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Gamma, alpha, delta, and theta oscillations govern cognitive processes

Erol Başar, [a], [b], Canan Başar-Eroglu[c], Sirel Karakaş[b], [d] and Martin Schürmann[a]

[a] Institute of Physiology, Medical University Lübeck, 23538 Lübeck, Germany

[b] Tübitak Brain Dynamics Research Unit, Ankara, Turkey

[c] Institute of Psychology and Cognition Research, 28334 Bremen, Germany

[d] Institute of Experimental Psychology, Hacettepe University, Beytepe, Ankara, Turkey

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Abstract

The increased interest in gamma oscillations, now widely regarded as functionally relevant signals of the brain, underlines the importance of the concept of event-related oscillations for bridging the gap between single neurons and neural assemblies. Taking this concept further, we review experiments showing that oscillatory phenomena such as alpha, theta, and delta responses to events are, just as the gamma band, strongly interwoven with sensory and cognitive functions. This review argues that selectively distributed delta, theta, alpha and gamma oscillatory systems act as resonant communication networks through large populations of neurons. Thus, oscillatory processes might play a major role in functional communication in the brain in relation to memory and integrative functions.

Author Keywords: Delta; Theta; Alpha; Gamma oscillations; Sensory processing; Cognitive processing

Article Outline

1. Why this special issue

A great change has taken place in Neuroscience. Brain scientists have recognized the importance of oscillatory phenomena and the functional EEG. This new development will not only govern improvements in Neuroscience within the next two or three decades, it will probably create the basic approach for the biophysical understanding of brain machinery. At the beginning of the 1970s only few research scientists emphasized the importance of oscillatory brain activity. Now this branch of Neuroscience is rapidly growing.

The reports in this special issue were collected from various laboratories by working with several colleagues from San Diego, Copenhagen, Vancouver, New York, Ankara, Istanbul, Sofia, Perth, Buenos Aires, Moscow, Stockholm and Shanghai. Working this way and with a broad aim we have gained much multidisciplinary experience which we intend to review and communicate to other scientists or graduate students working in the field.

A very important landmark in this special issue is the emphasis given to the alphas, i.e. distributed oscillatory processes in the 10-Hz frequency range as well as the other frequency bands. At present, most neuroscientists associate only the gamma band with the expression ‘oscillations’. We have very recently edited a volume on functional correlates of alpha activity and we clearly indicated a renaissance of alphas in the understanding of brain function (Basar; Basar et al., 1997b and Basar). The present publication further incorporates the newest 10-Hz results at the cellular, sensory and cognitive levels, and highly extends the integrative functions of the alpha activity. Besides this, theta and delta frequencies are treated extensively. Furthermore, spectral analyses and the chaos approach indicate the existence of event-related oscillations in the highest frequency range between 100 and 1000 Hz (Basar and Basar).

Some important features of the reports are:

1. In the last 20 years new important mathematical algorithms have been developed. These methods are chaos analysis, wavelet analysis and single trial recordings.

2. Great change has occurred in measurement at the cellular level. Gamma oscillations and alpha oscillations were measured with sophisticated experimental setups at the cellular level.

3. Concepts of cooperation phenomena and synchronization of cell assemblies has opened new avenues in brain research.

4. It is important to note that the most general dynamics in the brain are governed by the brain's natural oscillations (alpha, theta, delta,

gamma, etc.). It is hypothesized that these oscillations provide basic links to brain functions, especially for communication and associative functions. The author's team belongs to the scientist group who published the first gamma band responses almost 30 years ago. However, it is the major aim of this collection of reviews and original reports to demonstrate that other basic frequencies are as important as the oscillations in the gamma band. Multiple oscillatory responses provide the integrative brain functions.

5. The following working hypothesis is strongly emphasized: selectively distributed alpha, theta, delta and gamma oscillatory systems control the integrative brain functions at all sensory and cognitive levels. This view is strongly based on data obtained from diverse ranges of experiments.

6. The results show that brain oscillations are correlated with multiple functions depending on task, sensation and structures. At least 50 different functional correlates of brain oscillations are analyzed and summarized. These descriptions include sensory registration, perception, movement and cognitive processes related to *attention*, *learning* and *memory*.

7. A large ensemble of functions related to different frequencies or to superimposition of different frequencies are described. This step provides a tentative start to formulate an integrative neurophysiology based on EEG-oscillations.

8. Complex functions are, as a rule, manifested with several *superimposed oscillations* with varied degrees of amplitudes, duration and delays.

