Selectively distributed gamma band system of the brain

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Abstract

Experiments from the cat brain demonstrate that gamma responses can be recorded in cortex, hippocampus, cerebellum, formatio reticularis and thalamus, independent of the mode of sensory stimulation. These results support the hypothesis of a selectively distributed gamma system of the brain. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Various rhythms in the EEG and their possible functional meanings have been investigated in a number of studies during the past 70 years. Spontaneously existing EEG rhythms in delta (0–4 Hz), theta (4–8 Hz), alpha (8–13 Hz) and beta (13–30 Hz) frequency ranges have been found to correlate with various normal and pathological brain states. In connection with these studies, some authors have reported evoked, induced or emitted rhythms in the EEGs (e.g. ERPs), which are correlated with external and/or internal events (Adrian, 1942; Brazier, 1960; Freeman, 1975; Başar, 1980, 1983a,b, 1992; Gray and Singer, 1987, 1989; Eckhorn et al., 1988, 1989a,b; Galambos and Makeig, 1988; Gray et al., 1989; Bullock, 1992). In this class of brain electromagnetic rhythmicities, a rhythm of approximately 40 Hz, which is called 40 Hz- or gamma-rhythm Freeman, 1975; Başar, 1980, 1992; Gray and Singer, 1987, 1989; Eckhorn et al., 1988, 1989a,b; Galambos and Makeig, 1988; Gray et al., 1989; Bullock, 1992), has gained importance during the past years. We will use the term ‘gamma rhythm’ or ‘gamma band activity’,
because — according to the studies performed up to date — activities with similar characteristics can be shown in the range between 25 and 110 Hz and it has not to be strictly tuned at 40 Hz (Eckhorn et al., 1988; Galambos, 1992).

Gamma band (40 Hz) activities exist in a number of brain structures of different species, with seemingly different functional/behavioral correlates. This rhythm has also different dynamics in various structures and under different experimental conditions: it exists spontaneously and/or can be evoked, induced or emitted with different latencies and relations to sensory-cognitive events.

Even the neurophysiologist who is not working in this field is nowadays familiar with gamma rhythms. Studies include conventional spike analysis in anaesthetized animals, sensory evoked potentials and most markedly higher nervous activity, i.e. electrophysiology of cognitive processes. The functional correlates proposed so far include linking of perceptual information ('binding') and vibrations in memory leading to the question whether 'grandmother is an oscillation' Stryker, 1989. The functional correlates of the gamma response and its origin, now being investigated in several outstanding laboratories, however, often lead to controversies. These controversies are encountered (1) in descriptions related to localization or origin of gamma generators (visual cortex, frontal cortex, thalamus); (2) in functional properties of gamma rhythms (obligatory sensory processes, cognitive processes); and (3) in temporal properties of this signal: Are gamma band responses phase locked, or time locked; does the response occur immediately or does a long latency exist between excitation and response? For surveys of these findings see Başar and Bullock (1992) and Pantev et al. (1994).

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 30–60-Hz range. Starting from 1942 to this date, the studies on the 40-Hz rhythmicity have passed a total of four phases according to Başar-Eroğlu et al. (1996): initiated by the classical work of Adrian (1942), the induced character of the gamma band was studied in the first phase. The second phase took place between 1960 and 1980. The phase 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 rhythmicity. The third phase started with the work of Galambos (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 started with the work of Gray and Singer (1987) which led to investigations of 40 Hz at the cellular level. The present phase, the fifth phase, is marked by the heterogeneity of approaches and techniques applied toward the aim of solving the gamma puzzle.

Our aim in this report was to review evidence that the brain has a distributed neural population system of generators which are excitable in the 40-Hz frequency range. In this chapter, first, an account on pioneering work in this rapidly developing branch of electrophysiology is given. Our scope concerning the selectively distributed gamma response system of the brain has also been explained extensively in other papers in this volume.

2. Gamma responses to auditory stimuli recorded from various structures

The gamma band limits have been selected after inspection of the AFCs of each animal in each localization (not shown). The center frequencies of the gamma peaks varied between 30 and 70 Hz in different cats and in different localization’s. Therefore, a broad gamma band filtering between 30 and 70 Hz has been carried out on the data to be able to include all these peaks into further analysis and comparisons and to avoid the possible artifacts induced by narrow band filtering.

Fig. 1 shows the power spectra of the grand average prestimulus EEGs (left column) and the AFCs of the grand average EPs (right column) of seven cats in four brain structures to give a general idea of the frequency domain transformation of the data. Even though the gamma band peaks occurred in different cats with different center frequencies, both the grand average power spectra of the prestimulus EEGs and the grand average AFCs of the EPs show globally the mean effect of these gamma peakings.

Fig. 2 shows the averaged evoked responses of seven cats in four brain structures — gyrus ectosylvianus anterior (GEA, auditory cortex), hippocampus (HI), formatio reticularis (RF), and acoustical vermis of the cerebellum (CE) - filtered in the gamma frequency range. All of the averaged responses demonstrated an enhancement in the gamma band activity following the stimulation, which shows the time-locked nature of the response.

Fig. 3. The superimposed gamma band (30–70 Hz) filtered single sweeps of a AEP recording of one cat (upper row) and the gamma band filtered average AEPs of the same cat (bottom row) in different brain structures. (Modified from Başar et al. (1995), IEEE Eng. Biol. Med. 14: 400–410).

