

Induced Gamma activity in primary visual cortex is related to luminance and not color contrast: An MEG study

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Gamma activity in the visual cortex has been reported in numerous EEG studies of coherent and illusory figures. A dominant theme of many such findings has been that temporal synchronization in the gamma band in response to these identifiable percepts is related to perceptual binding of the common features of the stimulus. In two recent studies using magnetoencephalography (MEG) and the beamformer analysis technique, we have shown that the magnitude of induced gamma activity in visual cortex is dependent upon independent stimulus features such as spatial frequency and contrast. In particular, we showed that induced gamma activity is maximal in response to gratings of 3 cycles per degree (3 cpd) of high luminance contrast. In this work, we set out to examine stimulus contrast further by using isoluminant red/green gratings that possess color but not luminance contrast using the same cohort of subjects. We found no induced gamma activity in V1 or visual cortex in response to the isoluminant gratings in these subjects who had previously shown strong induced gamma activity in V1 for luminance contrast gratings.

Keywords: functional imaging, visual cortex, color vision, magnetoencephalography, beamformer, gamma activity

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Introduction

Recently, there has been a great deal of interest in the role of visual cortical gamma (20–60 Hz) activity in cognition and perception. For example, Tallon-Baudry and Bertrand (1999) have argued strongly for the significance of non-stimulus-locked gamma activity in response to the appearance of coherent figures. Using EEG, these authors have observed stronger spectral power in the 20- to 60-Hz band for coherent images compared to a condition in which no coherent object is perceived. At the heart of the argument is the temporal correlation, or

binding, hypothesis according to which temporal synchronization in the gamma band occurs in response to illusory figures versus incoherent images that do not form a recognizable percept. From a psychological perspective, feature binding is defined as the temporal linking of the common features of a stimulus (Gray & Singer, 1989). In Gestalt psychology, such common features of high visual salience include continuity, proximity, similarity, closure, and common fate motion (e.g., two bars that move together). Some mechanism is therefore needed by way of which attributes of an image that belong together are distinguished from other attributes that may be present simultaneously. Because of the sensitivity of neurons to

timing of their synaptic inputs, it has been argued that synchronization of neuronal firing of a cell assembly is the signature of common features and of relatedness. Indeed, microscopic and macroscopic measurements of the visual cortex have shown that high-frequency responses to bars that move in the same direction are stronger than those which have opposite motion (Eckhorn et al., 1988; Singer & Gray, 1995). Tallon-Baudry, Bertrand, Delpuech, and Pernier (1996) showed that stronger 40-Hz responses occur to Kanizsa triangles compared to non-triangles, which can be associated with feature-binding since Kanizsa triangles comprise aligned lines that constitute continuity (see also Keil, Müller, Ray, Gruber, & Elbert, 1999; Müller et al., 1996; Tallon, Bertrand, Delpuech, & Pernier, 1995; Tallon-Baudry, Bertrand, Wienbruch, Ross, & Pantev, 1997).

We used an MEG beamformer analysis method (Hillebrand, Singh, Holliday, Furlong, & Barnes, 2005; Vrba & Robinson, 2001) to study the visual cortex responses to simple gratings. We have previously shown that gamma activity in the visual cortex, and in particular V1, is modulated by changes in the fundamental aspects of gratings such as spatial frequency and contrast (Adjamian et al., 2004; Hall et al., 2005). These findings suggest that gamma activity in V1 may be related to features other than those related to formation of perceptual Gestalten.

