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Visual stimulus eccentricity affects human gamma peak frequency

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ABSTRACT

The peak frequency of neuronal gamma-band synchronization has received much attention in recent years. Gamma peak frequency shifts to higher frequency values for higher contrast, faster moving, and attended stimuli. In monkey V1, gamma peak frequency for a drifting grating is higher for a parafoveal as compared to an eccentric stimulus (Lima et al., 2010). This effect might be due to the cortical magnification factor: the higher cortical magnification for parafoveal stimuli increases the velocity with which the cortical representations of the moving grating stripes move across the cortical surface. Since faster moving stimuli lead to higher gamma frequency, a faster moving cortical representation might do the same. This explanation predicts that the eccentricity effect on gamma peak frequency is absent for stationary stimuli. To test this, we investigated the effect of eccentricity on gamma peak frequency by recording magnetoencephalography in human subjects while they viewed moving or stationary gratings. We found that both the moving and the stationary stimuli induced lower peak frequencies for larger eccentricities, arguing against an explanation based on the cortical magnification factor. We further investigated whether this eccentricity effect was explained by differences in the size or the spatial frequency of the expected cortical activation. Neither of those explained the eccentricity effect. We propose that the different stimulus and top-down factors leading to higher gamma peak frequency all result in higher stimulus salience, that salience is translated into gamma peak frequency, and that gamma peak frequency might subserve the preferential processing of neuronal activity induced by salient stimuli.

Introduction

Neuronal synchronization in the gamma frequency band (30–100Hz) has been implicated in several cognitive functions (Buschman and Miller, 2007; Buzsaki and Draguhn, 2004; Colgin et al., 2009; Fries, 2009; Singer and Gray, 1995). Gamma-band synchronization is observed during visual (Hoogenboom et al., 2006; Muthukumaraswamy et al., 2009), somatosensory (Bauer et al., 2006), and auditory (Brosch et al., 2002) stimulation; it is involved in memory processes (Fell et al., 2001; Howard et al., 2003) and motor control (Brown et al., 1998; Schoffelen et al., 2005). It is enhanced during attention (Bosman et al., 2012; Fries et al., 2001), and its moment-by-moment fluctuations predict the behavioral benefits of attention (Hoogenboom et al., 2010; Womelsdorf et al., 2006). Gamma synchronization is also affected in cognitive disorders, notably schizophrenia, with patients showing lower gamma power than healthy controls (see Uhlhaas and Singer (2010), for a review).

In recent years, the peak frequency of the visually induced gamma-band activity has gained much attention. Several studies have shown that the peak frequency is modulated by a number of factors, and thus may carry information about visual stimulus properties. For example, (Ray and Maunsell, 2010) reported that macaque V1 gamma peak frequency is positively correlated with visual stimulus contrast. Also stimulus velocity is positively correlated with gamma peak frequency: in macaque V1, gamma peak frequency increased systematically when grating drift speed increased from 1 to 12°/s (Gray et al., 1990). In human subject visual cortex, gamma peak frequency is higher for moving as compared to stationary gratings (Muthukumaraswamy and Singh, 2013; Swettenham et al., 2009). Stimulus size is negatively related to gamma peak frequency: in monkey V1, larger stimuli induced lower peak frequencies than small-diameter stimuli (Gieselmann and Thiele, 2008; Ray and Maunsell, 2011). The presence of this effect in the human is however inconclusive (Busch et al., 2004; Perry et al., 2013). Recently, Bosman et al. (2012) demonstrated that also attention to a visual stimulus can modify the induced gamma peak frequency: neuronal groups showed a gamma peak frequency that was 2–3 Hz higher, when their activating stimulus was attended as compared to unattended.

Recently, Lima et al. (2010) found a negative relation between stimulus eccentricity and gamma peak frequency. They recorded from two sites in V1 with receptive fields at eccentricities of 3 and 10° while the monkey was shown a single, moving grating that encompassed the receptive fields of both recording sites. For the more eccentric site, the gamma response had a lower peak frequency than for the parafoveal site (53 vs 67 Hz, respectively). The authors proposed that this effect can be explained by the cortical magnification factor, i.e. the phenomenon that the central visual field is overrepresented in the visual cortex relative to the periphery (Daniel and Whitteridge, 1961). The decline in representation volume is

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roughly linear (Slotnick et al., 2001), so if a given stimulus activates a cortical volume V when presented at the fovea, it will activate a cortical volume V/M, when placed in the periphery, with M describing the amount of cortical magnification at the fovea relative to this specific peripheral location. In this context, the moving grating stripes of the stimuli used by Lima et al. (2010), will move faster across the cortical surface when presented peripheral, than when presented perifoveally. We will refer to this concept as "cortical velocity". These differences in "cortical velocity" would then lead to differences in gamma peak frequency, in line with the findings by Friedman-Hill et al. (2000) and Swettenham et al. (2009). The eccentricity effect they found would thus in fact be a velocity effect.

This "cortical velocity" hypothesis predicts that stationary stimuli will induce gamma-band responses whose peak frequencies are not modulated by stimulus eccentricity. We set out to test this prediction by showing moving and stationary gratings at different eccentricities to human subjects, while their brain activity was recorded using magnetoencephalography (MEG). We found that the peak frequency of gamma-band responses to stationary stimuli is similarly modulated by stimulus eccentricity as for moving stimuli, arguing for an alternative explanation of the eccentricity effect.

