

Responses to reader queries for

Stimulus Dependence of Gamma Oscillations in Human Visual Cortex

D. Hermes, K.J. Miller, B.A. Wandell, J. Winawer
Cerebral Cortex, 2014 [doi:10.1093/cercor/bhu091](https://doi.org/10.1093/cercor/bhu091)

Below are several questions we received by email about our paper (Hermes et al., 2014, referred to subsequently as "HMWW"). In our answers, we refer to figures in the main text of HMWW as 'Main Figure X', supplementary figures included in HMWW as 'Supplementary Figure X', and new figures created for, and contained in, this document as 'Archive Figure X'.

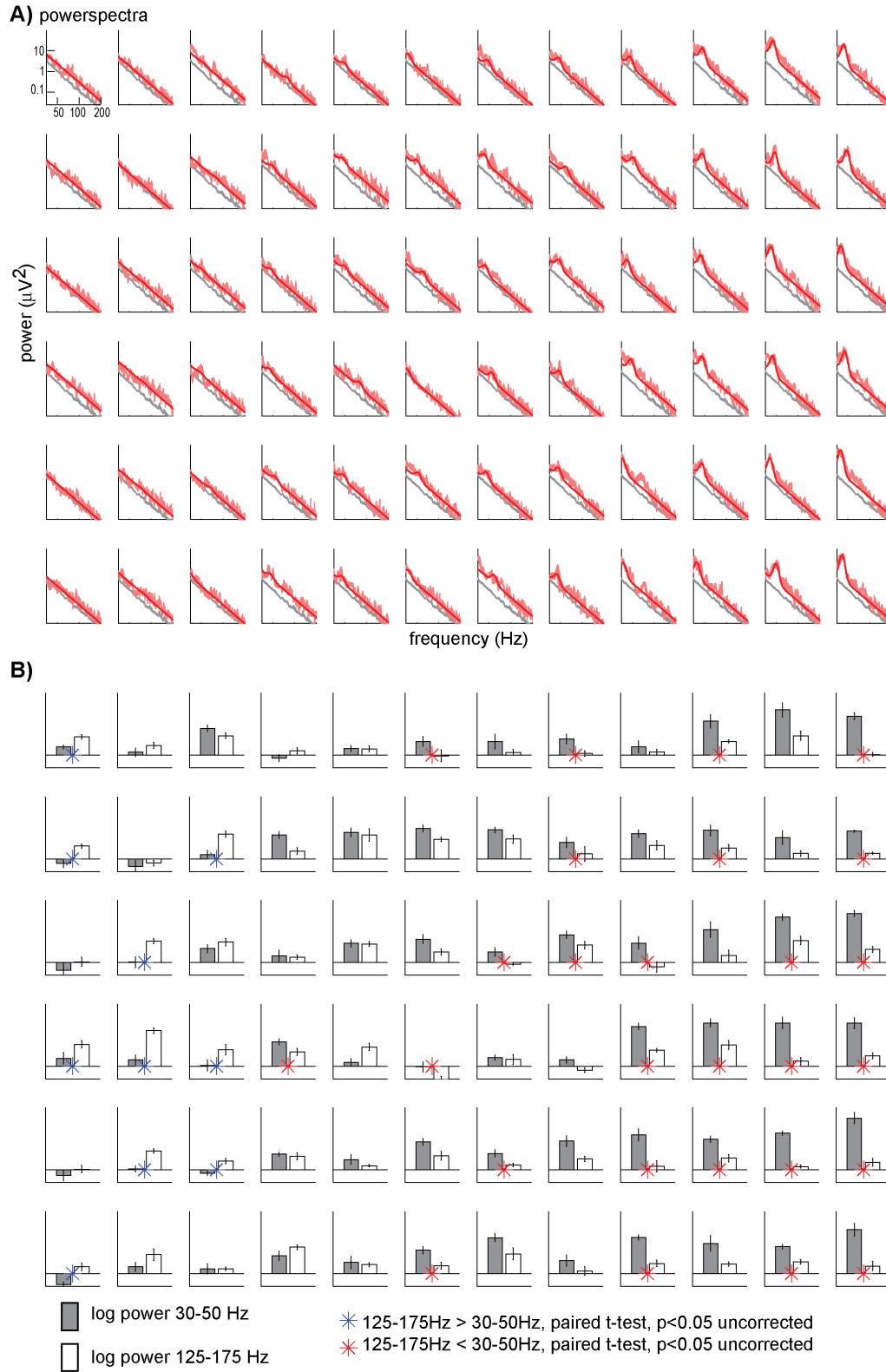
Q1. For supplementary figure 3, the patient fixated, but was there any task besides fixation? If so, what was the task, and did you select trials based on task performance?