Gamma power as a function of spatial frequency

We have previously shown that luminance gratings induce gamma band activity as increases in power within the primary visual cortex (Adjamian et al., 2004). The strength of this activity is dependent upon the spatial frequency (SF) of gratings with maximal activity for gratings of 2–4 cycles per degree (cpd). Moreover, we detected no activity arising from extrastriate visual areas for most SFs, particularly those of 2–4 cpd. This finding indicated that local gamma activity in V1 is highly sensitive to and contingent upon this elementary feature of the visual stimulus. Moreover, spectral analysis of the stimulus-related induced activity for gratings of 3 cpd demonstrated that this activity develops its maximum with stimulus onset, lasting the duration of its presentation, and ceases rapidly after the removal of the stimulus. In a similar study, Hall et al. (2005) have recently shown that gamma activity in the visual cortex has a linear relationship with stimulus contrast such that as grating contrast increases so does the induced gamma activity. Moreover, they show that gamma activity in V1 is represented such that the location of the activity depends on the quadrant in which the grating stimulus is displayed, thus conforming to retinotopic organization of early visual areas. We have also shown that in addition to the varying magnitude and spatial extent of induced gamma activity, its temporal

characteristics also vary with stimulus SF (Hadjipapas, Adjamian, Swettenham, Holliday, & Barnes, 2007). These results together show that local gamma activity induced in the primary visual cortex is highly sensitive to independent and fundamental properties of gratings such as spatial frequency, contrast, and temporal frequency.

To extend our investigation of the role of fundamental properties of gratings, we investigated visual cortical responses to isoluminant chromatic gratings of varying spatial frequency. Color perception is believed to be a higher order cognitive process and is involved in other areas of the visual cortex, including area V4 (e.g., McKeefry & Zeki, 1997; Zeki, Watson, Lueck, Friston, & Kennard, 1991) and area V8 (Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998). In this study, we have used photometrically isoluminant red/green gratings rather than luminance contrast gratings that we used in a number of previous studies. For these gratings, chromatic contrast is high while luminance contrast is low. We can therefore test the hypothesis that gamma band activity is related to luminance contrast processing specifically and not color contrast. We use the same cohort of subjects in order to facilitate the comparison between MEG cortical responses to isoluminant and contrast gratings.

Methods

Seven subjects (3 males, 4 females, aged 24 to 47 years) gave their consent to participate in the study. MEG data were collected using a 151-channel CTF Omega system (CTF Systems Inc., Port Coquitlam, Canada) with a third-order synthetic gradiometer configuration and a sampling rate of 625 Hz. We used isoluminant red/green gratings presented at SFs ranging from 0.5 to 6 cpd. We opted for a square wave luminance profile in order that the results become directly comparable to those we obtained with black and white contrast gratings, which optimally induce visual abnormalities (Adjamian et al., 2004). The chromaticity coordinates of the three phosphors were $r_x = 0.625$, $r_y = 0.340$, $g_x = 0.280$, $g_y = 0.595$, $b_x = 0.155$, and $b_y = 0.070$. The mean luminance of the red and the green components of the isoluminant grating were equal and maintained at 12 cd/m^2 , measured with a Minolta photometer, and the display was gamma corrected linearly over the range of contrast used. Red and green gratings were generated and modulated independently for physical luminance. They were then combined 180 degrees out of phase to produce the physically isoluminant red/green gratings. The mean luminance of the gratings was set at the same level as the achromatic gratings used in our previous study (Adjamian et al., 2004). Each grating was presented for 5 s in static mode and was replaced by a yellow blank screen with the same mean luminance. This

sequence was repeated 20 times for each SF of the grating. The gratings were generated using a Cambridge Research Systems VSG 2/3 grating generator and were displayed on an Eizo Flexscan T560i, gamma-corrected color monitor with 14-bit luminance resolution at a frame rate of 100 Hz. The gratings subtended six degrees of visual angle and were centrally fixated.

