



## Invited Review

## A review of alpha activity in integrative brain function: Fundamental physiology, sensory coding, cognition and pathology

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## ABSTRACT

**Aim of the review:** Questions related to the genesis and functional correlates of the brain's alpha oscillations around 10 Hz (Alpha) are one of the fundamental research areas in neuroscience. In recent decades, analysis of this activity has been not only the focus of interest for description of sensory-cognitive processes, but has also led to trials for establishing new hypotheses.

The present review and the companion review aim to constitute an ensemble of “reasonings and suggestions” to understand alpha oscillations based on a wide range of accumulated findings rather than a trial to launch a new “alpha theory”.

**Surveyed descriptions related to physiology and brain function:** The review starts with descriptions of earlier extracellular recordings, field potentials and also considers earlier alpha hypotheses. Analytical descriptions of evoked and event-related responses, event-related desynchronization, the relationship between spontaneous activity and evoked potentials, aging brain, pathology and alpha response in cognitive impairment are in the content of this review. In essence, the gamut of the survey includes a multiplicity of evidence on functional correlates in sensory processing, cognition, memory and vegetative system, including the spinal cord and heart.

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## 1. Introduction

The present review and the companion report (Başar and Güntekin, in press) aim, where possible, to combine analyses related to the spontaneous alpha activity, evoked alpha responses, event-related alpha responses, ERDs; and also, ideally, they aim to encompass applications of these measuring strategies over the entire cortex, by also taking into account resting states and evoked coherencies. Namely, to understand sensory-cognitive processes, it is almost imperative to attain reliable information over the whole brain, and information concerning evolving brain (neuroethology), aging brain and pathologic brain. Basic studies of “alpha at the cellular level” are also most pertinent for understanding the crucial role of *alpha in the integrative brain machinery*. This view will be further considered in Section 2. A review of the history of work on alpha oscillations is also necessary to illuminate the basic views.

According to Storm van Leeuwen (1977), if one understands the alpha rhythm, one will most probably understand the other EEG phenomena. Alpha rhythm was first observed and described by the German psychiatrist Hans Berger (1929). Mountcastle (1992) described that,

after Berger's first report of electroencephalogram, a great excitement pervaded the neurological word, in the late 1920s and early 1930s. The use of electroencephalography reached a peak in the 1940s; thereafter, such studies plateaued and ceased to be attractive to most experimental neuroscientists. The significance of the alpha rhythm was also poorly understood, and Ross Adey reported that several neuroscientists previously considered this pattern as a “noise”, “smoke” or idling of the brain.<sup>1</sup>

Thirty years ago, a paradigm shift occurred: According to Mountcastle (1992), our percepts are generated by the integration of the brain activity triggered by sensory stimuli with the activation of the neural images of past or current experience. This meant that brain mechanisms involved in perception could be studied directly, by measuring changes in the electrical activity of the human brain via a large number of EEG recordings, or the use of multiple microelectrodes implanted in primates. Furthermore, Mountcastle (1992, 1998) states that the paradigm change

<sup>1</sup> Ross Adey (1988) described the situation of EEG as follows: “...In 1953, Sir John Eccles delivered the Waynflete Lectures in Hilary. He considered EEG as an epiphenomenon. At that time EEG was considered nothing more than the noise of the brain's motor” (Ross Adey, 1988).

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introduced by using brain oscillations has become one of the most important conceptual and analytic tools for the understanding of cognitive processes. He proposes that a major task for neuroscience is to devise ways to study and analyze the activity of distributed systems in waking brains, in particular, human brains.

There remain many misconceptions about alpha rhythm, in relation to the functions of the brain and states of consciousness that need to be addressed and put in perspective. The literature shows that alpha rhythm is not a unitary phenomenon; rather, it demonstrates considerable variation and changes, depending on age, mental state, the cognitive task being performed and the cerebral location from which the EEG signal is being recorded.

Although between the 1950s and 1980s, EEG was regarded as noise and human alpha activity only as the idling state of the brain, during the two decades between 1990 and 2010, a significant number of reports were published related to cognitive correlates of alpha activity. Most of the recent work on “alpha” seems to be focused on psychological work that is often detached from physiological and clinical observations. The newly developed hypotheses are mostly based on new strategies and do not take into consideration the most general findings or framework established a few decades ago. More than 50 years ago, Gray Walter (1950) already pointed out that the alpha rhythm in one subject is composed of, and is the end product of, many alpha rhythms. In 1964, Walter stated:

“We have managed to check the alpha band rhythm with intracerebral electrodes in the occipital–parietal cortex; in regions which are practically adjacent and almost congruent, one finds a variety of alpha rhythms, some of which are blocked by opening and closing the eyes, some are not; some are driven by flicker, some are not; some respond in some way to mental activity, some do not. What one can see on the scalp is a spatial average of a large number of components, and whether you see an alpha rhythm of a particular type or not depends on which component happens to be the most highly synchronized process over the largest superficial area; there are complex rhythms in everybody.”

Now, at the turn of the 21st century, a number of publications on alpha oscillations consider “alpha” as an almost pure cognitive signal. Further, only thalamic pacemakers are discussed as generators of alpha activity. Fundamental and still valid works of Ross Adey et al. (1960), Rémond and Lesèvre (1967), Hernandez-Peon (1961), and Moruzzi and Magoun (1949) are usually not considered in new theories. Further, new generalizing results on animal physiology and clinical neurophysiology experiments have become rare.

According to Gasser et al. (1985), the alpha band has the best test-retest reliability compared with other EEG bands, and can therefore be treated as an intra-individually-stable trait. In the last decade of the 20th century, an efficient trend was initiated by several authors for understanding the functional correlates of alpha (Lehmann, 1989; Von Stein and Sarnthein, 2000; Başar et al., 2001; Nunez et al., 2001), as also reviewed by Başar et al. (1997b) and Klimesch (1999). Further, it is described that alpha activity is the most common component of the human brain's electrical activity (Başar and Güntekin, 2006; Shaw, 2003).

### 1.1. Aims of the review

The major aim of this review is to follow the fundamental questions posed by Gray Walter and Storm van Leeuwen by considering the following *structural descriptions*:

- 1) Extracellular recordings of the spontaneous and evoked alphas;
- 2) Intracellular recordings of alpha activity;
- 3) Selectively distributed alpha system of the brain;
- 4) Neuro-clinical bases and neurotransmitters.

Further, a survey of publications on functional correlates of alpha activity and alpha responses will be provided, including:

- a) Alpha in sensory function;
- b) Alpha in evolution of species;
- c) Alpha in vegetative functions;
- d) Alpha in the maturing brain;
- e) Alpha in cognitive processes (companion report);
- f) Alpha in cognitive impairment (companion report).

The present review also strongly emphasizes the observation of Gray Walter (1950), presented in the previous section, and also that, according to measurements, alpha oscillations or “alphas” are correlated with several basic functions. Research also suggests that a profound understanding of alpha activity can be only achieved by encompassing observations in *the maturing brain, evolving brains, emotional brain and pathologic brains* (Başar, 2011). During the last twenty years, 10-Hz observations were also recorded in the vegetative system (Barman and Gebber, 1993, 2009) and, in the future, this observation will be of considerable importance for the understanding of brain–body integration.

The present review includes around 180 references in an attempt to address the questions: Can the level of presented results and related theories lead to a new general “alpha theory”? Can new progress be achieved in the light of the above-mentioned critics? Is the time ripe for pronouncing a general alpha theory? Başar (2011) concluded that “Alpha is one of the fundamental functional operators of the brain for signal processing and communication in sensory/cognitive processes in the brain”. Further, according to results from the research group of Barman and Geber, “alphas are operating oscillations also in the spinal cord and the organs of the vegetative system”.

The final question will be: *Is the time ripe for a general theory of alpha?*

This question will be repeated at the end of the companion report.

The results of present studies generally depict a number of divergent results, indicating that it is still too early to launch an alpha theory. Therefore, at the end of the review, we include only a chain of “reasonings and suggestions for understanding alpha” that may provide the basic steps for establishing tenable hypotheses in the future.