The subject pressed a button when the fixation dot changed color, as reported in Parvizi et al (2012). There was no selection of trials – we used all trials for all 72 stimuli, shown 6 times each. (A number of other stimuli were shown once each, and were not included in the analysis.) We know from this data set that for the electrode depicted in Supplementary Figure 3, as reported in HMWW, 69 of 72 stimuli produced a significant broadband response. We also know that electrodes on the fusiform gyrus responded robustly and selectively to the face stimuli in this experiment, and that an electrode on the parahippocampal gyrus responded more to house stimuli than any other category in this experiment (Parvizi et al., 2012, Figure 1A). Clearly, the subject saw the stimuli.

Q2. Supplementary figure 3 sorts the images according to the strength of narrowband gamma. According to the text, the first 32 images did not reach a significant narrowband gamma in the fitting procedure. Why do many of the respective fits nevertheless show a clear Gaussian component, e.g. all fits in the fourth and fifth column?

The model fit to the spectra is a line plus a Gaussian, on log frequency-log power axes. The Gaussian is constrained to be centered within 35-80 Hz and to be greater than or equal to 0. Because the weight on the Gaussian cannot be negative, the model fits are biased to show positive Gamma responses in the presence of symmetric noise. To quantify the significance of the Gaussian term, we compared the value of the weight on the Gaussian for each stimulus condition to that obtained from the baseline (inter-trial intervals) via bootstrapping over trials. The model fits shown in Supplementary Figure 3 were based on the average spectrum across the images, independent of whether the Gaussian component was significant.

Here we add a different test of the significance of narrowband gamma, similar to the calculations used by Brunet et al (2013). We compared the average log₁₀ power increase from 30-50 Hz (the frequency range in which gamma peaked for this electrode) to the log₁₀ power increase from 125-175 Hz. See Archive Figure 1 underneath. We find very similar results to those obtained from the bootstrap analysis on the line plus Gaussian model fits. Fewer than half of the images showed a significantly larger increase in power from 30-50 Hz than 125-175 Hz (n=27). Many images did not result in a significant difference (n=35), and a number showed the opposite pattern (n=10), a bigger power increase in the high frequency range than the low frequency range. If we pick different frequency ranges for gamma (e.g., 30-80 Hz) and broadband (e.g., 100-200 Hz), the pattern of results does not change.



Archive Figure 1. (a) Spectral responses to natural images from a V1 electrode, re-plotted from Supplementary Figure 3A. (b) Power spectral elevation relative to baseline, summarized for 30-50 Hz band (gray bars) and 125-175 Hz band (white bars). Stimuli ordered as in (a). Asterisks indicate a statistically

significant difference in the power spectral elevation between the two bands (red = greater response for 30-50 Hz; blue = greater response for 125 – 175 Hz).

Q3.Experiment 1, subject 2: Did this subject perform no task at all? How can you demonstrate that this subject perceived the stimulus in each trial?

Subject 2 was continuously monitored to ensure his fixation. We report the following in the discussion and methods:

Discussion: “It is unlikely that the stimuli that did not elicit gamma rhythms were not perceived, because all stimuli were large (at least $10 \times 10^\circ$), had an abrupt onset during central fixation, and remained on the screen for at least 500 ms, sufficiently long to allow for conscious perception (Dehaene and Changeux, 2011). Moreover, the grating stimuli (which reliably elicited gamma oscillations) and the noise stimuli (which did not) were randomly interleaved and presented at a rapid rate (1 stimulus per second), ruling out the possibility that the subjects’ attentional state differed between the stimulus classes. “

Methods: “Subjects fixated on a dot in the center of the screen that alternated between red and green, changing colors at random times. Subject 1 pressed a button when the fixation dot changed color. Subject 2 fixated the dot but did not make manual responses because these responses were found to interfere with visual fixation.