The MEG data were analyzed using a beamformer technique called Synthetic Aperture Magnetometry (SAM) (Vrba & Robinson, 2001). SAM generates volumetric images of power changes between the active and the passive states within pre-selected frequency bands. A detailed description of SAM and its applications is beyond the scope of this paper but is adequately described in the literature elsewhere (for example, see the review by Hillebrand et al., 2005). Briefly, with SAM, each voxel in the brain is scanned using an optimal spatial filter for that voxel. This spatial filter provides a measure of source power in each voxel as a function of time and is constructed using the weighted sum of all the MEG sensors (Vrba & Robinson, 2001). The differential power estimates between active and passive states are then

divided by MEG sensor noise projected through the beamformer (Van Veen, van Drongelen, Yuchtman, & Suzuki, 1997; Vrba & Robinson, 2001) to obtain pseudo-*t* values. The output can be seen as a synthetic depth electrode or as a *virtual electrode* that has the same millisecond temporal resolution as the original MEG signals (Barnes & Hillebrand, 2003). Here, SAM images were generated by comparing the responses to the chromatic and the contrast stripe (active states) to those for the uniform yellow and gray screen (passive states) in frequency bands that ranged from 1 to 100 Hz.

Results

For each subject in the study, gamma activity was locally present in V1 in response to luminance contrast gratings and was maximal for 3-cpd gratings. On the other hand, the red/green chromatic gratings of the same spatial composition induced relatively little or no gamma activity

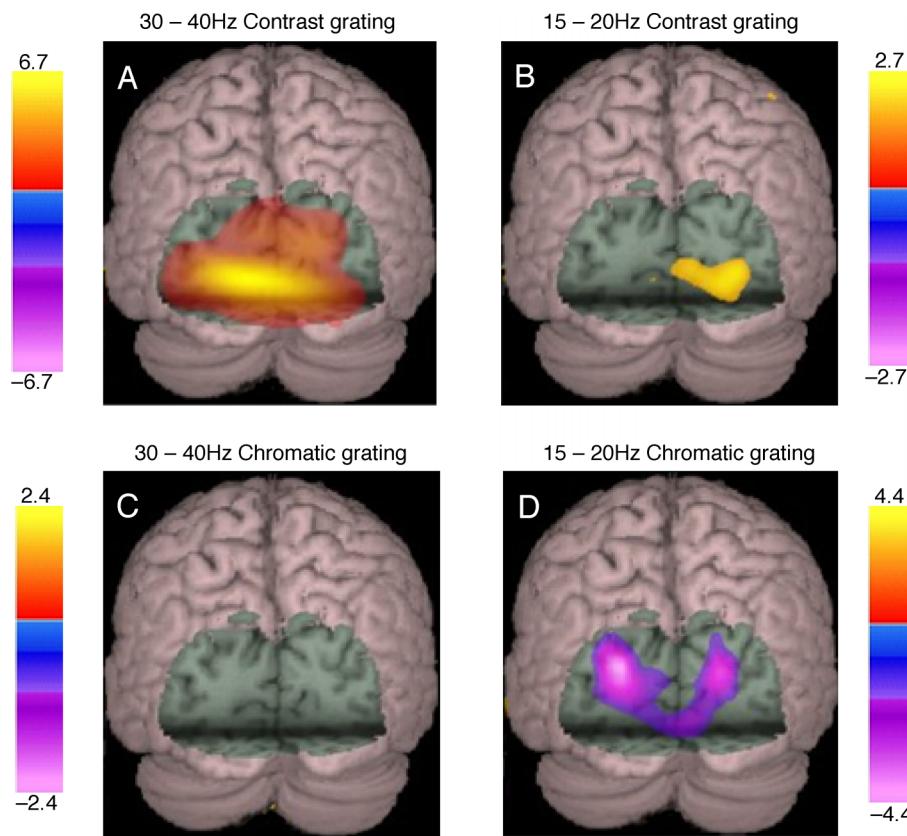


Figure 1. Beamformer images of differential activation in visual cortex in response to contrast and isoluminant chromatic gratings. Beamformer analysis was conducted on the entire 5 s of active versus passive periods. Each color bar depicts increase (red/yellow) or decrease (white/purple) in cortical power (pseudo-*t*). (A) Activity in the 30- to 40-Hz band to a black/white maximum contrast grating showing increase in power on the bank of the calcarine sulcus; (B) oscillatory power in the 15- to 20-Hz (beta) band is significantly reduced in response to the same contrast grating; (C) at photometric isoluminance, the power in the gamma band is absent; (D) at photometric isoluminance, the main effect is seen in the 15- to 20-Hz beta band as a decrease in cortical power. This decrease in power in the extrastriate cortex for the chromatic gratings may be indicative of color-related processing.