## 2. A short historical survey of physiological theories on the generation of alpha rhythms

### 2.1. Some fundamental remarks on single cell recording and EEG: from Ramon y Cajal (1911) to Mountcastle (1992)

At the turn of the 20th century, the morphological studies carried out by Ramon y Cajal's (1911) and Charles Sherrington's (1948) physiological approach opened the way to the “single-neuron doctrine” by introducing the notion of “one ultimate pontifical nerve-cell” that integrates the CNS function. In this concept, integration was related to motor activity; the functional mapping was a type of movement mapping. Although this approach dominated 20th century-neuroscience, it had a major shortcoming in that cognitive functions and memory were not integrated into the “neuron doctrine” or within its derivatives; even the cerebellum was omitted from Sherrington's model.

The single- (or several) neuron hypothesis was proposed by Horace B. Barlow (1972) and was updated in 1995. Barlow's general principle is that single neurons detect peripheral events with features that are of behavioral significance to the organism. This is the feature-detector idea (see also Sokolov<sup>2</sup>). However, in relation to this point, Mountcastle states that “This seems unlikely, however, that there are a sufficient number of feature detectors to account for the

<sup>2</sup> E. Sokolov Private Communication and Sokolov, E.N., 2001. Toward new theories of brain function and brain dynamics. *Int. J. Psychophysiol.* 39, 87–89.

virtually infinite number of sensory stimuli we readily perceive, nor for solving the binding and relational problems in perceiving complex scenes” (Mountcastle, 1998, p. 343).

The description of integration requires morphological descriptions, measurements in time–space and the analysis of coherence functions. Therefore, the role of time–space and coherence also gained considerable importance for the development of new concepts from the study of brain oscillations (Gray and Singer, 1989; Freeman, 1975).

Further to the work of Mountcastle (1992, 1998), Bullock et al. (2005) and Bullock (2006) discussed recent evidence suggesting that the neuron doctrine, conceived nearly a century ago by Ramon y Cajal, cannot encompass important aspects of information processing in the brain. Intercellular communication by gap junctions, slow electrical potentials, and action potentials initiated in dendrites, neuromodulatory effects, extrasynaptic release of neurotransmitters and information flow between neurons and glia all contribute to information processing. Revisiting the neuron doctrine, these authors suggest that future research beyond its limits may lead to new insights into the unique capabilities of the human brain.

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 gives 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 delta: 0.5–3.5 Hz, theta: 3.5–7 Hz, alpha: 8–13 Hz, beta: 18–30 Hz and gamma: 30–70 Hz). See further publications by Başar (1980), Yordanova and Kolev (1998), Klimesch et al. (1997); see reports in Başar and Bullock (1992), Gurtubay et al. (2004), Buszaky (2006), Schürmann et al. (1995, 1997) and Başar-Eroğlu et al. (1991).

## 2.2. Survey by Andersen and Andersson and the facultative pacemaker theory

In 1941, Adrian already reported that rhythmic 10/s activity following a single afferent volley could be recorded within or at the dorsal surface of the thalamus, even if the appropriate cortical area was removed. In other words, the thalamic nuclei contain a mechanism for the transfer of a single volley to a rhythmic 10/s sequence without the presence of the cortical area to which the thalamo-cortical fibers project. In 1950, Chang advanced the hypothesis that a cortico-thalamic reverberating circuit should be the basis for the evoked rhythmic activity. The arguments for this explanation were the presence of a similar rhythmic activity in the thalamus and cortex, and the difficulty of recording thalamic rhythmic activity after removal of the appropriate cortical projection area. However, this theory is contradicted not only by the early reports of Adrian (1941) and Bremer and Bonnet (1950), but also by observations by Adrian (1951), who critically tested the cortico-thalamic reverberating hypothesis; and by Galambos et al. (1952). Full support for the statement of Adrian and Bremer was given by Andersen et al. (1967a,b).

On the basis of their observations, Andersen et al. (1967a,b) and Andersen and Andersson (1968) advanced the hypothesis that facultative pacemakers in the thalamus influenced activity in the corresponding cortical areas. It is assumed that rhythm generation occurs at many independent thalamic locations and that each group is able to produce rhythmic activity of intra-spindle frequencies. Via

the specific thalamo-cortical fibers, the burst discharges of the thalamic rhythmic entity are imposed on a cortical area, which may correspond to a cortical column (Mountcastle, 1957; Hubel and Wiesel, 1962). Each thalamic burst will induce neuronal activity in the cortex, thus giving correspondence between thalamic and cortical rhythmicity. Since each thalamic rhythm generator may act as an independent unit, the same individuality in rhythmic activity will also occur at the cortical level.

Andersen and Andersson (1968) estimated the maximal number of rhythm-generators in the cat thalamus to be of the order of 30,000–40,000, while the number of cortical columns in one hemisphere of the cat was around 25,000. These authors noticed that the high degree of synchrony of rhythmic activity usually found in thalamic and cortical areas indicates that the activity of individual generators of the rhythm is coordinated into larger units. This may be done by “distributor neurons”, for example of the type described by Scheibel and Scheibel (1966) and Tömböl (1966). However, experiments with decorticated preparations led Andersen and Manson (1971) to assume that a mechanism in the thalamus produces widespread synchronization of individual rhythm-generators, and that the coordination of rhythmic activity in large cortical areas is primarily an intra-thalamic event.

## 2.3. The scope of Lopes da Silva and coworkers

Contrary to the viewpoint of Andersen and Andersson (1968), Lopes da Silva et al. (1973b) did not make any a-priori assumption that all rhythmic activities falling within the alpha range should be considered equivalent. In their investigations, the latter authors recorded spontaneous alpha rhythms and barbiturate spindles in dogs from the same recording site. The alpha rhythms were found to differ from barbiturate spindles with respect to their cross-spectra and topographic distribution. Lopes da Silva et al. (1973b) concluded that, in a state of alpha rhythms, the thalamic and cortical sites act more independently of one another than under a state of light barbiturate anesthesia. Further, the same group of investigators (Lopes da Silva et al., 1973a) tested the hypothesis of Andersen and Andersson by specifically studying the relationships between alpha rhythms recorded in the lateral geniculate nucleus and visual cortex. The strength of thalamo-cortical relationship was measured by means of coherence functions.

Although significant thalamo-cortical coherences were found, cortico-cortico coherences generally exceeded high thalamo-cortical coherences. The high cortico-cortical coherences were found over relatively large areas (diameters of 5 or 6 mm). The model of Andersen and Andersson, according to which the rhythmic activity of discrete cortical areas is paced by relatively small groups of neurons in thalamic nuclei, would imply the existence of low coherences between different cortical areas, with high thalamo-cortical coherences of some specific sites; however, this implication is completely contradicted by the results of Lopes da Silva et al. (1973a).

The view of Lopes da Silva et al. (1973a) on the pacemaker concept is as follows: “In our view, this problem cannot be solved by using a deterministic pacemaker concept. In a general sense, a deterministic pacemaker has two main properties: It has auto-rhythmicity; and it can impose its rhythm upon other systems. This implies absolute correlation, i.e., coherence of one, or nearly one if it is assumed that there is measurement of noise in all records.”