Material and methods

Subjects

14 neurologically healthy volunteers (10 females) were recruited via the participant database of the Radboud University Nijmegen. Their mean age was 22.1 years (SD 3.4) and they had normal or corrected-to-normal vision. The experiment was approved by the local ethics committee (CMO region Arnhem-Nijmegen).

Experimental setup

Subjects performed the experiment while seated upright in a 275-channel whole-head magneto-electroencephalography (MEG) system (CTF Systems, Canada) that was inside a magnetically shielded room (MSR). MEG data was recorded at 1200 Hz, stored and downsampled to 600 Hz. Four bipolar EMG electrodes were placed at the sides of both eyes, as well as above and below the left eye. These respective horizontal and vertical EOG signals were co-recorded with the MEG signal for offline artifact rejection (blink detection). Eye movements were recorded, for both eyes separately, at 1000 Hz each, using an Eyelink 2000 eyetracker system, to check subjects' fixation accuracy. Stimuli were backprojected onto a translucent screen 90 cm in front of the subjects (projection dimensions: 45 × 34 cm, W × H) using an EIKI LCD projector that was outside the MSR.

Paradigm and stimuli

Each trial (Fig. 1) started with a pre-baseline fixation of 0.33 s, in which a gray circular Gaussian (standard deviation 0.25°) was presented centrally as fixation point on an isoluminant background of 50% grey value. Subjects were instructed to keep fixation at the fixation point throughout the trial. After the pre-baseline, the fixation point turned white, indicating the start of a 1.33 s long baseline period. Hereafter, one stimulus of varying eccentricity was presented. The subjects' task was to press a response button with their right index finger when the fixation point changed from white to yellow. This could happen any time between 0.75 and 3.0 s after the onset of the stimulus. The trial ended after a response (whether correct or too early), if no button press was made within the response window of 0.5 s, or if the maximum stimulation period of 3.0 s was reached.

The stimulus was a circular grating of 4.2° diameter and a spatial frequency of 3 cycles/°, presented at maximum contrast. The experiment consisted of 6 stimulus conditions, following a 3 × 2 design (eccentricity × velocity). The stimulus was presented with its center either at 6°, 3°, or 0° left of the center of the screen, and was either static or contracting towards the grating center with a velocity of 0.66°/s (Hoogenboom et al., 2006, 2010). Irrespective of eccentricity and velocity, there was an aperture of 1.0° diameter at the center of the stimulus (effectively turning the stimulus into an annulus), which allowed the fixation Gaussian to be visible in the 0° conditions. Each condition was presented in 120 trials, for a total of 720 trials in the experiment. Conditions were randomly interspersed, and the total experiment lasted approximately 60 min. Before the actual experiment started, subjects performed a couple of practice trials. Note that this stimulus configuration might result in partial cancellation of activation by the activities on either bank of the calcarine sulcus. In the present configuration however, the cancellation is kept as similar as possible for the three eccentricity conditions, as opposed to when stimuli were e.g. presented on a diagonal from the center downwards.

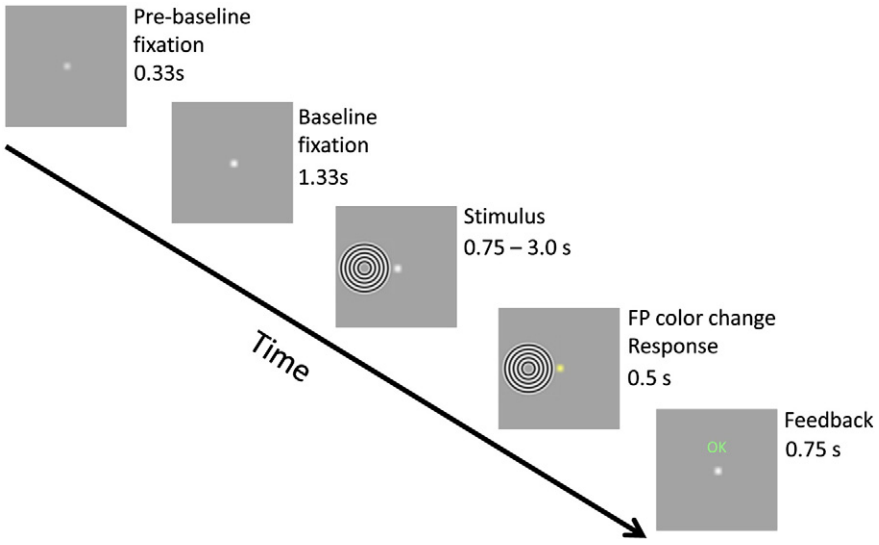

Fig. 1. Experimental paradigm. Each trial started with a 0.33 s pre-fixation baseline, followed by 1.33 s of actual baseline. Then, a visual stimulus was presented at three possible locations in the visual field: either at fovea, or 3° or 6° left of the fixation point (FP). The stimulus could either be moving inwards at 0.8°/s or be stationary. After a variable time period post stimulus onset (0.75–3.0 s) the FP assumed a yellow color, cueing the subject to respond as quickly as possible by pressing a response button. After this, feedback on performance was presented, and the subsequent trial started. Stimulus size and location not to scale.