

NEUROSCIENCE FOREFRONT REVIEW

EARLY GAMMA OSCILLATIONS

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Abstract—Gamma oscillations have long been considered to emerge late in development. However, recent studies have revealed that gamma oscillations are transiently expressed in the rat barrel cortex during the first postnatal week, a “critical” period of sensory-dependent barrel map formation. The mechanisms underlying the generation and physiological roles of early gamma oscillations (EGOs) in the development of thalamocortical circuits will be discussed in this review. In contrast to adult gamma oscillations, synchronized through gamma-rhythmic perisomatic inhibition, EGOs are primarily driven through feedforward gamma-rhythmic excitatory input from the thalamus. The recruitment of cortical interneurons to EGOs and the emergence of feedforward inhibition are observed by the end of the first postnatal week. EGOs facilitate the precise synchronization of topographically aligned thalamic and cortical neurons. The multiple replay of sensory input during EGOs supports long-term potentiation at thalamocortical synapses. We suggest that this early form of gamma oscillations, which is mechanistically different from adult gamma oscillations, guides barrel map formation during the critical developmental period. © 2013 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: gamma oscillations, neonate, cortex, thalamus, electroencephalogram.

Contents	
Introduction	240
EGOs: electrographic features	241
Developmental profile of EGOs and relevance to premature human electroencephalograms (EEGs)	241
Time lock to stimulus	242

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Abbreviations: CSD, current source density; dLGN, dorsal lateral geniculate nucleus; EEG, electroencephalograms; EGO, early gamma oscillation; EPSC, excitatory postsynaptic current; IPSC, inhibitory postsynaptic current; L2/3, layer 2/3; L4, layer 4; LFP, local field potential; MUA, multi-unit activity; NMDA, N-methyl-D-aspartic acid; P0, postnatal day 0; PSTH, peristimulus time histogram; PTX, picrotoxin; STDP, spike timing-dependent plasticity; VPM, ventral posteromedial nucleus of the thalamus; VSD(I), voltage-sensitive dye (imaging).

Spatial characteristics of EGOs	243
Synaptic correlates of EGOs	244
Thalamic origin of EGOs	245
Perisomatic inhibition	248
EGOs, synaptic plasticity and critical period	248
Summary points	249
Conflict of interest statement	250
Acknowledgments	250
References	250

INTRODUCTION

Neuronal synchronization in gamma (30–90 Hz) oscillations is fundamental for cortical functions. In the adult brain, gamma oscillations have been hypothesized to subservise perceptual binding and facilitate the transient formation of functional assemblies through the synchronization of neuronal firing, thereby supporting synaptic plasticity. A number of excellent reviews have addressed the physiological mechanisms underlying the generation and role of gamma oscillations in cognitive functions in the adult brain (Gray and Singer, 1989; Singer and Gray, 1995; Fries et al., 2001; Buzsaki and Draguhn, 2004; Fries, 2009; Wang, 2010; Whittington et al., 2011; Buzsaki and Wang, 2012). Considerable evidence indicates that the synchronization of neurons in gamma oscillation is based on synchronous inhibition through fast-spiking perisomatic parvalbumin-containing basket interneurons (Bartos et al., 2007; Whittington et al., 2011; Buzsaki and Wang, 2012). Gamma oscillations have long been considered to emerge relatively late in development. In humans, gamma oscillations emerge several months after birth and show a developmental increase until adulthood (for review, Uhlhaas et al., 2010). Similarly, in rodents, gamma oscillations emerged during the second postnatal week (Leinekugel et al., 2002; Lahtinen et al., 2002; Doischer et al., 2008). This delayed development of gamma oscillations likely reflects the delayed maturation of the perisomatic inhibition. Indeed, in rodents, basket cells develop fast-spiking features, forming synapses with excitatory cells and establishing chemical and electrical synapses with other basket cells from the end of the first postnatal week, and the maturation of these cells proceeds through the first postnatal month (Du et al., 1996; Chattopadhyaya et al., 2004; Daw et al., 2007; Huang et al., 2007; Doischer et al., 2008; Okaty et al., 2009; Wang and Gao, 2010; Goldberg et al., 2011;

Pangratz-Fuehrer and Hestrin, 2011; Yang JM et al., 2012). The long-range gamma synchronization of neuronal activity also depends on the development of supragranular cortical layers and horizontal intracortical connections that also show delayed development from the second postnatal week in rodents (Luhmann et al., 1986; Bureau et al., 2004; Borgdorff et al., 2007). Therefore, similar developmental profiles of gamma oscillations, perisomatic inhibition and intracortical connectivity fit the widely-accepted theory of gamma rhythmogenesis.

Recent studies have revealed that oscillations at gamma frequencies are transiently expressed in the rat barrel cortex during the first postnatal week (Yang et al., 2009; Minlebaev et al., 2011; Yang JW et al., 2012), well before the emergence of perisomatic inhibition and the development of supragranular layers. In the present review, we will describe the distinct features, generative mechanisms and potential physiological roles of these early gamma oscillations (EGOs) during cortical development.