According to Lopes da Silva et al. (1973a), alpha rhythms should be considered as signals produced by stochastic processes. More specifically, thalamic and cortical alpha rhythms would result from the filter properties of neural networks when submitted to a random input:

“Neural networks with similar design and frequency selectivity should exist in different brain areas (cortical and thalamic), where they give rise to alpha rhythms with the same frequency spectra



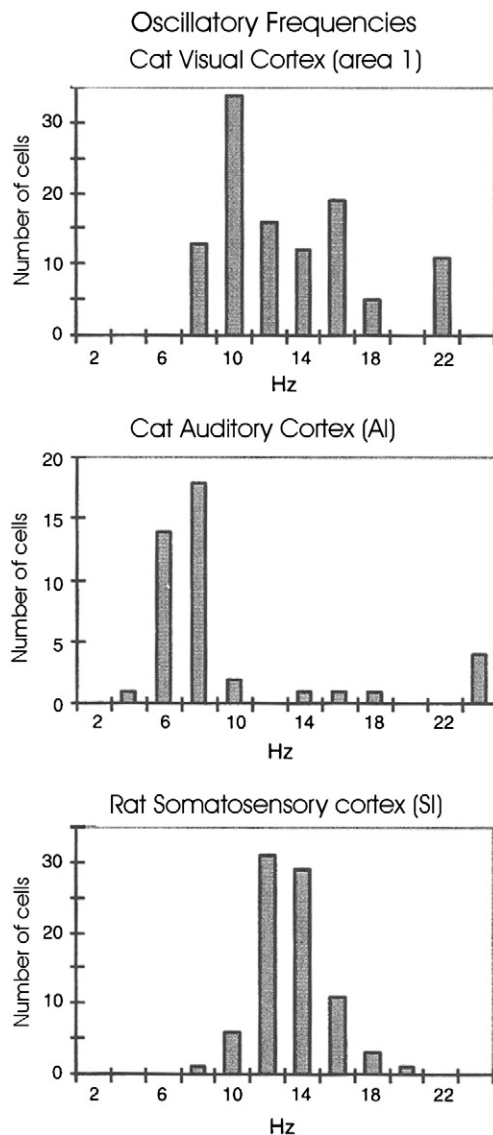


Fig. 1. Distribution of mean oscillatory frequencies for neurons of the primary visual area (area 17), auditory (AI) and somatosensory cortex (SI). Modified from Dinse et al. (1997).

but not necessarily with large coherence values. Instead of thinking in terms of pacemakers, these authors proposed to think in terms of statistical correlations.”

The investigation by Lopes da Silva et al. (1973a,b), in dogs with electrodes inserted through the cortex, and those with a large number of electrodes spaced closely together on the surface of the cortex, elucidated that, at a distance ranging from 0.5 mm to 2.5 mm on the cortex, there may be good coherence of alpha rhythm, but also that this coherence is often not absolute. In practice, a good deal of dissimilarity may be observed, even from electrodes spaced closely together in different cortical layers. The waveform of alpha rhythms recorded by means of intracortical electrodes is rather different from that derived from the surface. The alpha waves may be much spikier and present an arcade. Lopes da Silva et al. (1970a,b, 1973a,b) suggest that, in the occipital cortex, many small generators are present which, averaged over a period of time, are largely in synchrony, although they may vary considerably from moment to moment. This holds not only vertically, for the generators at different depths in one area, but also horizontally, for the generators distributed over the cortex.

Başar et al. (1975a,b) and Başar (1980) argued that the idea of alpha pacemakers and possible transmission between thalamus and cortex is useful; however, pacemaker hypotheses should be extended to other structures including brainstem and hippocampus, and also to other frequency bands, since coherences between hippocampus and cortex, and between reticular formation and cortex, may be greater than thalamo-cortical coherences (Schürmann et al., 2000). Başar and coworkers also supported the theory of Hernandez-Peon (1961), attributing to reticular formation a control function in the whole brain. Despite these findings, the group of Klimesch et al. (2007) and Uhlhaas and Singer (2006) defended the facultative pacemaker theory as also being supported by Başar's group. As will be explained in the following section, this is not in accordance with the interpretation by Başar's group, including the reticular formation and also the cerebellum in the selectively distributed “alphas”. In addition to neurophysiological findings in recent analyses by Babiloni et al. (2009), it is shown that progressive atrophy of the hippocampus correlates with decreased cortical alpha power, as estimated using LORETA source modeling, in the continuum from mild cognitive impairment (MCI) to Alzheimer conditions. These results further support the view that the hypothesis of thalamo-cortical networks is limited.

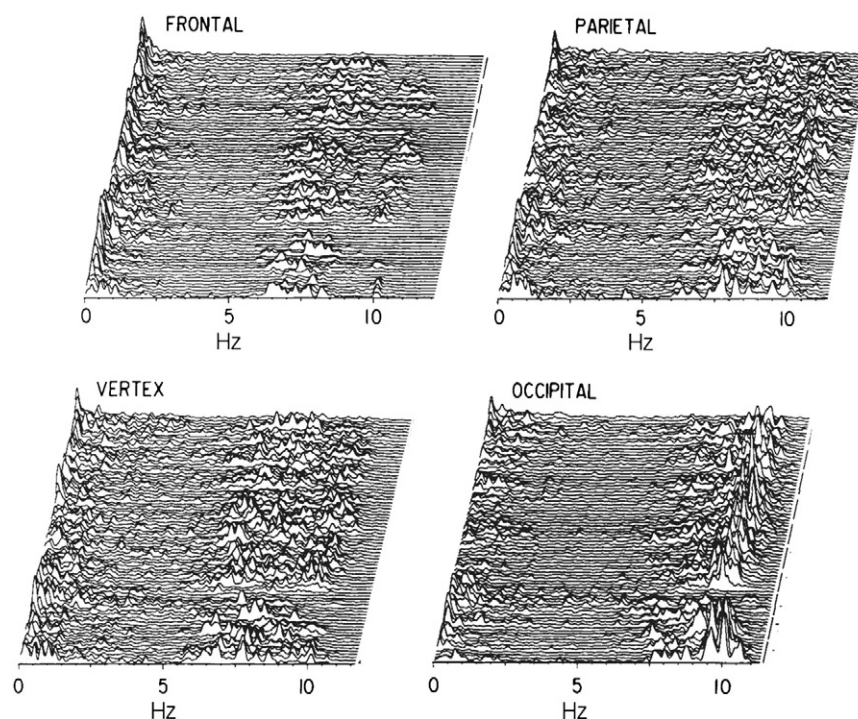
#### 2.4. Multifunctional and selectively distributed 10 Hz oscillations —a renaissance of alphas

Başar (1980) further reviewed the “induced” and “evoked” alpha by stating that the rhythms are generated in distributed parts of the brain, and not in a given, unique structure. Furthermore, if the brain is brought to an excited state, either by means of sensory stimulation or cognitive tasks, it can generate evoked alpha rhythms. These rhythms are not the alpha states fitting the conventional description of alpha activity, as stated by the rules of the EEG-Society. On the contrary, if the brain is excited by sensory stimulation, it shows short, damped oscillatory behavior of approximately 300 ms duration upon stimulation. The volume edited by Başar et al. (1997a) includes reports of the physiological bases of the 10-Hz activities and their functional correlates, with emphasis on sensory, cognitive and motor states that accompany the 10-Hz oscillations. This endeavor, which aimed to establish a new trend regarding the functional implications of the alpha activity, led to a “renaissance of alpha” 80 years after the first discovery by Hans Berger. Thus, a new nomenclature was proposed by the authors of the special issue (Başar et al., 1997a), the expressions “alpha's” or “brain's 10-Hz oscillations” were utilized to emphasize the multiplicity of phenomena in the alpha band (see also Klimesch, 1999). Such usage helps to draw attention to the existence of multiple phenomena in the alpha band, which have hitherto been generally regarded as a single rhythm and, therefore, a single phenomenon. In this approach, the mu and the tau rhythms are also regarded as components within the associated ensemble of phenomena that are classed as “alpha's”.

### 3. Studies at the cellular level

Creutzfeldt et al. (1966, 1969) analyzed post-stimulus time histograms (PSTHs) of lateral geniculate cells and of cortical cells and cortical visual EPs following light flashes. The single cell responses may vary with recording depth, but a common type of response is seen at all levels of the cortex. The experimental data revealed a good correlation between the 10-Hz components of the surface EP and cellular events. A phase reversal of all components is observed at a depth between 800 and 1200  $\mu\text{m}$ . Furthermore, with bipolar recordings, no significant potential differences are measured within the upper 600–800  $\mu\text{m}$  of the cortex, and the steepest gradient is found within a short distance at that depth.

The experimental results described by Creutzfeldt and colleagues indicate a close correlation between averaged EPs and cellular potentials.



