard to the spectral phase of the LFP recorded on neighboring electrodes (details are provided in *Methods*). (B) PPC from A as a function of trial bin number. (C) Slopes of regression analyses as shown in B, as a function of frequency. (D) Ratio of MUA firing rate with regard to the first trial bin, as a function of trial bin number, and the corresponding regression analysis. (E) Spike waveforms (averages per isolated single unit) and the distribution of the corresponding action potential waveform durations. Neurons with waveform durations in the black bin were discarded. norm., normal. (F) Change in PPC with regard to the first trial bin (diff. wrt bin 1), separately for NS and BS cells. (G) Ratio of the firing rate with regard to the first trial bin (ratio wrt. bin 1), separately for NS and BS cells. (H) Regression *t* statistics from two separate multiple linear regression analyses for the BS and NS cells, respectively. The multiple linear regressions fitted the dependent variable [slope of the regression between spike-LFP PPC and log(trial bin number)] as a function of the independent variables (firing rate in the baseline), with results shown as softly colored lines, and [firing rate during stimulation (FRstim)/firing rate in the baseline (FRbase)] NS (BS) waveforms. All panels show grand averages of all microelectrode recordings (i.e., averages across monkeys M1 and M2, across all recordings sessions, and across all sites or units, respectively). All recording sites were in area V4.



The index  $[(FR_{stimulation} - FR_{baseline}) / (FR_{stimulation} + FR_{baseline})]$  was, on average,  $0.23 \pm 0.12$  for BS cells with negative slope and  $0.49 \pm 0.11$  for BS cells with positive slope (difference not significant).

## Discussion

We found that in the course of a recording session, during repeated stimulus presentations, gamma-band activity in area V1 increased by approximately a factor of 2. The strength of gamma-band activity was linearly related to the logarithm of the repetition bin number. This repetition-related gamma increase was spatially specific for the sites with visually induced gamma, and the strength of the repetition-related increase was systematically related to the strength of the visually induced gamma before any repetition-related increase. Furthermore, the repetition-related gamma increase did not appear to be dependent on selective visual attention. A very similar repetition-related increase was also present for the interareal gamma-band coherence between areas V1 and V4 and for the gamma-band activity in area V4. In a separate dataset from area V4, we showed that multiunit synchronization to the gamma rhythm increased by roughly 30%, whereas the multiunit rate decreased by roughly 12%. When separating single units into BS and NS cells, the NS cells showed qualitatively the same synchronization and rate changes as the multiunit. The BS cells showed a strong trend for a repetition-related decrease in gamma synchronization, which was significant for the weakly stimulus-driven cells but absent for the strongly driven ones.

Repetition-related increases in area V1 gamma-band activity and area V1–V4 gamma-band synchronization are expected to lead to an increasing impact of area V1 input onto area V4 (7, 11, 12). Because this increasing impact is rhythmic in the gamma-frequency band, it is expected to result, in area V4, in increasing gamma-band activity and increasing gamma spike-field synchronization but not necessarily in increasing overall firing rates, in line with the results reported here. It is conceivable that the overall firing rate decrease in area V4 is related to the

increased gamma-rhythmic impact and the increased local gamma spike-field synchronization. We have shown previously that spikes that are maximally synchronized to the local gamma rhythm are more stimulus-selective than less gamma-synchronized spikes (27). With repeating stimulation, increasing area V1–V4 coherence, and corresponding impact, the less gamma-synchronized spikes in area V4 seem to disappear, leaving the more gamma-synchronized spikes from the more stimulus-driven neurons (Fig. 4H). The precise mechanisms of this pruning of non-gamma-synchronized spikes are unclear. They might well be a consequence of the increasing gamma-band synchronization, or they might be independent of the mechanisms behind gamma and its repetition-related increase.

From a methodological point of view, the present results are important for the interpretation of previous studies and for the optimal design of future studies on gamma-band synchronization. Typically, neurophysiological studies use multiple repetitions of a given experimental condition. Where previous studies confounded their experimental conditions with repetitions (e.g., by presenting conditions in blocks of trials without sufficient counterbalancing), this might have resulted in apparent condition effects that actually were repetition effects. Where previous studies properly randomized conditions across repetitions, the repetition-related effect described here might have led to an underestimation of the significance and/or size of the effect of the respective experimental conditions. For future studies on gamma-band synchronization, the present results emphasize the importance of proper condition randomization in the experiment design and of taking repetitions into account in the data analysis. A discussion of related studies (22–24, 28–36) is provided in *SI Discussion* and Fig. S8.

In Fig. 4, we analyzed the changes in gamma synchronization separately for MUA, NS cells, and BS cells. NS cells are putative interneurons, although this cannot be proven in the awake monkey preparation at this moment. Networks of interneurons are the core generators of gamma-band synchronization (26, 37). Consistent with this, the gamma synchronization of the NS cells

increased similar to the gamma power/coherence within/between ECoG signals. Intriguingly, the BS cells showed repetition-related changes in gamma synchronization that depended on their stimulus-driven activation. Weakly driven BS cells showed repetition-related decreases in gamma synchronization, whereas strongly driven BS cells kept their gamma synchronization unchanged across repetitions. Thus, across repetitions, the gamma-synchronized spike output contained fewer and fewer spikes from weakly stimulus-driven BS cells and relatively more spikes from strongly stimulus-driven BS cells, which amounts to a sharpening of the stimulus representation in the gamma-synchronized spike output (27). We have recently described a very similar effect of selective attention on cell type-specific gamma-band synchronization (26). It is particularly the gamma-synchronized spikes that have an impact on postsynaptic target neurons, and in this postsynaptic target group of neurons, the different input neurons always mutually reduce impact through normalization mechanisms (38). Thus, if the gamma-synchronized spike output contains relatively more spikes from strongly stimulus-driven BS cells, this lends those cells a stronger effective impact.

## Methods

A detailed description of the methods used in this study is provided in *SI Methods*. If not stated otherwise, data are from recording sessions in which

the monkeys performed a selective visual attention task. They kept fixation on a central dot while two patches of drifting grating were presented, of which one fell into the receptive field of the recorded neurons. In monkeys E1 and E2, ECoG grid electrodes were implanted over the left hemisphere to obtain LFPs (7, 39, 40). We use electrodes over areas V1, V2, and V4 and the temporal-occipital area (TEO). When we refer to area V1 (V4), this also includes some electrodes that might be over area V2 (TEO). LFPs from immediately neighboring electrodes were subtracted to obtain local bipolar derivations, which avoid a common reference in interareal coherence analysis. In monkeys M1 and M2, standard techniques were used to record with four microelectrodes simultaneously in visual area V4 (20, 41).

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