Regarding this issue, we did note in the discussion that: “We cannot rule out the possibility that for stimuli near detection or recognition threshold, the presence or absence of gamma oscillations will modulate an observer’s judgments. However, since very large differences in the gamma response can be observed across different stimuli, it is unlikely that the gamma amplitude is the principal determinant of stimulus detection or recognition.”

Q4.Experiment 2: How many repetitions were obtained per stimulus? Only one?

There were 99 stimuli across the two classes (50 faces and 49 houses). The individual exemplars within each category were shown once each. Main Figure 4 shows the mean response across all exemplars in each class. Main Figure 5 shows the response in one channel on every individual trial. Note that this channel shows the largest narrowband gamma responses; other channels showed little or no narrowband gamma.

Q5.You write: "A recent ECoG measurement in macaque showed that gamma oscillations were elicited during the free viewing of natural images (Brunet et al. 2013). The gamma response was present for several of the images shown and in the mean response across all images." By contrast [Brunet et al] explicitly report in the paper that gamma responses were present for

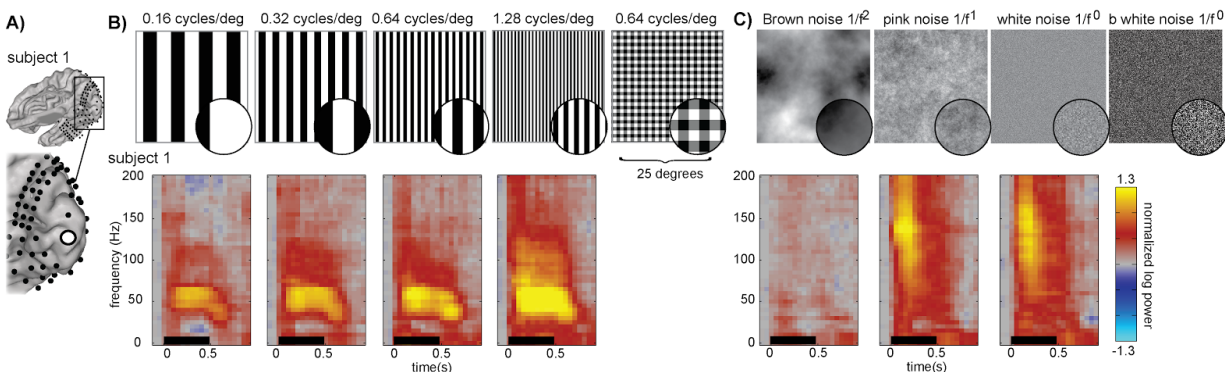
ALL images: "...for each image, power enhancements during natural viewing compared with prestimulus baseline (i.e., \log_{10} [power during natural viewing/power during prestimulus baseline]) were significantly stronger in the gamma-frequency band (50-80 Hz) when compared with a 150- to 200-Hz band (largest P-value was 0.0007, paired t-test across trials), indicating that gamma power enhancements are most likely not due to broadband power enhancements as have been found in other ECoG recordings (Miller et al. 2009)." What leads you to write that gamma responses ... were present for several images and for the mean across all images, which claims implicitly that gamma responses were not present for some images?

We did not intend to assert that gamma responses were absent for some images. We tried to describe the figures as clearly as possible: Figure 3 in Brunet et al (2013) shows the presence of clear gamma oscillations for several natural images, and Figure 4 shows significant increases between 50 and 80 Hz for all images and we stated these two things. Spectra were not shown for most of the images and we have no comment on those stimuli.

We are however interested in understanding the differences between the results of Brunet et al (2013) and our own results. Specifically, we are interested in whether Brunet et al (2013), like HMWW, measured any broadband increases, and at what frequency the noise floor starts in the measurements of Brunet et al (2013).