**Fig. 2.** A comparative presentation of power spectra (compressed spectral arrays). Simultaneous recordings from the same subject in frontal, central, parietal and occipital locations. Bickford's spectral array. Along the abscissa is the EEG frequency in Hz. Along the coordinate the EEG-epochs in increasing time axis. Modified from Başar (1990).

It is possible to find a strikingly close correlation between unit recordings and recordings of population response. The degree of correlation depends on the recording site and the type of experiments.

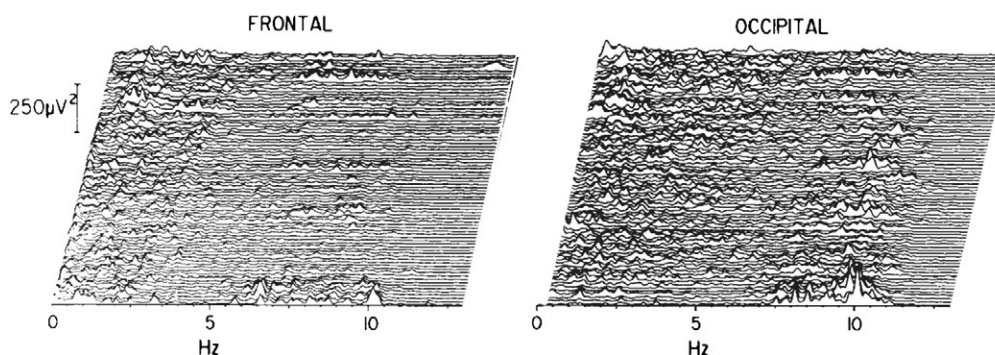
Dinse et al. (1991, 1997) investigated a highly significant and reproducible temporal structure that can already be identified in post-stimulus time histograms (PSTHs) using simple flashed stimuli. Fig. 1 shows the histograms of this oscillator structure: a low-frequency oscillation in the range of approximately 10 Hz, in different cortical areas. Based on spectral analysis of their data, these authors suggest that high-frequency band (30–90 Hz) and slow-frequency oscillatory patterns are present in the neural discharge simultaneously, but with different amplitude characteristics (Dinse et al., 1997).

In a number of electrophysiological studies carried out in various laboratories, it has been demonstrated that the receptive fields of the retina and the lateral geniculate nucleus (LG) are not homogenous systems with uniform characteristics and properties. Dudkin et al. (1978)

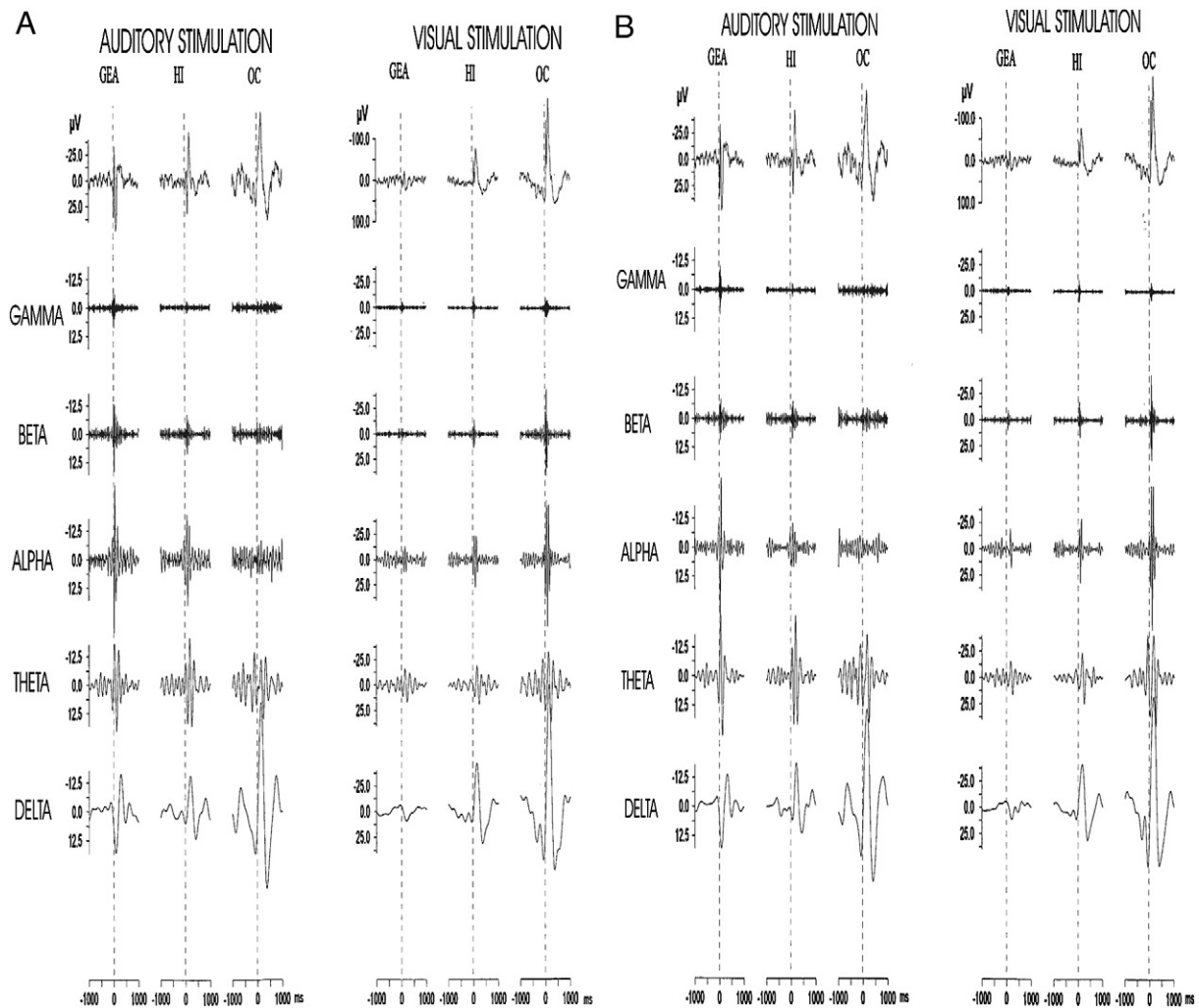
showed that changing the stimulus area and contrast against a background allows one to recognize three types of receptive fields in the cat lateral geniculate nucleus.

To reveal the differences in the dynamics of receptive fields to luminance, Dudkin et al. (1978) studied the temporal frequency characteristics of the lateral geniculate nucleus and their dependence on the spatial parameters of light stimulus. They recorded the PSTHs of responses of neurons belonging to different types of receptive fields and applied a Fourier transform to determine their frequency characteristics. The results indicate that type I and type II receptive fields have different frequency characteristics.

Moreover, the study of single frequency characteristics obtained from single visual stimuli reveals distinct frequency peaks around 10 Hz and 20 Hz. It is to be expected that the gross electrodes pick up responses of various neural groups in the lateral geniculate nucleus. Certainly, experiments with freely moving, chronically implanted cats



**Fig. 3.** A comparative presentation of power spectra for frontal and occipital locations of another subject. Bickford's spectral array. Along the abscissa is the EEG frequency in Hz. Along the coordinate the EEG-epochs in increasing time axis. Modified from Başar (1990).



**Fig. 4.** (A) Results of band-pass filtering in a typical animal: left, auditory stimulation; right, visual stimulation. Each column refers to an electrode site (auditory cortex: GEA; visual cortex: OC; hippocampus: HI). The uppermost row shows the wide-band filtered curve. The remaining rows show the frequency components gamma (32–64 Hz), beta (16–32 Hz), alpha (8–16 Hz), theta (4–8 Hz) and delta (0.5–4 Hz). (B) Results of wavelet decomposition in a typical animal: left, auditory stimulation; right, visual stimulation. Each column refers to an electrode site (auditory cortex: GEA; visual cortex: OC; hippocampus: HI). The uppermost row shows the wide-band filtered curve. The remaining rows show the frequency components gamma (32–64 Hz), beta (16–32 Hz), alpha (8–16 Hz), theta (4–8 Hz) and delta (0.5–4 Hz). (A) Modified from Başar et al. (1999). (B) Modified from Başar et al. (1999).

cannot easily be compared with electrophysiological experiments with unit recording. However, a comparison of the results of Dudkin et al. (1978) shows that the grossly recorded EPs reflect the information that could be obtained from single recordings in the time and frequency domains.