in V1. Visual cortical responses to these latter gratings gave rise to decreases in power in the lower 15–20 Hz beta band arising mainly from the extrastriate cortex. This is consistent with previous metabolic studies showing activation within this region due to chromatic gratings (e.g., Hadjikhani et al., 1998; McKeeffry & Zeki, 1997; Zeki et al., 1991). **Figure 1** shows this difference in one subject. Note that for each image, the peak response is in a different slice and the maximum task-related power change between the stimulus on and off states is indicated by the color bars. The statistical pseudo-*t* values are

metrics of the change in electrical power in the cortex between the active period (gratings) relative to the passive or baseline period (uniform yellow screen of same mean luminance).

For both chromatic and achromatic activity in V1, time-frequency analysis was performed using a wavelet bootstrap method (Graimann, Huggins, Levine, & Pfurtscheller, 2002) for activity in the voxel corresponding to the peak gamma activity (i.e., the voxel that showed maximum power change (pseudo-*t*) in the 30- to 40-Hz band in the beamformer image). **Figure 2** depicts this analysis for

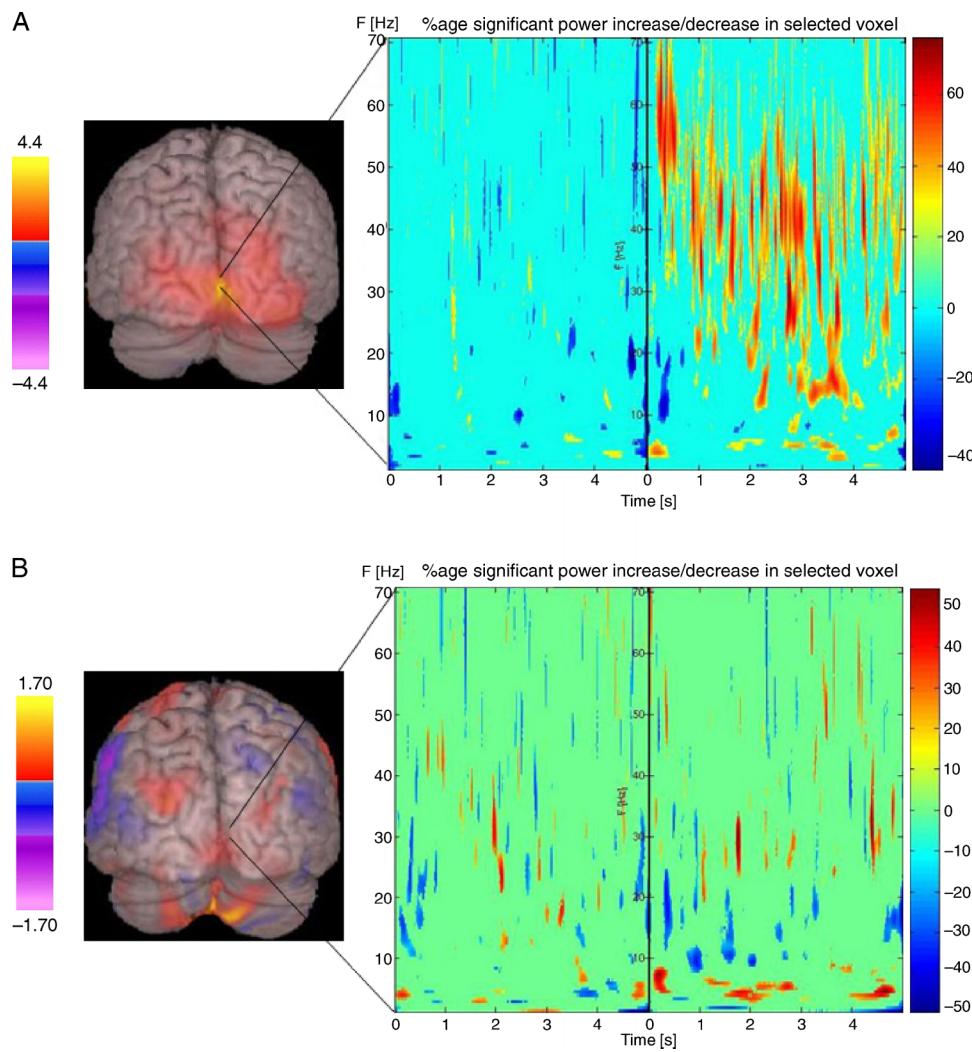


Figure 2. Bootstrap time-frequency representation of a voxel in V1. (A) Image on the left shows significant power increase in the 30- to 40-Hz band in V1 induced by the onset of the 3-cpd contrast gratings. The analysis was conducted on the entire 5 s active versus passive periods (black/white gratings vs. uniform gray). The yellow/red colors at the occipital pole indicate relative increase in power (pseudo-*t*). The time-frequency representation on the right shows the difference between the two 5 s states in the peak V1 voxel. Note the sustained activity around 40 Hz for the duration of the stimulus presentation. (B) On the left, the beamformer image of power change, also in the 30- to 40-Hz band, due to the onset of the isoluminant 3-cpd red/green stripe. The analysis was conducted on the entire 5 s active versus passive periods (red/green gratings vs. uniform yellow). Note the significant reduction of gamma activity in V1 compared to the black and the white gratings, also depicted in the spectral analysis on the right. In the time-frequency representation, the blue and the red colors represent the percentage of significant power decrease and power increase in the selected voxel, respectively.