Q6. For some conditions, the baseline seems to show power reductions, e.g. Fig. 1C, subject 2, pink noise. I guess, this is due to calculating the baseline as average across all inter-stimulus intervals. Correct? But do these power reductions then not demonstrate that this baseline was not stable across stimulus conditions?

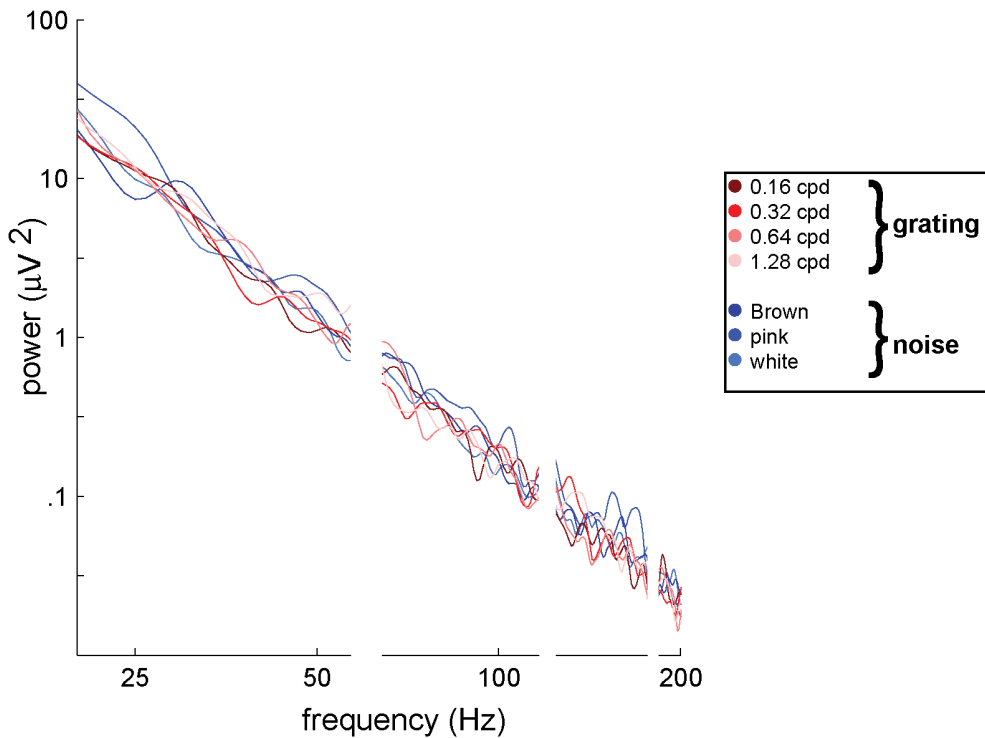
The baseline is indeed computed as the average across inter-stimulus intervals. The same pattern of results is obtained if the baseline is defined as the pre-stimulus period of each individual trial, as shown in Archive Figure 2.



Archive Figure 2. Time–frequency power estimates in V1/V2 for gratings and noise stimuli. All plotting conventions are the same as Main Figure 1A&B except for the new baseline calculation: here, the baseline is

computed as the pre-stimulus period of each individual trial, rather than the mean across all inter-stimulus intervals.