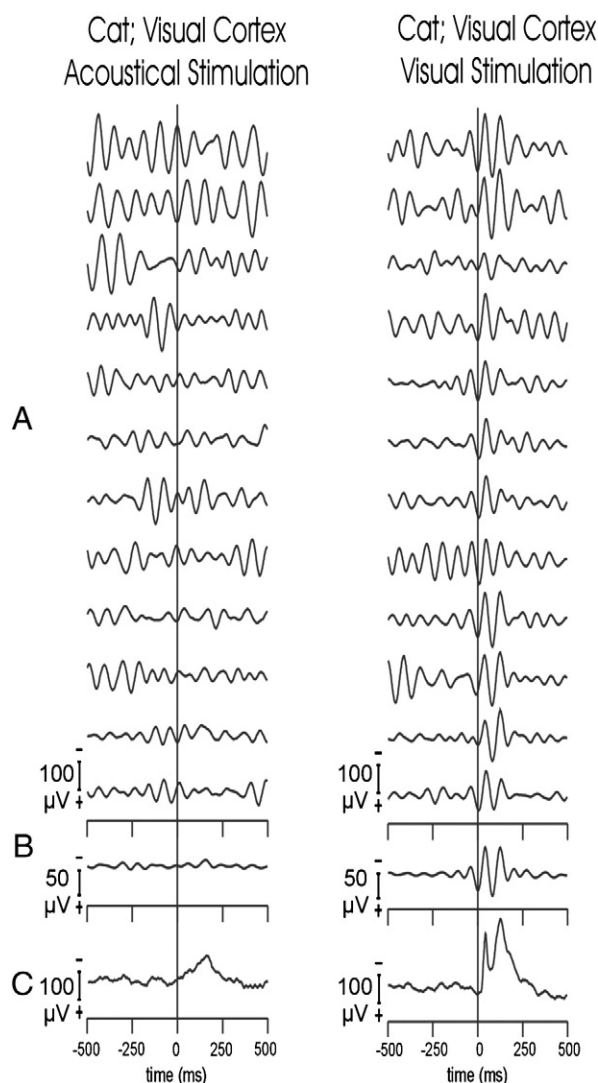
As Shepherd (1988, pp. 518–519) states, “the thalamic circuits are recognized to include both the specific relay nuclei (such as the lateral geniculate nucleus) and the nonspecific reticular thalamic nucleus. The latter receives three types of inputs, from (1) the brainstem reticular system (see below); (2) collaterals of specific thalamocortical relay neurons; and (3) cortical pyramidal neurons. The intrinsic organization of the thalamic nuclei consists mainly of inhibitory dendrodendritic and axo-dendritic synapses; the output is directed solely at the specific relay nuclei, and is also inhibitory. Thus, the reticular neurons constitute a special system for inhibitory control of the thalamic relay neurons and, through them, of thalamocortical circuits”.

The membrane properties of thalamic neurons have been revealed by electrophysiological analysis of in-vitro slice preparations. Jahnson and Llinás (1984) showed that the thalamic neurons have two modes of impulse firing. In one mode, the resting membrane potential is relatively hyperpolarized and the cell fires in brief bursts at a rate of 6/s; In the other mode, the resting membrane potential is relatively

depolarized and the cell fires at a rate of 8–12/s—the range of the alpha rhythm. These two modes of firing depend on different ion channels being differentially activated at these membrane potential levels. The membrane potential, in turn, is controlled by the synaptic inputs.

A study by Silva et al. (1991) reported that minipyramidal neurons in layer 5 of the neocortex showed prolonged 5–12 Hz rhythmic firing at the threshold, which was due to intrinsic membrane properties. The data suggest the presence of an oscillatory mechanism intrinsic to the membrane of each rhythm-generating neuron. The same study also explored the possibility that intrinsically rhythmic neurons of layer 5 can generate synchronized cortical oscillations. The authors interpreted their results as indicating that a network of intrinsically rhythmic neurons in layer 5 can initiate synchronized rhythms and project them onto neurons of other layers. Thus, many of the pyramidal neurons of layer 5 had the intrinsic ability to fire unstable, rhythmic patterns at 5 to 12 Hz; fragments of cortex containing only layer 5 were sufficient to generate synchronized oscillations at 4 to 7 Hz; fragments of cortex without layer 5 did not oscillate synchronously. The authors made the following conclusions based on the observed responses: “Neurons generate rhythms in a variety of ways. Some have an intrinsic property to oscillate, and groups of these may interact synaptically to





**Fig. 5.** EPs recorded from the cat brain by using intracranial electrodes. (A) Single EEG-EP trials, filtered 8–15 Hz; (B) averaged EP, filtered 8–15 Hz; (C) averaged EP, wide-band filtered. Left column, inadequate stimulation (visual cortex recording with auditory stimulation). Right column, adequate stimulation (visual cortex recording with visual stimulation).  
Modified from Schürmann et al. (1997).

produce synchronous patterns. Synchronized rhythms can also arise as an emergent property of a network of neurons that, as individuals, are non-rhythmic. Neurons in the middle layers of the neocortex can initiate some non-rhythmic forms of synchronized activity" (Silva et al., 1991).

Hughes and Crunelli (2007) identified a subset of thalamocortical (TC) neurons in the lateral geniculate nucleus (LGN) that exhibit dendritic calcium channel-dependent rhythmic high-threshold bursting at 2–13 Hz, and which are interconnected by gap junctions (GJs). These cells combine to generate a locally synchronized continuum of alpha and theta oscillations, thus providing direct evidence that the thalamus can act as an independent pacemaker of alpha and theta rhythms. Furthermore, GJ-coupled pairs of TC neurons can exhibit both in-phase and anti-phase synchrony, and will often spontaneously alternate between these two states. The authors interpret this by proposing that the local field oscillation amplitude is not only simply linked to the extent of cell recruitment into a single synchronized neuronal assembly but also to the degree of destructive interference between dynamic, spatially overlapping, competing anti-phase groups of continuously-bursting neurons. The authors further argue that these

network dynamics might have important implications for relating changes in the amplitude of EEG rhythms and also alpha and theta rhythms in the activity of thalamic networks.

#### 4. Spontaneous alpha, sensory-evoked alpha and event-related alpha

##### 4.1. Spontaneous alpha distributed in the whole cortex

Fig. 2 shows the power spectra that were simultaneously evaluated from four different locations of a subject (vertex, parietal, occipital and frontal) during waking stage with eyes closed. During the analysis of such compressed arrays of power spectra, the following observation was usually made: In the central electrode (vertex), the power was usually centered between 7 and 10 Hz, with large peaks in frequencies lower than 10 Hz. In occipital locations, the subjects usually showed high amplitude alpha activity centered at 10–12 Hz. In frontal electrodes the 10-Hz component usually had lower amplitudes; high amplitude activities were mostly associated with lower frequencies, including the theta band.

Additional to the illustration in Fig. 1, another case is added of a subject who did not show any relevant alpha activity during the periods of eyes closed, especially in the frontal region. The important message from the illustrations in Figs. 2 and 3 is that two different locations in the brain may show completely different behaviors. These results might help to account for the discrepancies in the results of several authors by facilitating hypotheses based on alpha activity. The activities of a unique location (spontaneous EEG, EPs and EROs) cannot be representative of the whole cortex. Hypotheses related to alpha activity must encompass all locations, since the correlations and coherences between all locations are also functionally relevant (see also Section 9).