EGOs: electrographic features

EGOs are short-lived oscillations lasting approximately 200 ms in the gamma frequency range (peak frequency about 55 Hz), reliably evoked through sensory stimulation (Minlebaev et al., 2011; Yang JW et al., 2012). EGOs can also occur spontaneously (Yang et al., 2009) in the rat barrel cortex during the first postnatal week. EGOs characterize the initial part of a complex sensory-evoked response, which also comprises spindle-burst (8–25 Hz) oscillations (Khazipov et al., 2004; Minlebaev et al., 2007; Yang JW et al., 2012). EGOs and spindle-bursts, in turn, are nested in a delta-wave lasting approximately 500 ms (Marcano-Reik and Blumberg, 2008; Minlebaev et al., 2009). EGOs are best observed in the layer 4 (L4) of a cortical barrel column after a brief deflection of a single principal whisker. However, EGOs are hard to detect in responses evoked through the stimulation of multiple whiskers, during which slower spindle-burst oscillations dominate the activity (Minlebaev et al., 2007, 2009; Colonnese et al., 2010).

Developmental profile of EGOs and relevance to premature human electroencephalograms (EEGs)

As a part of the immature sensory response, EGOs are expressed in the barrel cortex during a restricted developmental time window, i.e., the first postnatal week, where the cortical barrel map is formed, representing a critical period of sensory-dependent thalamocortical plasticity in the barrel cortex (Fig. 1) (Van der Loos and Woolsey, 1973; Fox, 1992, 2002; Erzurumlu and Gaspar, 2012). The close of the critical period in the L4 barrel cortex by the end of the first postnatal week coincides with an abrupt disappearance of EGOs and immature bursting (Colonnese et al., 2010; Minlebaev et al., 2011). This coincidence suggests an involvement of the immature activity

patterns, including EGOs, in barrel map development during the critical period.

Although there is agreement on the developmental disappearance of EGOs in the barrel cortex after P7–8, the onset of these oscillations is somewhat controversial. Yang and colleagues have reported that EGOs are observed at birth (postnatal day 0 (P0)) (Yang JW et al., 2012), whereas Minlebaev and colleagues (Minlebaev et al., 2011) have observed only delta-waves, occasionally organized in groups of 2–3 delta-waves, without any significant patterning of activity in the gamma frequency at P0–1 (see an example response at P1 in Fig. 1B), and an emergence of gamma oscillations starting from postnatal day P2 (Minlebaev et al., 2011).

In human premature neonates aged <25 gestational weeks, corresponding to the earliest stages of thalamocortical development compared with the late embryonic/term rat (Higashi et al., 2002; Kostovic and Judas, 2010), intermittent “smooth” delta waves lacking rapid oscillatory components (“brushes”) dominate the electroencephalographic activity. These delta wave oscillations, reminiscent of the responses evoked through sensory stimuli in the P0–1 rat barrel cortex shown in a previous study (Minlebaev et al., 2011), become intermixed with rapid rhythms (“delta-brushes”) by the seventh month of gestation in humans. Delta-brushes constitute dominant activity patterns in all cortical areas and fade near term (Anderson et al., 1985; Stockard-Pope et al., 1992; Lamblin et al., 1999; Scher, 2006; Andre et al., 2010). Similarly in rats, delta-brushes are also reliably evoked through sensory stimuli in the somatosensory and visual cortex of premature neonates (Hrbek et al., 1973; Milh et al., 2007; Colonnese et al., 2010; Stjerna et al., 2012). Therefore, from the developmental standpoint, a similar developmental sequence of smooth delta waves followed by delta-brushes is also expected in the rat. Thus, it would be of interest to know whether delta waves without EGOs are present in fetuses and preterm neonates in rats, which display EGOs at birth, and mice, in which barrel map development is delayed 1–2 days compared with rats (Rhoades et al., 1990; Schlaggar et al., 1993; Rebsam et al., 2002).

The rapid rhythms of delta-brushes in premature human neonates typically occur within an 8–25 Hz frequency band, and the association of delta-brushes with an activity at gamma frequency has not been reported (Ellingson, 1958; Dreyfus-Brisac, 1962; Parmelee et al., 1969; Nolte et al., 1969; Goldie et al., 1971; Watanabe and Iwase, 1972; Hrbek et al., 1973; Engel, 1975; Vanhatalo et al., 2002, 2005; Milh et al., 2007; Colonnese et al., 2010; Dreyfus-Brisac, 1962). Therefore, it remains unknown whether EGOs are present in humans. Notably, in the rat, EGOs are restricted to the L4 of a single cortical column and are hardly detected, even during intracortical recordings near the cortical surface (Fig. 2C) (Minlebaev et al., 2011), suggesting that EGOs would also be hard to detect using conventional scalp EEG recordings from premature human babies. However, it might become

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