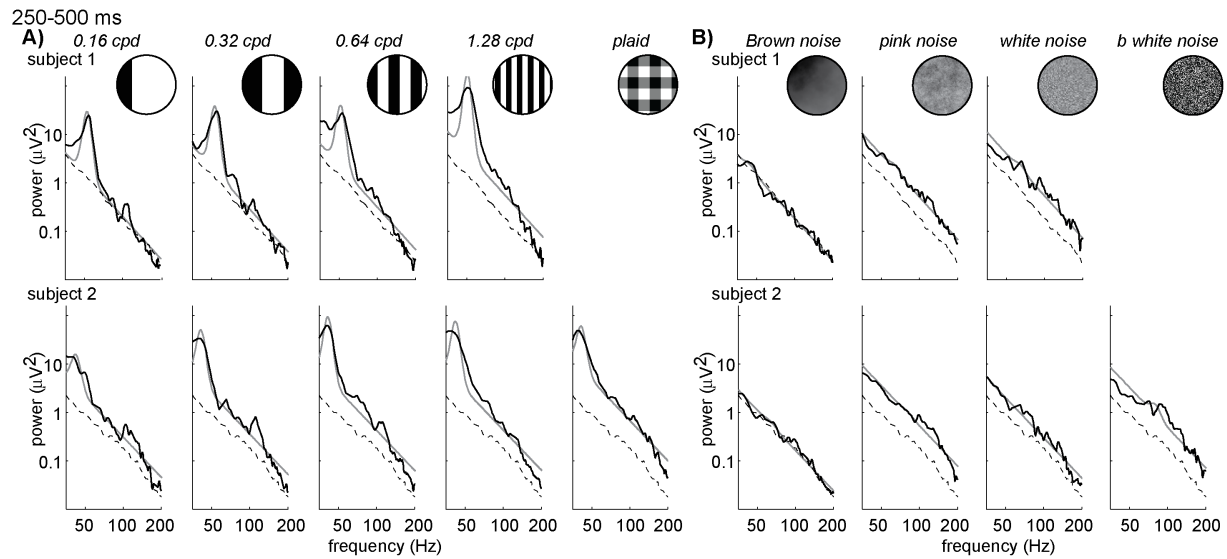
Similarly, the power spectra of the pre-stimulus baseline (-250-0 ms before stimulus onset) are similar across conditions, as indicated in Archive Figure 3.



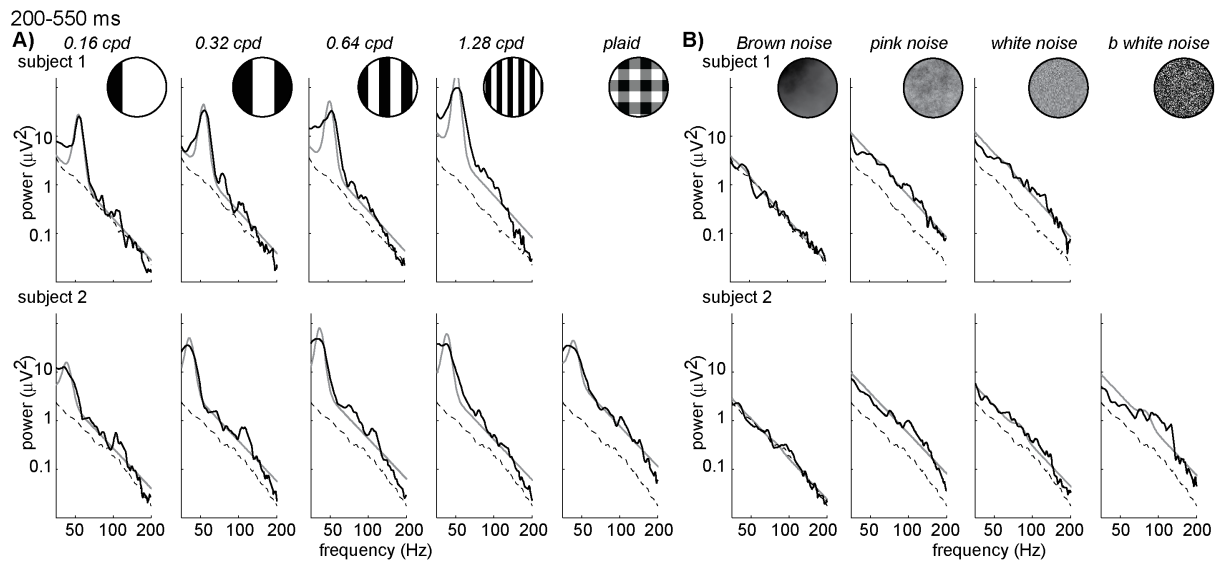
Archive Figure 3. Power spectra of the pre-stimulus baseline of each condition for subject 1 (*cf.* Main Figure 2).

Q7.The line fits are done on spectra calculated on 0-500 ms post stimulus. This entails the early broadband-dominated response. It excludes the response after stimulus offset, even though visual cortex responses in humans trail retinal changes by about 50 ms. How do those spectra look if one analyses 200 - 550 ms post stimulus onset?

