International Journal of Psychophysiology 90 (2013) 99–117

Contents lists available at ScienceDirect

International Journal of Psychophysiology

journal homepage: www.elsevier.com/locate/ijpsycho

Review

A review of gamma oscillations in healthy subjects and in cognitive impairment

Erol Başar *

Istanbul Kultur University, Brain Dynamics, Cognition and Complex Systems Research Center, Istanbul, Turkey

ARTICLE INFO

Article history:
Received 3 April 2013
Received in revised form 2 July 2013
Accepted 17 July 2013
Available online 23 July 2013

Keywords:
Gamma oscillations
Cognition
Bipolar disorders
Schizophrenia
Memory

ABSTRACT

This review describes a wide range of functional correlates of gamma oscillations in whole-brain work, in neuroethology, sensory–cognitive dynamics, emotion, and cognitive impairment. This survey opens a new window towards understanding the brain's gamma activity.

Gamma responses are selectively distributed in the whole brain, and do not reflect only a unique, specific function of the nervous system. Sensory responses from cortex, thalamus, hippocampus, and reticular formations in animal and human brains, and also cognitive responses, were described by several authors.

According to reviewed results, it becomes obvious that cognitive disorders, and medication—which influence the transmitter release—change entirely the understanding of the big picture in cognitive processes.

Gamma activity is evoked or induced by different sensory stimuli or cognitive tasks. Thus, it is argued that gamma-band synchronization is an elementary and fundamental process in whole-brain operation. In conclusion, reasoning and suggestions for understanding gamma activity are highlighted.

1. Introduction

This review aims to encompass a wide range of results on gamma oscillations in whole-brain work, in neuroethology, sensory–cognitive dynamics, emotion, and cognitive impairment. A review of such a broad spectrum of data is a difficult mission; however, the trial is important for opening new avenues in understanding brain gamma activity.

Neuronal gamma-band oscillations, which can be recorded in many cortical and sub-cortical areas in the mammalian brain and in invertebrate ganglia, are evoked or induced by different stimuli or tasks. Many different gamma-band oscillatory processes are involved in diverse functions (Herrmann et al., 2004). Further, there are several views related to the role of gamma activity in the communication processing of the brain. These results often lead to controversies.

The present review argues that gamma-band activation is a fundamental process that serves as an elementary operator of brain function and communication. It was previously proposed that gamma band activities are selectively distributed in the brain, and do not reflect a specific function in the nervous system (Başar-Eroglu et al., 1992). In recent decades, several reviews were published that supported this conclusion (Fries, 2009; Herrmann et al., 2004; Uhlhaas and Singer, 2006). An extended discussion on gamma activity in cognitive impairment was included in recent conference proceedings under the umbrella of the World Federation on Clinical Neurophysiology (Başar et al., 2013).

The empirical background of the gamma band dates back to Adrian (1942), who reported that the application of odorous substances to the olfactory mucosa of the hedgehog induced trains of sinusoidal oscillations within the 30 to 60-Hz range. The studies on the 40-Hz oscillation passed a total of seven phases initiated by Adrian (1942) in the first phase. According to Lavin et al. (1959) and Hernandez-Peon et al. (1960), 40-Hz activity was not restricted to olfactory stimuli, but could be elicited by a wide range of other conditions.

The second phase took place between 1960 and 1980, and was characterized by the works of Freeman (1975), Başar et al. (1975a,b,c) and Sheer (1976), in which a variety of functions were ascribed to the gamma oscillations. Başar and Özesmi (1972) introduced the term 'gamma-response' to describe hippocampal gamma-range activity to external stimuli in cats. Enhanced gamma activity was especially seen in structures that were able to fire spontaneously in this mode ('gamma resonance'). In addition, 40-Hz oscillatory responses were also observed in humans (Sheer, 1989; Başar et al., 1976; Galambos et al., 1981). Further studies found gamma-range activities associated with visual (Eckhorn et al., 1988; Gray et al., 1989) and olfactory (Freeman, 1975, 1979) sensation. For a comprehensive review, see Başar-Eroglu et al. (1996b) and Başar (1999).