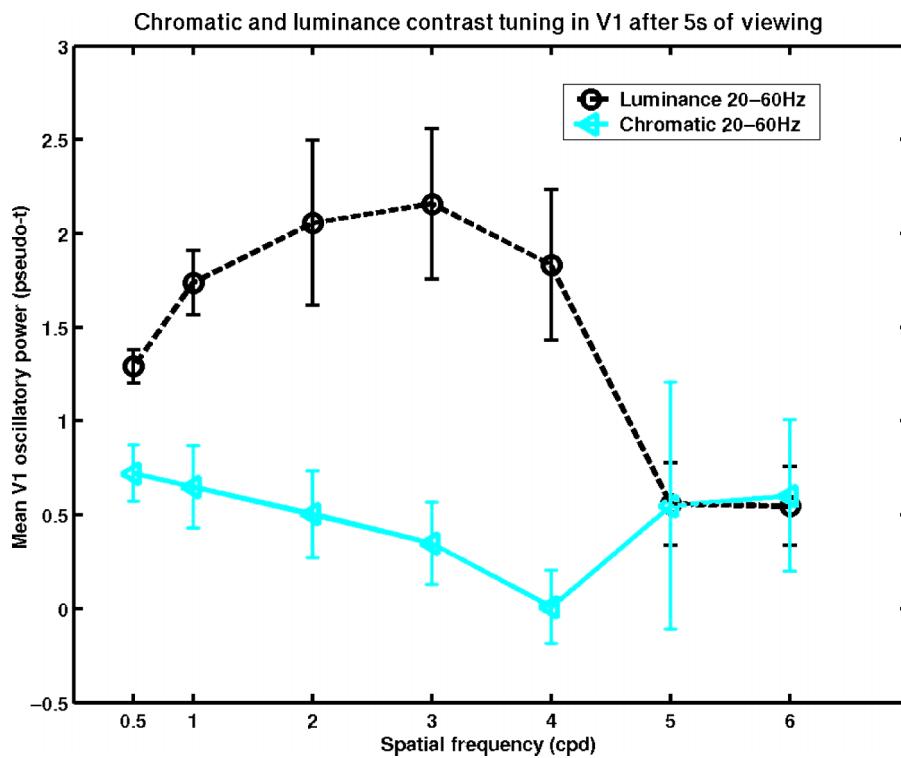


Figure 3. Two curves showing group-averaged tuning function of V1 to luminance gratings (dashed black line) and to isoluminant color gratings (solid light blue line), in the gamma frequency band, as a function of SF. The measures represent relative increases and decreases in cortical power. The error bars represent one standard error of the mean. Note the clearly discernible effect of SF upon the gamma activity in response to luminance contrast but not isoluminant chromatic gratings. Also note that the *t* values are obtained from the average of all voxels in V1 based on the calcarine fissure and are therefore different from the peak *t* values that are shown in Figure 2.

another subject in the study. The color code in the time-frequency plots (on the right) represents significant power change (thresholded at $p = 0.05$) for a given time and in a given frequency band, assessed against the average power across the whole passive period in that frequency band (Graimann et al., 2002).

Average activity in the voxels of V1 for each subject and each condition was compared to illustrate the differences between chromatic and luminance responses of V1. In Figure 3, the dashed and solid lines represent responses to luminance and chromatic gratings, respectively, as a function of SF. SF of luminance gratings modulates gamma activity in V1, which is not the case with chromatic gratings.

per-se. Indeed, these oscillations develop, in anesthetized animals, due to very basic stimulus properties such as contrast (Henrie & Shapely, 2005; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001) and contour (Gail, Brinksmeyer, & Eckhorn, 2000) and persist for the entire stimulus duration (Figure 2A; Hadjipapas et al., 2007; Logothetis, 2002; Rols, Tallon-Baudry, Girard, Bertrand, & Bullier, 2001) long after perception has occurred.

Previously much work has linked gamma oscillations at the cellular level (Gray & Singer, 1989; Singer & Gray, 1995) or the scalp (Tallon-Baudry & Bertrand, 1999) to conscious perception of form. Our study serves to emphasize that modulations in gamma power in primary visual cortex can be achieved (or abolished) using stimulus manipulations that concern *local* rather than *global* stimulus attributes.