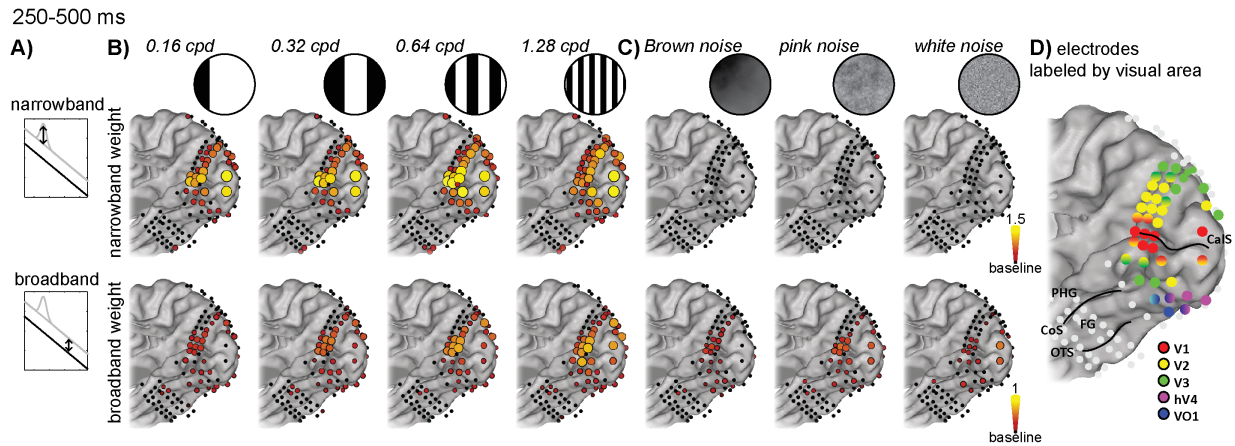
Our main results do not change using a 250-500 ms window. See Archive Figures 4, 5, 6 and 7 below using a 250-500 ms and 200-550 ms window. (Compare to Main Figures 2 and 3):



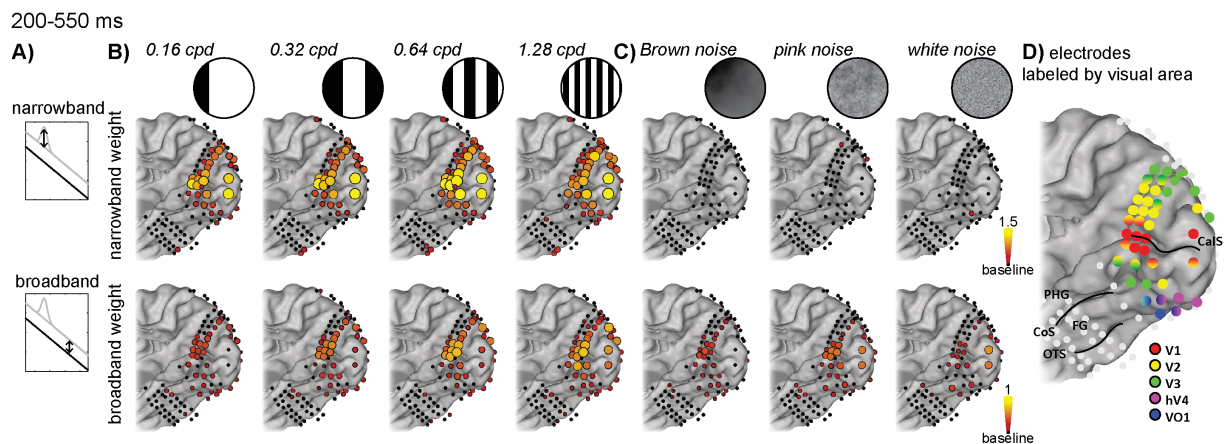
Archive Figure 4 Power spectra in V1/V2 for gratings and noise stimuli computed over the 250-500 ms post-stimulus interval. All plotting conventions are the same as Main Figure 2A&B, except that the power spectrum is calculated for the 250-500 ms after stimulus onset rather 0-500 ms.