The third phase started with the work of Galambos et al. (1981). This work led to investigations concerning the sensory and cognitive correlates of the gamma oscillation, primarily in humans.

The fourth phase is shaped by the fundamental works of Eckhorn et al. (1988), and Gray and Singer (1989), which led to investigations of 40-Hz at the cellular level.

* Tel.: +90 212 498 43 92; fax: +90 212 498 45 46.
E-mail address: e.basar@iku.edu.tr.

0167-8760/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.ijpsycho.2013.07.005

The fifth phase is marked by the heterogeneity of approaches and techniques applied with the aim of fully describing gamma. During this fifth phase, Galambos (1992) suggested classifying various findings of gamma-band activities measured in different species using a categorical system, in a workshop in New York (See Galambos, 1992), as follows:

1. The *spontaneous* gamma-activity, i.e., a fraction of the total EEG energy at any given moment without intentional stimulation (Başar and Özesmi, 1972; Sheer, 1976).
2. The *induced* gamma-activity, i.e., activity initiated by—but not tightly coupled to—a stimulus (Adrian, 1942; Freeman, 1975; Freeman and Skarda, 1981).
3. The *evoked* gamma-activity, which is both elicited by and strictly time-locked to a stimulus. Numerous examples have been studied in different brain regions of human and cat models.
4. The *emitted* gamma-activity, i.e., activity that is not bound to a stimulus but rather to an internal process; demonstrated, for instance, by the use of the 'omitted stimulus' paradigm in non-mammalian vertebrates like fish (Bullock et al., 1990) or mammals like cat (Başar-Eroglu and Başar, 1991).

From the late 1990s to the present, a sixth phase is observed, during which research on gamma activity increased significantly, prompted by interest in the effects of neurotransmitters (Traub et al., 2003; Whittington et al., 1995, 2000). Further, several studies suggested that 40-Hz oscillatory activity is not restricted to sensory processing, but can also be modulated or triggered by cognitive processes (Tiitinen et al., 1993; Pulvermuller et al., 1995; Tallon-Baudry et al., 1998). Başar et al. (1995) argued that gamma responses occur throughout the brain, i.e., in a selectively distributed way, as correlates of brain functions, which can be sensory and cognitive in origin.

The seventh phase began in the 2000s, and is shaped by strategies on cognitive gamma responses, and also by increasing numbers of studies on cognitive impairment.

2. Natural frequencies of the brain. Superposition of oscillations

The functional significance of oscillatory neural activity begins to emerge from the analysis of responses to well-defined events (*event-related oscillations, phase- or time-locked to a sensory or cognitive event*). Among other approaches, it is possible to investigate such oscillations by frequency domain analysis of event-related potential (ERP), based on the following hypothesis:

> The EEG consists of the activity of an ensemble of generators producing rhythmic activity in several frequency ranges. These oscillators are usually active in a random way. However, by application of sensory stimulation, these generators are coupled and act together in a coherent way. This synchronization and enhancement of EEG activity give rise to "evoked" or "induced" rhythms. Evoked potentials, representing ensembles of neural population responses, were considered to be a result of the transition from a *disordered* to an ordered state. The compound ERP manifests a *superposition* of evoked oscillations in the EEG frequencies, ranging from delta to gamma ("*natural frequencies of the brain*" such as alpha: 8–13 Hz, theta: 3.5–7 Hz, delta: 0.5–3.5 Hz and gamma: 30–70 Hz). See further publications by Başar (1980), Yordanova and Kolev (1998), and Klimesch et al. (1997); see reports in Başar and Bullock (1992), Gurtubay et al. (2004), and Buszaky (2006).

3. Gamma oscillations: functional multiplicity

Herrmann et al. (2004) distinguish the evoked gamma and induced gamma oscillations as follows: Oscillations in the brain can either occur *spontaneously*, that is, without relation to external stimuli, or they can be related to the processing of stimuli. In the latter case, a distinction is usually made between '*evoked*' and '*induced*' oscillations (Başar-Eroglu et al., 1996b). If an oscillation appears with the same latency and phase after each stimulus, it is considered *evoked activity*, which is usually the case for early gamma activity before 150 ms after stimulus presentation (peak latencies are typically around 50 ms for auditory and around 100 ms for visual stimuli) (see also Figs. 1, 3A,B).