Note also that the color contrast gratings used were set at photometric isoluminance and formed from square wave gratings. That is, they possessed significant luminance artifact. Despite this fact, there is still a considerable difference in the cortical response to the two gratings types. It may be argued that afterimages affected the results presented here, particularly as the phase of the red/green bars was not reversed across trials. Afterimages may be a complicating factor at low contrast, reducing sensitivity for detection. However, as the stimuli we used

Discussion

The results of this MEG study clearly show that gratings defined by chromaticity do not give rise to the gamma band changes in V1 characteristic of luminance gratings. That is, gamma oscillations in primary visual cortex seem to relate to very low level stimulus attributes (such as luminance contrast) rather than stimulus gestalts (gratings)

were considerably above threshold, performance would not be strongly affected by the presence of afterimages. Furthermore, identical spatial and temporal stimulus parameters (stationary square-wave grating without temporal phase modulation) were used in our previous study with achromatic luminance contrast gratings (Adjamian et al., 2004), and yet entirely different results were obtained with chromatic contrast modulation. The absence of gamma activity in V1 to chromatic gratings does not indicate that this region is silent for such stimuli but rather reflective of the analysis methodology particularly with regards to the fact that the analysis was performed over 5 s of stimulus presentation. McKeefry and Zeki (1997) have shown that chromatic responses do occur in V1, but within the first second of stimulus presentation.

In conclusion, using the same cohort of subjects, we have shown that visual cortex responses to chromatic and achromatic gratings are different to each other in significant ways. We found a significant reduction in gamma activity in response to chromatic gratings arising from V1 relative to achromatic contrast gratings. Furthermore, the change in SF of chromatic gratings did not seem to alter the activity. Both findings are in stark contrast to results obtained with black and white gratings. Our results indicate that activation of V1 in the gamma band represents local induced activity, the strength of which varies with subtle changes in stimulus features such as contrast, luminance, and SF. In this regard, V1 gamma activity may be related to stimulus representation instead of cognitive processing.

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