



## Review

## Cortical gamma responses: Searching high and low

Nathan E. Crone\*, Anna Korzeniewska, Piotr J. Franaszczuk

Department of Neurology, The Johns Hopkins University School of Medicine, 600 N. Wolfe St., Meyer 2-147, Baltimore, Maryland 21287, United States

## ARTICLE INFO

## Article history:

Received 19 August 2010  
 Received in revised form 22 October 2010  
 Accepted 26 October 2010  
 Available online 23 November 2010

## Keywords:

Gamma band  
 High gamma  
 Oscillations  
 Electroencephalography  
 Electroencephalography  
 Functional mapping  
 Induced responses  
 ERD/ERS

## ABSTRACT

In this paper, a brief, preliminary attempt is made to frame a scientific debate about how functional responses at gamma frequencies in electrophysiological recordings (EEG, MEG, ECoG, and LFP) should be classified and interpreted. In general, are all gamma responses the same, or should they be divided into different classes according to criteria such as their spectral characteristics (frequency range and/or shape), their spatial-temporal patterns of occurrence, and/or their responsiveness under different task conditions? In particular, are the responses observed in intracranial EEG at a broad range of “high gamma” frequencies (~60–200 Hz) different from gamma responses observed at lower frequencies (~30–80 Hz), typically in narrower bands? And if they are different, how should they be interpreted? Does the broad spectral shape of high gamma responses arise from the summation of many different narrow-band oscillations, or does it reflect something completely different? If we are not sure, should we refer to high gamma activity as oscillations? A variety of theories have posited a mechanistic role for gamma activity in cortical function, often assuming narrow-band oscillations. These theories continue to influence the design of experiments and the interpretation of their results. Do these theories apply to all electrophysiological responses at gamma frequencies? Although no definitive answers to these questions are immediately anticipated, this paper will attempt to review the rationale for why they are worth asking and to point to some of the possible answers that have been proposed.

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## 1. Introduction

Since the advent of EEG recordings in humans and animals, investigators have observed that functional brain activation is associated with suppression of resting EEG rhythms (e.g. alpha, mu, beta, etc.) and the appearance of low voltage activity at faster frequencies (Adrian and Matthews, 1934; Berger, 1930; Jasper and Carmichael, 1935). Subsequent research on EEG activity at gamma frequencies (>30 Hz) related both spontaneous and evoked activity, particularly at 40-Hz, to cortical function in both animals and humans (Bressler and Freeman, 1980; Galambos et al., 1981; Loring and Sheer, 1984; Spydell et al., 1979). Interest in this activity was further intensified by experimental and theoretical work in the 80s and 90s suggesting a role for gamma oscillations in basic mechanisms of neural coding (Gray, 1999; Gray and Singer, 1989; Singer, 1993). In particular, LFP recordings in cat visual cortex showed that during appropriate visual stimulation, oscillatory neuronal firing in a frequency range of 30–80 Hz became synchronized between spatially separate columns in area 17 (Gray et al., 1989), between areas 17 and 18 (Eckhorn et al., 1988), and even between areas 17 of the two hemispheres (Engel et al., 1991). Because this synchronization was

dependent upon global stimulus properties, it was proposed to serve as a mechanism in perceptual grouping. More generally, synchronization at gamma frequencies was hypothesized to form a temporal code that dynamically “binds” spatially segregated neurons (e.g. with different retinotopic receptive fields) into assemblies representing higher-order, or global, stimulus properties (e.g. an object common to different receptive fields) (Singer and Gray, 1995; Von der Malsburg, 1995). As a corollary, synchronization was proposed to identify neurons belonging to different assemblies, solving the “superposition problem” of assembly coding (Gray, 1999). These hypotheses were linked with EEG gamma oscillations by experiments (Murthy and Fetz, 1992; Sanes and Donoghue, 1993) demonstrating synchronization of single unit firing with LFP gamma oscillations, suggesting that gamma oscillations facilitate and/or are facilitated by neuronal synchronization. The LFP gamma oscillations themselves are widely believed to depend on rhythmic and coherent firing in networks of inhibitory interneurons (Bartos et al., 2007; Buzsaki and Chrobak, 1995; Grenier et al., 2001).