Archive Figure 5 Power spectra in V1/V2 for gratings and noise stimuli computed over the 200-550 ms post-stimulus interval. All plotting conventions are the same as Main Figure 2A&B, except that the power spectrum is calculated for the 200-550 ms after stimulus onset rather 0-500 ms.



Archive Figure 6. Spatial distribution of narrowband (gamma) and broadband weights fit to data 250-500 ms post-stimulus onset. All plotting conventions are the same as Main Figure 3A-D, except that narrowband and broadband weights are calculated on the power spectrum from the 250-500 ms window after stimulus onset rather than 0-500 ms.



Archive Figure 7. Spatial distribution of narrowband (gamma) and broadband weights fit to data 200-550 ms post-stimulus onset. All plotting conventions are the same as Main Figure 3A-D, except that narrowband and broadband weights are calculated on the power spectrum from the 200-550 ms window after stimulus onset rather than 0-500 ms.

Q8. Fig. 2B suggests that e.g. white noise induces a relatively broad but still somewhat band-limited power increase, rather than an increase that is appropriately fitted by a line.

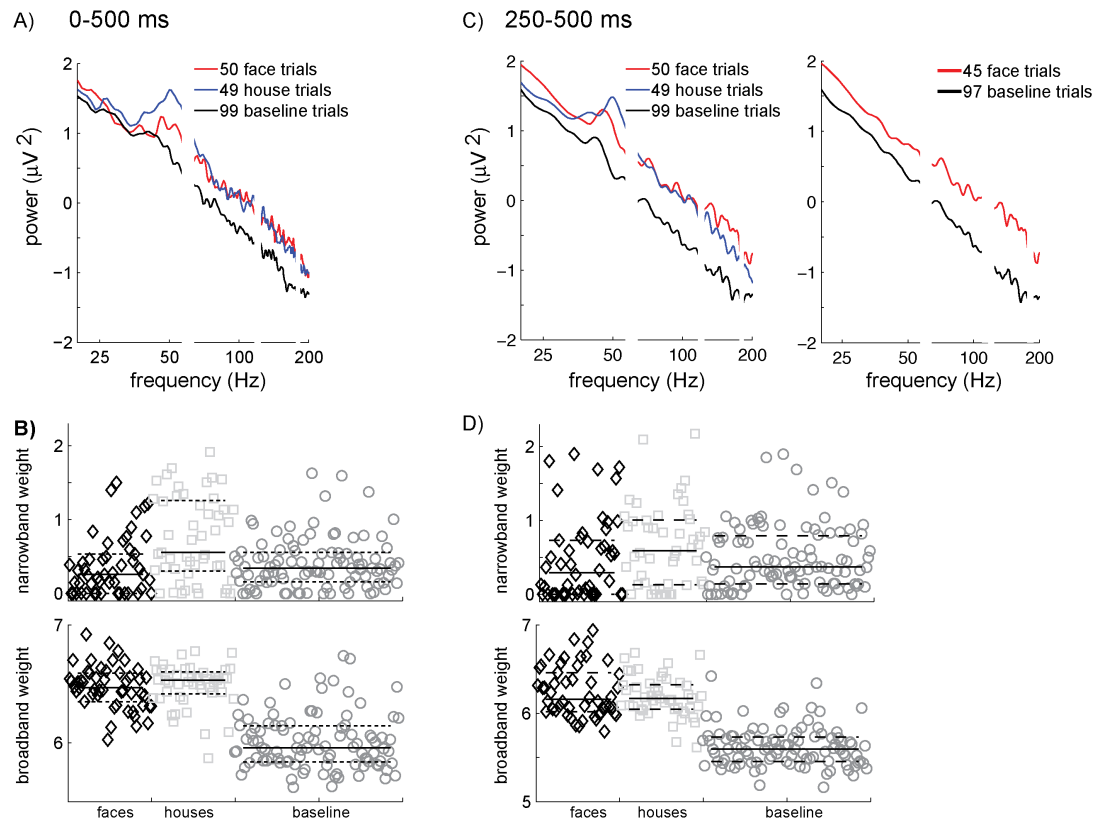
We tested for the presence of gamma oscillations between 35-80 Hz. We did not find evidence for these oscillations elicited by white noise stimuli. It is true that a line in log-log space is a simplified model and does not capture all the details of the power spectrum. The spectra for just the second half of the trials (250-500 ms), as in Archive Figures 4 and 5

above, are better fitted by a straight line than the spectra for the entire trial (0-500 ms) plotted in Figure 2 of the paper.