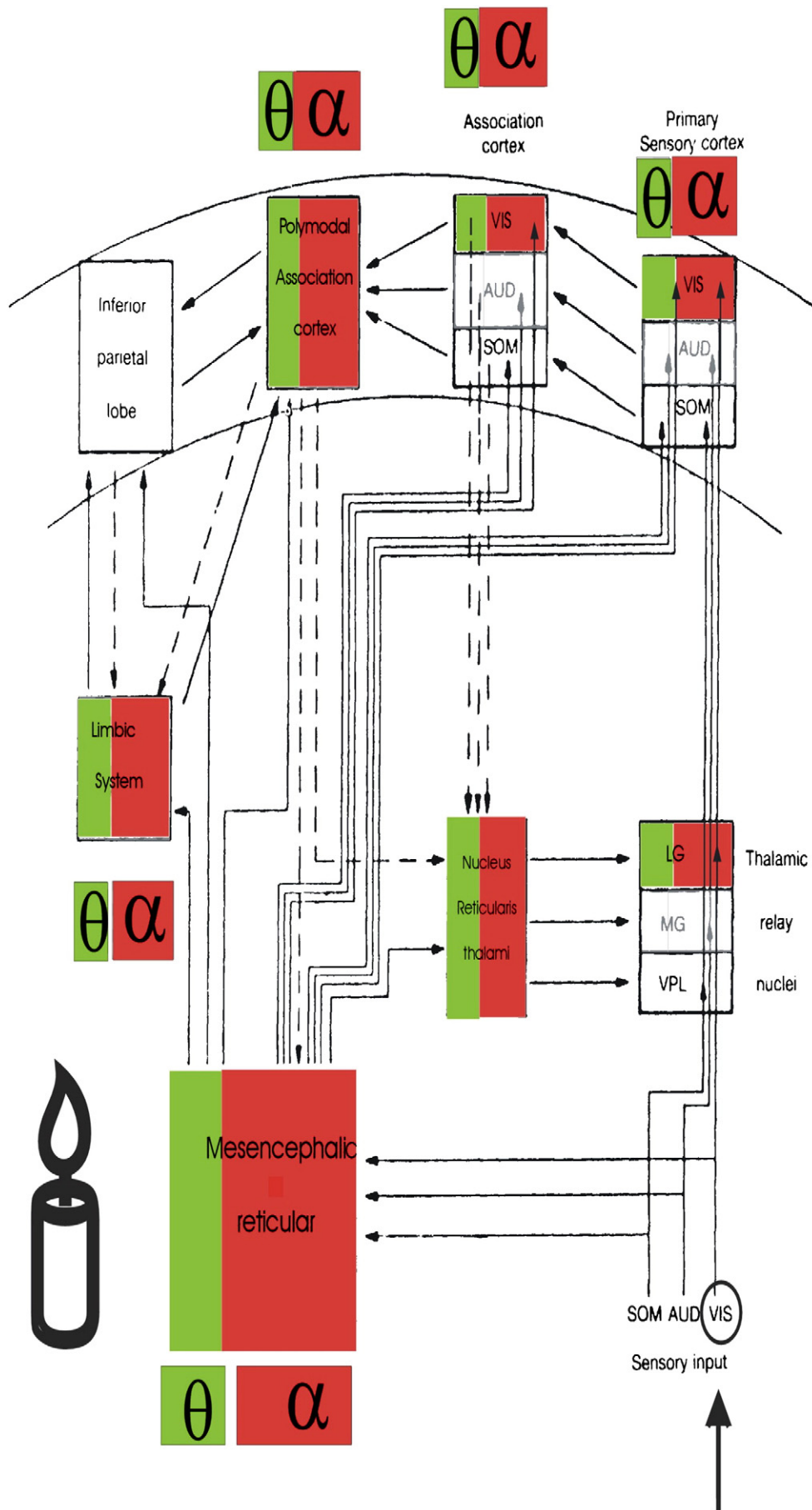
##### 4.2. Sensory-evoked alpha

Although research on experimental animals with sub-cortical electrodes analyzing the evoked/event-related oscillations is fundamental, such studies were not conducted during recent decades. Accordingly, this review is limited by the availability of relatively few publications.

Fig. 4A shows the results of band-pass filtering of the auditory and visual evoked potentials recorded from the auditory cortex (gyrus ectosylvian anterior), hippocampus (HI) and visual cortex, and occipital cortex (OC) of a representative cat. Fig. 4B shows the same results, evaluated by the wavelet analysis techniques applied to ERP analysis. Wavelet analysis confirms the results obtained using the amplitude frequency characteristics (AFCs) and digital filtering. In addition, wavelet analysis can be used for *signal retrieval and selection* from a large number of sweeps recorded in a given physiological or psychological experiment (see Fig. 4B) (Demiralp et al., 1999; Başar, 1999; Başar et al., 1999). Note that the uppermost rows in Fig. 4A and B are identical, since there are wide-band filtered EPs from the same cat.

The basic observation on the oscillatory response EPs in both A and B is generally in accordance. However, especially in higher frequency bands, the time localization capability of wavelet analysis was significantly better compared with the conventional band-pass filters. The ringing effects occurring in the conventional band-pass filtering techniques, which lead to oscillations before the stimulation time point, were smaller in alpha, beta and gamma frequency ranges. The noteworthy results are emphasized below:

1. The dominant frequency components of the visual EPs recorded in the OC area were of comparable weight in the delta and alpha ranges, whereas the auditory EPs (recorded in GEA) had a dominant component in the alpha range.
2. Alpha response components were most pronounced in the responses of OC and GEA to adequate stimuli, and in HI in visual





modality, whereas their amplitudes were markedly reduced in the responses of both GEA and OC to inadequate stimuli.

Besides frequency and site of oscillations, several other parameters are dependent on specific functions, namely *enhancement*; *time locking*, *phase locking*, *delay* and *duration of oscillations* (for a review of the methods to assess these parameters, see, for example, Kolev and Yordanova, 1997).

#### 4.3. Schematic explanation of visual and evoked auditory alpha responses distributed in the cat brain

##### 4.3.1. Sensory components

This section considers the *topographic differences* of frequency components, using the example of the alpha response in cross-modality measurements in the cat brain, as mentioned in the previous paragraph. In particular, the results of measurements from auditory and visual areas are summarized. As auditory and visual stimuli were used, the conditions were either “adequate stimulation” (auditory cortex recording of auditory EP; visual cortex recording of visual EP) or “inadequate stimulation” (visual cortex recording of auditory EP and vice versa). Such experiments are referred to as “cross-modality” measurements (Hartline, 1987).

Panel A in Fig. 5 shows the single-trial EPs filtered in the 8–15 Hz range. The left column refers to auditory stimulation with visual cortex recordings; the right column to visual stimulation with visual cortex recordings; i.e. inadequate vs. adequate stimulation. Responses to visual – adequate – stimulation show amplitude increase and time- and phase-locking. A distinct response is also seen in the filtered averaged EP in panel B. The unfiltered averaged EP also shows an alpha-like waveform. In contrast, responses to auditory stimulation are inadequate, and show neither amplitude increase nor phase locking, nor can an alpha response be seen in the filtered average. There is a type of response in the unfiltered EP in panel C, but this is not an alpha response.

Thus, alpha responses were recorded with adequate stimuli in primary sensory areas. Adequate vs. inadequate differences were larger for alpha responses than for theta responses, demonstrating the functional relevance of frequency components. As an aside, in “cross-modality” recordings from the auditory cortex (gyrus ectosylvianus anterior) of the cat brain, a complementary effect was observed, in that large alpha enhancements were present in auditory EP recordings; no such alpha enhancements were observed in visual EP recordings from the auditory cortex. These results provide an important message: In human recordings and in animal recordings, the concept of cross-modality implies that the alpha processes in the brain must be analyzed dependent on topology and stimulation modality. This is also valid for measurements upon application of cognitive load. In this case, modality of cognitive task and also the results from locations such as frontal lobes and parietal lobes will indicate the major functions.

When a subject (human or cat) is visually stimulated, large alpha enhancements are recorded in the *mesencephalic reticular formation*, lateral geniculate nucleus and, in parallel, in the hippocampus (Başar et al., 1975a, 1979a; Başar, 1980). There are also large alpha enhancements in the visual and association cortices. Information flows to the polymodal association cortex and to the limbic system. The results have also shown that large theta enhancements were recorded in the thalamus, hippocampus, primary cortex and association cortices, including the frontal lobes (Başar, 1999). Fig. 4A and B illustrates that alpha enhancements cannot be seen in the auditory areas of the cortex and thalamus upon visual stimuli; however, theta enhancements are also present in these structures following light stimulation.