Until recently, it was difficult to reliably record high frequency responses in humans, due in part to limitations in EEG recordings and in part to low signal-to-noise ratio for this activity at the scalp surface. This began to change, however, as digital EEG systems were introduced with more powerful specifications and as researchers began to exploit the investigative potential of intracranial EEG recordings in patients undergoing epilepsy surgery. Prior to these developments, most reports of EEG gamma responses in humans were

Abbreviations: ECoG, Electroencephalography; EEG, electroencephalography; MEG, magnetoencephalography; LFPs, local field potentials.

\* Corresponding author. Tel.: +1 410 955 6772; fax: +1 410 955 0751.

E-mail address: [ncrone@jhmi.edu](mailto:ncrone@jhmi.edu) (N.E. Crone).

observed as components of phase-locked (evoked) or steady-state responses at, or in the neighborhood of, 40 Hz (Galambos et al., 1981). In addition, non-phase-locked 40-Hz activity was observed in some subjects during activation of motor cortex (Pfurtscheller et al., 1994; Pfurtscheller and Neuper, 1992), auditory cortex (Pantev, 1995), and visual cortex (Tallon-Baudry et al., 1997). However, few studies had considered the possibility of non-phase-locked responses at higher gamma frequencies. Brindley and Craggs (1972), while searching for components of local field potentials in monkey motor cortex that could be used to drive prosthetics, had found that if the signal was filtered between 80 Hz and 250 Hz and then rectified and smoothed, it was reliably correlated with the monkey's movements. Although the potential utility of this activity for controlling prostheses was recognized at the time, it was not exploited until much later (Leuthardt et al., 2004; Miller et al., 2009b). Furthermore, the significance of this finding with respect to cognitive neurophysiology was not fully appreciated nor was it further explored, perhaps because the aforementioned excitement about gamma oscillations had not yet taken hold.

In the 1980s and 1990s, as the surgical management of intractable epilepsy increasingly relied upon long-term, extra-operative monitoring with subdural electrocorticography (ECoG) to better localize seizure foci, clinicians and researchers began to explore ECoG as a potential tool for both functional mapping and cognitive neuroscience research. Although significant early progress was made in these studies by focusing on phase-locked response, i.e. event-related potentials (Halgren et al., 1995; McCarthy and Wood, 1987; Nobre et al., 1994), other studies began to investigate non-phase-locked responses (Crone et al., 1994, 1995). Interest in these responses was based in part on a growing appreciation of them in non-invasive EEG and MEG studies, where they were known as induced responses (Herrmann and Knight, 2001; Pantev, 1995) or as event-related desynchronization (ERD) and event-related synchronization (ERS) (Pfurtscheller, 1977, 1992). In addition, their lower sensitivity to temporal jitter was considered advantageous for functional tasks involving downstream cortical processing with more variable latencies (Herrmann et al., 2004). Furthermore, these studies were influenced by the aforementioned experimental and theoretical accounts of gamma oscillations, which by then had gained substantial attention, and which did not assume phase-locking to a stimulus or event.

## 2. Experimental findings in humans

While exploring human ECoG as a tool for functional mapping and cognitive neuroscience, event-related, non-phase-locked responses to a variety of functional tasks were surveyed across a range of frequencies, including traditional alpha (8–13 Hz), beta (13–30 Hz), and gamma (>30 Hz) frequencies. Using tasks designed to activate sensorimotor, auditory, visual, and language cortices (Crone et al., 1994, 1995), these studies observed spectral perturbations (e.g. ERD/ERS) that were generally in agreement with the findings of previous non-invasive EEG and MEG studies. However, an unexpected but consistent finding across these studies was that cortical activation was accompanied by a power increase in a broad range of frequencies that were substantially higher than the traditional 40 Hz gamma band. Because these responses were discovered in the context of searching for gamma oscillations in lower frequencies, without any knowledge of the studies by Brindley and Craggs (1972) over two decades earlier, they were provisionally called “high gamma”, and their physiological significance was interpreted in the context of the burgeoning literature on gamma oscillations. However, as discussed later, investigations of high gamma responses have since revealed response properties that further distinguish them from “low” gamma oscillations and suggest potentially different interpretations with regards to their underlying neurophysiology.