The apparent band limited power increase for the pink noise stimuli cannot directly be taken to reflect an oscillatory process. There is no sharp peak in the spectrum, and the attenuation at high frequencies could be due to a measurement limit as well as an attenuation in the field potential at these frequencies. Because the signal amplitude is very low at high frequencies, spectral power elevation at high frequencies can be masked by noise in the amplifier (Miller et al., 2009, Miller et al., 2014). Because we did not measure the amplifier noise floor, we cannot rule out the possibility that some signal attenuation is due to measurement limits. In any case, there is clearly no observable gamma oscillation in the frequency range in which gratings elicit gamma oscillations (35-80Hz).

Q9. Fig. 4 suggests that this might also be the case for face and house stimuli, maybe even more so. Yet, for these stimuli, the line spectra are not shown in the paper. Can you provide those spectra? And can you provide them also for 200-550 ms post stimulus onset?

Archive Figure 8 shows the power spectra for face and house images for 0-500 ms (A) and for 250-500 ms (B). Consistent with the spectrograms shown in our paper (Main Figure 4b), Archive Figures 8a and 8c (left panel) show a modest elevation in narrowband gamma power when averaging across all trials, especially for house stimuli. This is due to responses in a few trials (Archive Figures 8b, d). Figure 8c, right panel, shows the average across 45 of 50 face trials for the 250-500 ms window. Note that in Main Figure 5, we also calculated the gamma amplitude on every individual trial, to show that a few face and several house trials show large gamma oscillations. Calculating the narrowband and broadband amplitude on every individual trials also allowed the frequency to vary from trial to trial, such that the average across trials does not mask gamma on individual trials (Archive Figures 8B and D).



Archive Figure 8. Spectral responses to face and house stimuli in a V1 electrode. A) Power spectra during baseline and while viewing faces or houses for an example V1 electrode averaged across all trials, computed over the 0-500 ms post-stimulus time interval. B) Narrowband gamma and broadband estimates for every individual trial, computed over the 0-500 ms post-stimulus time interval (re-plotted from Main figure 5B). Almost all trials show broadband responses above baseline; most trials do not show a gamma response above baseline. C) The left panel is the same as panel (A), but computed for the 250-500 ms interval after stimulus onset. The right panel in (C) plots the spectra for the face stimuli averaged across 45 trials rather than 50, excluding the 5 trials with the largest gamma responses. D) Narrowband and broadband estimates for the 250-500 ms interval for every individual stimulus. Almost all trials show broadband responses above baseline; most trials do not show a gamma response above baseline.

References

- Brunet N, Bosman CA, Roberts M, Oostenveld R, Womelsdorf T, De Weerd P, Fries P (2013) Visual Cortical Gamma-Band Activity During Free Viewing of Natural Images. *Cereb Cortex*.
- Dehaene S, Changeux JP (2011) Experimental and theoretical approaches to conscious processing. *Neuron* 70:200-227.
- Hermes D, Miller KJ, Wandell BA, Winawer J (2014) Stimulus Dependence of Gamma Oscillations in Human Visual Cortex. *Cereb Cortex*.

Miller KJ, Honey CJ, Hermes D, Rao RP, denNijs M, Ojemann JG (2014) Broadband changes in the cortical surface potential track activation of functionally diverse neuronal populations. *NeuroImage* 85 Pt 2:711-720.

Miller KJ, Sorensen LB, Ojemann JG, den Nijs M (2009) Power-law scaling in the brain surface electric potential. *PLoS Comput Biol* 5:e1000609.

Parvizi J, Jacques C, Foster BL, Witthoft N, Rangarajan V, Weiner KS, Grill-Spector K (2012) Electrical stimulation of human fusiform face-selective regions distorts face perception. *J Neurosci* 32:14915-14920.