Large alpha and theta enhancements are observed in the limbic system, reticular formation and lateral geniculate nucleus. No alpha enhancements are recorded in the nuclei of the auditory pathways. Although the theta enhancements are also one of the major response components in thalamus and cortex, the alpha responses are not recorded in the auditory cortex or the medial geniculate nucleus.

Although we do not mention here all the functions attributed to the reticular formation, we will describe a relevant working hypothesis, formulated by Hernandez-Peon (1961):

- (1) The brainstem reticular system is a region where impulses of all sensory modalities converge. It is reached by impulses from the lower segments of the specific afferent paths, as well as by those arising from the cortical receiving areas.
- (2) The same central region is able to decrease or increase the *excitability* of most sensory neurons. Therefore, it is able to inhibit or facilitate sensory transmission at all levels of the specific afferent paths. The centrifugal control of sensory paths exerted by the reticular system is tonic and selective.

According to the hypothesis of Hernandez-Peon, the core of the brainstem may be viewed as a form of *high command*, which constantly receives and controls all information from the external and internal environments, as well as from other parts of the brain itself. However, at a given moment only a limited part of the information reaches this central area, and a large number of informing signals are excluded. The exclusion of afferent impulses from sensory receptors takes place just as they enter the central nervous system. Therefore, it is assumed that the first sensory synapse functions as a valve, where sensory filtering occurs. This might lead to the concept that the reticular mechanism of *sensory filtering* is formed by a feedback loop with an ascending segment from second-order sensory neurons to the reticular formation and a descending limb carrying impulses in the opposite direction. Hernandez-Peon states that it is unlikely that both centripetal and centrifugal limbs of the loop contain specific facilitatory and inhibitory neuronal connections. Such an arrangement would prevent over-activation of sensory neurons and, therefore, an excessive bombardment of the brain by afferent impulses.

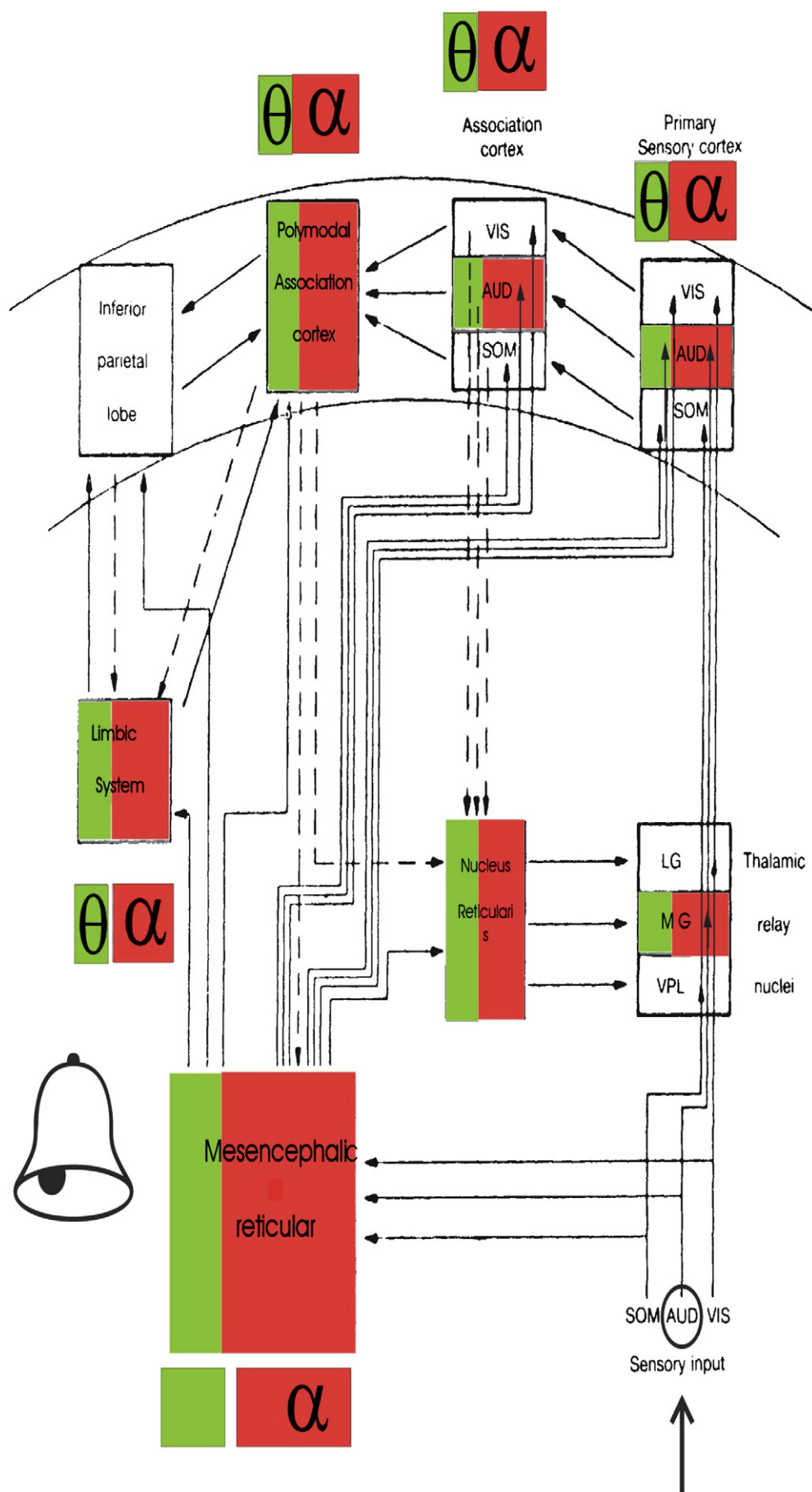
Fig. 6 describes, schematically and globally, the distribution of visual alpha responses in various structures of the cat brain according to empirical results.

Fig. 7 explains a similar hypothetical flow of information upon an auditory stimulation. In this case, alpha enhancements dominate the structure in the auditory pathways, i.e. reticular formation and the hippocampus. The neurophysiological processes in sub-cortical structures depict large alpha response components in reticular formation, medial geniculate nucleus and auditory cortex. It is noteworthy that reticular formation and hippocampus show large alpha responses, whereas lateral geniculate nucleus and visual cortex show only theta responses. Theta enhancements are present in all structures, regardless of whether the stimulus is inadequate or adequate. The way of approaching the responses to auditory stimulation can also be applied to visual stimulation, but the largest alpha enhancements are marked in temporal, parietal and occipital areas.

Fig. 7 describes, schematically and globally, the distribution of auditory alpha responses in various structures of the cat brain according to empirical results.

EROs in mice were measured by Ehlers and Criado (2009) using sensory and/or cognitive processes that influence the dynamics of the EEG. Using this method, EROs are estimated by decomposition of the EEG signal into phase and magnitude information for a range of frequencies, and then changes in those frequencies are characterized over a millisecond time scale with respect to task events. The

**Fig. 6.** Flow of oscillatory information in alpha and theta frequency channels in the visual pathway, reticular formation, limbic system and association areas of the cortex. Letters “alpha” and “theta” indicate the existence of strong enhancements. Sensory and cognitive neural pathways in this figure are modified from Flohr (1991) and Başar (2004).



results of these studies demonstrate that EROs can be generated in cortical sites in mice in the delta, theta, alpha/beta frequency ranges in response to auditory stimuli. Oscillations in the 7.5–40 Hz frequencies were significantly affected in the 0–50 ms time range in response to differences in tone frequency.