Early accounts of ECoG spectral responses (Crone et al., 1998a,b) focused on their localization within the relatively predictable somatotopic organization of sensorimotor cortex. This was done to validate these responses prior to their application to language cortex and other brain regions with less predictable functional anatomy. Compared to alpha power suppression (ERD) and “low gamma” power augmentation (ERS) during a visually cued motor task, augmentation of high gamma power (70–100 Hz in this case) appeared to be more discretely localized with respect to the expected anatomy and timing of cortical activation. In particular, high gamma responses were typically observed in fewer electrodes than responses at lower frequencies. Cortical stimulation at these sites usually interfered with movement of the same body part or caused involuntary movement of it. In addition, lower frequency responses appeared to have a slower temporal evolution, with more delayed latencies and longer durations, while high gamma responses had an abrupt onset and offset (Zygierevicz et al., 2005) that corresponded to the onset and offset of cued isometric muscle contractions, i.e. changes in muscle force. These basic properties of high gamma responses in sensorimotor cortex have been consistent across studies using a variety of motor tasks and signal analyses (Brovelli et al., 2005; Brunner et al., 2009; Dalal et al., 2008; Leuthardt et al., 2007; Miller et al., 2007; Ohara et al., 2000; Pfurtscheller et al., 2003). In addition, high gamma responses in sensorimotor cortex have since been shown to be of potential utility in the development of ECoG as a brain interface for controlling prosthetic devices (Gonzalez et al., 2006; Leuthardt et al., 2004; Miller et al., 2009b; Reddy et al., 2009).

Although a potential distinction between responses in high vs. low gamma frequencies was first reported in studies of sensorimotor cortex, this suspicion was deepened by the results of ECoG studies of auditory cortex (Crone et al., 2001a). As in studies of sensorimotor cortex, in comparison to non-phase-locked responses in lower frequencies, high gamma responses were observed in a smaller number of sites in posterior superior temporal gyrus (pSTG) critical for auditory discrimination. The temporal envelopes of these responses were again faster than those of lower frequency responses. In addition, high gamma responses in dominant pSTG were more robust during speech discrimination than during tone discrimination, consistent with the critical role of this site in processing the more complex acoustic features of speech. However, this study also afforded a more detailed analysis of the reactivity of the power spectrum during cortical activation. This showed that in ECoG recorded from dominant pSTG, speech discrimination was consistently associated with power augmentation at high gamma frequencies (in this case >80 Hz). However, depending on the electrode site or even the subject, power in lower gamma frequencies could either be increased or decreased. Furthermore, power augmentation was evident across a wide range of frequencies that extended well beyond 100 Hz, without any clear or consistent upper boundary. The picture that began to emerge was that cortical activation is associated with power augmentation over a large range of frequencies and that the lower boundary of this power augmentation is quite variable. Sometimes this extends down to traditional gamma frequencies, e.g. 40 Hz, but sometimes it does not. This variability in the direction of power changes at lower gamma frequencies may be due to variability in the frequency range over which event-related power suppression (ERD) occurs. For example, if task-related power suppression at alpha/beta frequencies extends into low gamma frequencies, it may mask any power augmentation in this frequency range. The most consistent power augmentation, however, can be observed at high gamma frequencies though the lower boundary of this response may sometimes extend down to low gamma frequencies. Subsequent studies of auditory cortical physiology in both humans (Chang et al., 2010; Edwards et al., 2005; Edwards et al., 2009; Kaiser and Lutzenberger, 2005; Lenz et al., 2008; Trautner et al., 2006) and monkeys (Brosch et al., 2002; Steinschneider et al., 2008) have found

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