Fig. 4. The broad band (1–70 Hz, thin line) and gamma band filtered (30–70 Hz, thick line) averaged auditory EPs of a representative cat in four brain structures. An extremely prominent gamma band response can be observed in cerebellum. (Modified from Başar E et al. (1995), IEEE Eng. Biol. Med. 14: 400–410).
gamma response. The grand averages of all the experiments filtered in the gamma range are presented at the bottom of the illustration.

In Fig. 3 the superimposed gamma band filtered single sweeps of one cat in four structures is shown. An evident time locking of the gamma responses in single sweeps to the stimulation time point can be observed also by superimposition of single sweeps.

Fig. 4 shows the superimposed broad band filtered (1–70 Hz) and gamma band filtered (30–70 Hz) averaged responses of one cat in four brain structures. The gamma band components of the evoked responses are also clearly visible in the broad band filtered signals, which is the evidence that we are not dealing with filter artifacts.

For a robust test of the gamma band enhancements due to stimulation, the maximum peak-to-peak amplitudes in the 1000-ms prestimulus time window (between −1000 and 0 ms) have been compared with those in the 200-ms post-stimulus time window (between 0 and 200 ms). Although the enhancement factor calculation, defined as the ratio of the peak-to-peak amplitude of the evoked response to the RMS amplitude of the prestimulus period by Başar (1980) would give a physically more meaningful measure of the gamma band response, we also used the peak-to-peak amplitudes in measuring the prestimulus activity to enhance the confidence range of the statistics. In this way any transient waveform occurring in the averaged prestimulus period EEG through phase-locking by chance is also considered. The differences between the pre- and post-stimulus period maximum gamma amplitudes of four leads have been tested by a two-way ANOVA test (stimulation × lead).

The results from two-way ANOVA are presented in Table 1. The main effect of the factor ‘stimulation’ (pre- and post-stimulus gamma band amplitudes) was significant \( F_{1,6} > 8.62, P < 0.03 \), whereas the effect of the factor ‘lead’ was not significant \( F_{3,18} > 1.08, P = 0.38 \). Also, the interaction for the maximal amplitude measurements between ‘stimulation’ and ‘lead’ was insignificant \( F_{3,18} > 1.01, P = 0.41 \). The mean values of the maximum gamma band amplitudes in pre- and post-stimulus periods are given in Fig. 5 in histogram form with mean percentual increase values.

3. Gamma responses to visual stimuli recorded from various structures

For measurements with visual stimuli, recordings were made from chronically implanted electrodes in the occipital cortex (area 17, referred to as OC), lateral geniculate nucleus (LG), superior colliculus (SC), dorsal hippocampus (HI), mesencephalic reticular formation (RF) and auditory

![Image](316x181 to 473x344)

Table 1

<table>
<thead>
<tr>
<th>Factor (d.f.)</th>
<th>F</th>
<th>P</th>
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<tbody>
<tr>
<td>Stimulation (1,6)</td>
<td>8.62</td>
<td>0.03</td>
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<tr>
<td>Lead (3,18)</td>
<td>1.08</td>
<td>0.38</td>
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<tr>
<td>S × L (3,18)</td>
<td>1.01</td>
<td>0.41</td>
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Table 1

Results from two-way analysis of variance (stimulation × lead) for the maximal amplitudes of the gamma band activities (modified from Başar et al. (1995), IEEE Eng. Med. Biol. 14: 400–410)
cortex ( gyrus ectosylvianus anterior, GEA). EPs were elicited by means of intense visual step function stimuli \( (N = 100) \) delivered via a fluorescent bulb (with pseudo-random interstimulus intervals of 2.5–3.5 s, mean: 3 s).

Fig. 6 shows the averaged evoked responses in nine cats filtered in the gamma frequency range. An enhancement in the gamma band activity following the stimulation is visible in all structures, thus showing the time-locked nature of the gamma response.

In Fig. 7 the superimposed gamma band filtered single trials of one cat in four structures are shown. A remarkable time locking of the gamma responses in single trials to the stimulation time point can be observed.

Fig. 8 illustrates the stimulus-evoked gamma enhancement. A significant difference between
Fig. 8. Maximal amplitudes of gamma band filtered averaged prestimulus EEG (‘pre’: −1000 to 0 ms) and averaged EP (‘post’: 0–200 ms) in nine cats and in five brain structures. (Modified from Schürmann et al. (1997), NeuroReport 8: 531–534)

pre- and post-stimulus gamma amplitudes was observed ($P < 0.01$), Wilcoxon, for OC, HI, RF; $P < 0.05$ for SC). Note that no significant difference was observed for the auditory cortex (GEA), and that differences were largest for the visual cortex (no test possible for LG due to small sample size).

4. Gamma responses — multiple functional correlates

Are gamma oscillations in the EEG functionally related to certain brain processes? Such a relation has been suggested for the processing of complex stimuli (of cognitive relevance). It is an open question whether this relation is a specific one. In contrast to previous studies, we observed gamma rhythms even in response to very ‘simple’ stimuli, measured in cats with electrodes implanted into several parts of the brain, i.e. gamma rhythms occur even when the demand for cognitive processing is minimal. We conclude that gamma rhythms are related to the processing of simple as well as complex stimuli. This supports the view that gamma rhythms are elementary signals of the brain, functionally related to diverse (not only cognitive) brain processes.

For an extended discussion of these results the reader is referred to Başar (1998, 1999) where the multiple functional features of gamma are discussed.

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