2. Oscillations and functions: introductory synopsis

“During the ‘Decade of the Brain’ neuroscience is coming to terms with its ultimate problem: understanding the mechanisms by which the immense number of neurons in the human brain interact to produce higher cognitive functions" (Freeman, 1998). As one of the candidate mechanisms, oscillatory neuroelectric activity has recently attracted much interest. In particular, this holds for synchronous gamma activity in spatially distributed cells. In this framework, the present review has several aims, namely:

1. To survey functionally related findings in *oscillatory brain activity*, in the frequency range between 0.5 and 100 Hz, i.e. by surpassing approaches centered on the gamma band. In particular, the aim is to demonstrate that the alpha band — so far mostly neglected — deserves more interest.

2. To develop a new integrative view emphasizing that oscillatory networks are selectively distributed and that oscillatory activities are related to sensory as well as cognitive processes. It is suggested we reconsider several controversies related to brain oscillations by introducing the synthesis that oscillatory networks are selectively distributed and have several functions.

3. To propose a new approach to a fundamental problem — searching for general communication properties in the brain. In particular, it is suggested that complex stimuli elicit superimposed alpha, gamma, theta responses (which are combined like letters in an alphabet; Başar, 1999)

As oscillatory responses (phase- or time-locked) to a sensory or cognitive event, evoked or event-related oscillations are usually classified according to the 'natural frequencies' of the brain (alpha: 8–13 Hz, theta 3.5–7 Hz, delta 0.5–3 Hz, and gamma 30–70 Hz). As will become clear below, this approach is well suited for comparative analysis of findings at the level of single neurons, field potentials, EEG or MEG.

As for event-related gamma oscillations, the most prominent examples nowadays are oscillatory responses in the frequency range of 40–60

Hz occurring in synchrony within a functional column in the cat visual cortex (Gray and Singer, 1989). This possibly reflects a mechanism of feature linking in the visual cortex (Eckhorn et al., 1988). This is related to the 'binding problem': how is the spatially distributed but temporally coherent electrical activity from a large number of elementary neural components integrated to functional activity? Despite its current popularity, the binding theory does not fully explain the 'ubiquity of gamma rhythms' (Desmedt and Sch). In this respect, it may be helpful to consider further studies of gamma oscillations, partly going back to Lord Adrian (Adrian, 1942). While the interpretations are heterogeneous, the empirical findings may be roughly classified into sensory (or obligatory) vs. cognitive gamma responses. Concerning the former,

1. Auditory and visual gamma responses are selectively distributed in different cortical and subcortical structures. They are phase-locked stable components of EPs in cortex, hippocampus, brain stem and cerebellum of cats occurring 100 ms after the sensory stimulation with a second window of approximately 300 ms latency (Basar; Basar and Sch).

2. A phase-locked gamma oscillation is also a component of the human auditory and visual response (Başar, 1980). A new strategy by application of six cognitive paradigms showed that the 40-Hz response in the 100 ms after stimulations has a sensory origin, being independent of cognitive tasks (Karakaş and Başar, in press). The auditory MEG gamma response is similar to human EEG responses with a close relationship to the middle latency auditory evoked response (Basar and Pantev).

3. An early phase-locked 40-Hz response was recorded in visceral ganglion of Helix pomatia using electrical stimulation (Schütt and Başar, 1992). In arthropods also, light-induced gamma responses have been observed (Kirschfield, 1992).

Several investigations dealt with cognitive processes related to gamma responses, some of them based on measuring the P300 wave. This positive deflection typically occurs in human ERPs in response to deviant (‘oddball’) stimuli or omitted stimuli interspersed as ‘target’ stimuli into a series of standard stimuli:

1. A P300–40 Hz component has been recorded in the cat hippocampus, reticular formation and cortex by utilization of omitted auditory stimuli as a target. This response occurs approximately 300 ms after the stimulation, being superimposed with a slow wave of 4 Hz (Başar-Eroglu and Başar, 1991). Preliminary data indicate a similar P300–40 Hz response to oddball stimuli in humans (Başar et al., 1993). However, a suppression of 40-Hz activity in response to target stimuli has also been reported (Fell et al., 1997).

2. Attention-related 40-Hz responses were reported in humans, especially over the frontal and central areas (Tiitinen et al., 1993).

3. During visual perception of reversible or ambiguous figures a significant increase (almost 50%) in the human frontal gamma EEG activity has been recorded during states of ‘perceptual switching’ (Başar-Eroglu et al., 1996a).

4. The spatiotemporal magnetic field pattern of gamma band activity has been interpreted as a coherent rostrocaudal sweep of activity repeating every 12.5 ms due to a continuous phase shift over the hemisphere (Llinas and Ribary, 1992).