Herrmann et al. (2004) also indicated that if the oscillation varies in either latency or phase from trial to trial, it is called induced activity. This is typically the case for the late gamma activity which occurs 200–300 ms after stimulus presentation and later (see also Section 3.2.2 and Fig. 3A). Gamma activity appears in a wide frequency band, between about 30 and 80 Hz. Evoked responses often oscillate around 40 Hz, whereas induced responses might also reveal higher frequencies. Computation of the average potentials across many experimental trials, as it is usually employs electrophysiology to yield the event-related potential, whereas evoked oscillations are summed because they are phase-locked to stimulation. Induced activity, on the other hand, almost cancels out completely in the averaged event-related potential. It should be noted that induced oscillations are highly reduced in the averaged curves but never cancelled out if the number of epochs do not attain high trials (see example in Fig. 3A).

To the noteworthy classification by Herrmann et al. (2004), we also add event-related oscillations. In this case, the stimulations include a task, such as the target signal in P300 oddball paradigm. The empirical findings on the gamma band may be roughly classified into sensory (or obligatory) versus cognitive gamma responses.

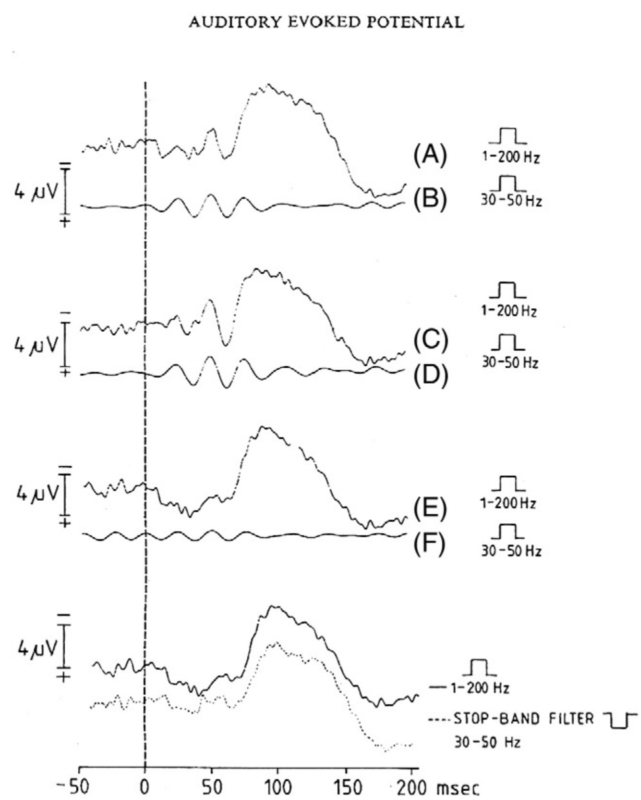

Fig. 1. (A) Spontaneous and evoked electrical activity recorded from the human vertex (Cz-electrode). The curve was evaluated by averaging 40 single, unselected sweeps (digital filter applied: pass-band filter of 1–200 Hz); (B) averaged EEG-EP of illustration (A), filtered using a 30–50 Hz pass-band filter; (C) spontaneous and evoked electrical activity recorded from the human vertex (Cz-electrode). The curve was evaluated by averaging 40 single, selected sweeps with large 40-Hz enhancement; selection criterion was X > 1.8; (D) averaged EEG-EP of illustration (C), filtered using a 30–50 Hz pass-band filter; (E) spontaneous and evoked electrical activity recorded from the human vertex. The curve was evaluated by averaging 40 single, selected sweeps without 40-Hz enhancement; selection criterion: enhancement factor X < 1.2; (F) averaged EEG-EP of illustration (E), filtered using a 30–50 Hz pass-band filter. (Bottom) The solid curve is that shown in (E); the dotted curve is (A), which here is filtered 30–50 Hz stop-band filters (modified from Başar et al., 1987).