This wide spectrum of experimental data is in accordance with a hypothetical ‘selectively distributed parallel processing gamma system’ with multiple functions. Rather than being highly specific correlates of a single process, gamma oscillations might be important building blocks of electrical activity of the brain. Being related to multiple functions, they may: (i) occur in different and distant structures; (ii) act in parallel; and (iii) show phase locking, time locking or weak time locking.

Particular support of this view stems from the observation that simple electrical stimulation of isolated invertebrate ganglia evokes gamma oscillations (in the absence of perceptual binding or higher cognitive processes). In conclusion, gamma oscillations possibly represent a universal code of CNS communication (Kirschfield; Sch; Basar and Basar). This view might also serve as a synthesis providing a real possibility to overcome controversies in various reports.

As to the alpha range, taking into account Adrian's observations of 'evoked alpha' as reactiveness of the brain and also due to new advances in measuring 10-Hz oscillations at the cellular level, a 'renaissance of functional alphas' is under way. Co-existing with the well-known 'spontaneous' alpha rhythm (maximal with eyes closed and blocked when the subject opens his or her eyes), several forms of 'work alpha' or 'functional alpha' are observed during sensory, cognitive and motor processes (Basar; Basar et al., 1997b; Basar; Basar and Basar):

1. Auditory and visual stimulations elicit alpha responses in the auditory and visual pathways, hippocampus and reticular formation (damped 10 Hz oscillations of approx. 300 ms), which are visible without filtering and can be analyzed with several methods, for example wavelet analysis (Başar, 1998). Multiple sclerosis patients with opticus neuritis show reduced alpha responses after visual stimulation, thus demonstrating the correlation of sensory functions with the alpha response (Başar, 1998).

2. Thalamo-cortical circuits are not unique in generating alpha responses. The hippocampus and the reticular formation may have a more general significance, since hippocampal and reticular 10-Hz responses are present in all modalities in contrast to thalamo-cortical circuits. Human alpha responses similar to those in the cat brain have also been described (Basar; Basar; Basar and Sch).

3. Cognitive targets significantly influence the alpha responses in

P300: using an oddball paradigm, prolonged event-related alpha oscillations up to 400 ms were observed (Basar and Basar).

4. Movement related alpha (Pfurtscheller et al., 1997) describes the ability of neural structures to generate oscillating potentials related to movement.

5. Memory related event-related alpha oscillations can be emitted from the brains of well-trained subjects 1 s before the delivery of an expected cognitive target. New results (Klimesch; Basar; Basar et al., 1997b and Basar) demonstrate that alpha activity is strongly correlated with working memory and probably with long-term memory engrams.

6. Further evidence suggesting that the alpha activity is not only recorded in mammalian thalamo-cortical networks are the spontaneous and electrically evoked 10-Hz oscillations in isolated cerebral or visceral ganglia of Helix pomatia and Aplysia (Sch; Bullock and Basar).

Similar to what was said for the gamma band, these results are consistent with a hypothetical selectively distributed alpha system interwoven with general communication functions. Event-related alpha oscillations may facilitate association mechanisms in the brain in the following way: when a sensory or cognitive input elicits ‘10-Hz wave-trains’ in several brain structures, then it can be expected that this general activity can serve as a resonating signal ‘par excellence’. Furthermore, EP amplitudes strongly depend on the amplitude of the prestimulus alpha activity (Basar and Basar).

As for the gamma band, parallel observations at the cellular level are noteworthy: evoked oscillations in the 8–10-Hz frequency range in visual cortex neurons upon visual stimulation suggest a relation to scalp-recordable alpha response (Silva and Dinse). The sum of these observations permits a tentative interpretation of alpha as a functional and communicative signal with multiple functions. This interpretation of

10-Hz oscillations (at the cellular level, or in populations) might be comparable to the putative universal role of gamma responses in brain signaling.

Experimental data concerning event-related theta oscillations hint at a basic role in cognitive processing and in the cortico-hippocampal interaction (for reviews see Miller; Basar; Klimesch and Basar). Some examples follow:

1. Theta response is the most stable component of the cat P300-like response (Basar and Basar).

2. Bimodal sensory stimulation induces great increases in frontal theta response thus demonstrating that complex events increase the frontal processing in the theta range (Başar, 1999).

3. Event-related oscillations in the theta band are prolonged and/or have a second time window approximately 300 ms after the presentation of the target in oddball experiments. Prolongation of theta is interpreted as being correlated with selective attention. (Başar-Eroglu et al., 1992).

4. Event-related theta oscillations are also observed after an inadequate stimulation whereas event-related alpha oscillations are not existent if the stimulation is an inadequate one. Accordingly the associative character for event-related theta oscillations is more pronounced than for higher frequency event-related oscillations (Başar, 1999).

5. Event-related potentials obtained with paradigms inducing focused attention, P300, and with stimuli giving rise to high expectancy states, have shown marked electrophysiological changes in the frontal cortex, parietal cortex and the limbic system. (Basar and Basar).

6. 'Orienting' — a coordinated response indicating alertness, arousal or readiness to process information — is related to theta oscillations

and manifested in cat experiments during exploration and searching and motor behavior (Basar and Basar).

According to the statements above it is clear that event-related theta oscillations can be considered as important building blocks of functional signaling in the brain.

As to delta oscillations, experimental data hint at functional correlates roughly similar to those mentioned for theta oscillations, i.e. mainly in cognitive processing:

• The responses to visual oddball targets have their highest response amplitude in parietal locations, whereas for auditory target stimuli the highest delta response amplitudes are observed in central and frontal areas (Sch; Basar and Basar).

• Cognitive functions: The amplitude of the delta response is considerably increased during oddball experiments. Accordingly, it has been concluded that the delta response is related to signal detection and decision making (Başar-Eroglu et al., 1992).

• In response to stimuli at the hearing threshold delta oscillations are observed in human subjects. This confirms the hypothetical role of the delta response in signal detection and decision making (Başar, 1999).

• A waveform observed in response to deviant stimuli not attended by the subject, the mismatch negativity (Näätänen, 1992) is shaped by a delayed delta response superimposed with a significant theta response.

• Phase-locked delta responses are probably the major processing signals in the sleeping cat and human brain (Başar, 1980).

The topographic distribution of the results is again consistent with a distributed response system.

3. Selectively distributed oscillatory systems

To end this survey of experimental data, it is suggested that event-related oscillations might help us to understand what Fessard called ‘principles that govern the most general transformations — or transfer functions — of multiunit homogeneous messages during their progression through neuronal networks’ (Fessard, 1961). The transfer function describes the ability of a network to increase or impede transmission of signals in given frequency channels. The transfer function, represented mathematically by frequency characteristics or wavelets (Basar and Basar) constitutes the main framework for signal processing and communication. The existence of general transfer functions would then be interpreted as the existence of networks distributed in the brain having similar frequency characteristics facilitating or optimizing the signal transmission in resonant frequency channels (Basar and Basar). Further experiments are needed to find out whether the brain has such subsystems tuned in similar frequency ranges or common frequency modes and whether they are principles dominating the operations of heterosensory communication and cognitive processes.

Some hints, however, can be derived from the results reviewed above: they demonstrate frequency selectivities in several brain structures or selectively distributed oscillatory networks (delta, theta, alpha, beta, gamma) related to general transfer functions of the brain. The degree of synchrony, amplitudes, locations and duration or phase lags are continuously varying, but similar oscillations are most often present in activated brain structures.

In a model of cognition, the formation of specific templates belonging to objects and memories occurs as selectively distributed processing with considerable specialization and in anatomically differentiated localizations (Mesulam, 1994). An important strategy in memory research emphasizes that memory reflects a distributed property of cortical systems (Fuster, 1997). The present review emphasizes that the selectively distributed oscillatory systems may provide a general communication framework parallel to the morphology of distributed memory networks and also that fundamental functional mapping of the brain should be complementary to morphological studies.

In this report we have described numerous types of oscillatory activities with definitive or tentative explanations of their functional relations. The results from several laboratories clearly demonstrate that it is not possible to assign a single function to a given type of oscillatory activity. These oscillations have multifold functions and act as universal operators or codes of brain functional activity. Moreover, besides the frequency and site of the activity some other parameters are also strongly involved in brain functioning. These parameters are enhancement, time locking, phase locking, delay of the oscillation and prolongation of oscillation.

In conclusion, our hypothesis about the functional role of event-related brain oscillations is as follows: complex and integrative brain functions are manifested in the superimposition of several oscillations, and can be illustrated with a comment on Stryker's question ‘Is grandmother an oscillation?’ (Stryker, 1989). According to our review selectively distributed oscillatory networks (for delta, theta, alpha and gamma responses) are activated by sensory and cognitive events. These events evoke superimposed and/or parallel oscillations (‘multiple oscillations’) that are transferred to distributed structures with various degrees of intensity, synchronization, duration and delay.

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Corresponding author. Institute of Physiology, Medical University of Lübeck, Ratzeburger Allee 160, D-23538 Lübeck, Germany. Tel.: +49-451-500-4170; fax: +49-451-500-4171; email: erol.basar@deu.edu.tr

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