#### 4.4. Human evoked sensory alpha

It is useful to compare the cat data with EEG recordings in humans. Fig. 8 shows filtered curves computed from grand averages of occipital recordings ( $O_1$ ). The alpha response to auditory stimulation (adequate for the visual cortex, occipital located) is on the left, showing low-amplitude response; the response to visual stimulation on the right, however, has a distinct alpha response. Note that the adequate–inadequate difference is less for the theta response. This supports the hypothesis given previously: as observed in cats, it is mainly the alpha response, which is dependent on whether or not a stimulus is adequate. A correlation between the alpha response and primary sensory processing is thus plausible both for human and for cat EEG-EP data.

#### 4.5. Brief comments on alpha and motor processes

The results of Pfurtscheller et al. (1996) on motor correlates of alpha activity were explained in detail. At this stage, we should again mention the statements of Llinás (1988), who assigned oscillations and resonances in the central nervous system to diverse functional roles. This author assumed that oscillations play a role in determining global functional states (for example, 1. sleep–wakefulness or attention; and 2. timing in motor co-ordination). Both these examples, and especially the results of Pfurtscheller et al. (1996), show how the alpha activity is involved in movements.

Pineda (2005) described that mu and alpha-like rhythms are independent phenomena because of differences in source generation sensitivity to the frequency and power of sensory events. According to this author, alpha networks (visual, auditory and somatosensory-centered domains), typically producing rhythmic oscillations in locally independent sources of alpha, become coherently engaged in transforming perception to action.

### 5. 10-Hz activity in sympathetic nerves of the heart, the spinal cord and cerebellum

In recent decades, the group led by Gebber and Barman in Michigan studied the frequency links of the spinal cord to the heart and kidneys. Such studies are rare; however, they provide core information for the oscillatory integration between the central nervous system and the vegetative system.

In their early studies, Barman and Gebber (1993) recorded a variable mixture of 10-Hz and 2- to 6-Hz discharges from sympathetic nerves in decerebrate cats. The data supported the view that lateral tegmental field neurons (LTF) have a permissive role in governing the 10-Hz rhythm sympathetic nerve discharge (SND), probably by acting on elements of the rhythm generator located elsewhere.

In further studies by the Michigan group (Barman et al., 1995), coherence analysis revealed that the 10-Hz rhythm in SND was not correlated to that in either inferior olivary activity of decerebrate cats; or to neocortical spindles of urethane-anesthetized cats. Also, the discharges of some ventrolateral medullary and raphe neurons contained a 10-Hz rhythm that was not correlated to that in SND. These data support the hypothesis that a 10-Hz rhythm reflects the organization of a brainstem network that specifically governs sympathetic outflow.

In order to evaluate the role of pontine neurons, Barman et al. (1997) hypothesized whether pontine neurons are elements of the network responsible for the 10-Hz rhythm in sympathetic nerve discharge (SND). The first series of experiments tested whether chemical inactivation of neurons in the rostral dorsolateral pons (RDLP) or caudal ventrolateral pons (CVLP) affected inferior cardiac postganglionic SND of urethane-anesthetized cats. Barman et al. (1997) supported the view that pontine neurons are involved in the expression of this rhythm. Additional experiments were designed to determine whether pontine neurons are activity correlated to the 10-Hz rhythm in SND or whether they merely provide a tonic (nonrhythmic) driving input to the rhythm generator. Coherence analysis revealed that local field potentials recorded from the RDLP or CVLP had a 10-Hz component that was significantly correlated to SND. Additionally, spike-triggered averaging and coherence analysis showed that the naturally occurring discharges of individual RDLP or CVLP neurons were correlated to the 10-Hz rhythm in SND.

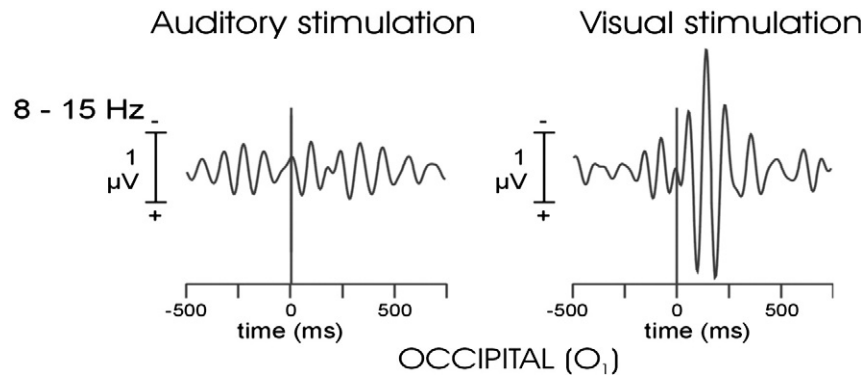
Gebber et al. (1999) used time and frequency domain analyses to examine the changes in the relationships between the discharges of the inferior cardiac (CN) and vertebral (VN) postganglionic sympathetic nerves produced by electrical activation of the midbrain periaqueductal gray (PAG) in urethane-anesthetized, baroreceptor-denervated cats. Further, CN–VN coherence and phase angle in the 10-Hz band served as measures of the coupling of the central oscillators controlling these nerves. The 10-Hz rhythm in CN and VN discharges was entrained 1:1 to electrical stimuli applied to the PAG at frequencies between 7 and 12 Hz. CN 10-Hz discharges were increased and VN 10-Hz discharges were decreased when the frequency of PAG stimulation was equal to or greater than that of the free-running rhythm. In contrast, stimulation of the same PAG sites at lower frequencies increased, albeit disproportionately, the 10-Hz discharges of both nerves. In either case, PAG stimulation significantly increased the phase angle between the two signals (VN 10-Hz activity lagged CN activity); coherence values relating their discharges were little affected. However, the increase in phase angle was significantly more pronounced when the 10-Hz discharges of the two nerves were reciprocally affected. Importantly, partialization of the phase spectrum using the PAG stimuli did not reverse the change in CN–VN phase angle. Gebber et al. (1999) discussed the possibility that the increase in the CN–VN phase angle reflected changes in the phase relations between coupled oscillators in the brain stem.

Barman and Gebber (2007) recorded changes in right inferior cardiac and either left inferior cardiac or left vertebral sympathetic nerve discharge (SND) produced by unilateral microinjections of GABA-A and excitatory amino acid (EAA) receptor antagonists into the ventrolateral medulla (VLM) of urethane-anesthetized, baroreceptor-denervated cats. Their observations suggest that: 1) GABAergic transmission in VLM is critical for generation of the 10-Hz rhythm; 2) the caudal and rostral portions of VLM act together to generate the 10-Hz rhythm; and 3) 10-Hz rhythm generation depends, at least in part, on tonic or phasic excitatory drive to GABAergic interneurons in caudal VLM and presympathetic neurons in rostral VLM.

Barman and Gebber (2009) further studied the changes in inferior cardiac sympathetic nerve discharge (SND) and mean arterial pressure (MAP) produced by aspiration or chemical inactivation (muscimol microinjection) of lobule IX (uvula) of the posterior vermis of the cerebellum in cats anesthetized with urethane. Autospectral analysis was used to decompose SND into its frequency components. These results are the first to demonstrate a role of cerebellar cortical neurons of the posterior vermis in regulating the frequency composition of naturally occurring SND.

**Fig. 7.** Flow of oscillatory information in alpha and theta frequency channels in the auditory pathway, reticular formation, limbic system and association areas of the cortex. Letters “alpha” and “theta” indicate the existence of strong enhancements. Sensory and cognitive neural pathways in this figure are modified from Flohr (1991).





**Fig. 8.** Alpha responses of grand average EPs ( $N = 11$ ). Filter limits: 8–15 Hz, “alpha response”. Left, acoustic stimulation; right, visual stimulation. Modified from Schürmann et al. (1997).

## 6. Alpha in neuroethology

### 6.1. What is neuroethology?

Neuroethology is the biological approach to the study of the neural basis of behavior. The ethological approach emphasizes the causation, development, evolution and the function of behavior. Neuroethologists seek to understand this in terms of neural circuits. Neuroethology is the study of natural behavior, which, in the older scientific literature, was called “innate behavior”. The neural approaches used in neuroethology are as diverse as the field of neuroscience itself. Often, neuroethologists use behavioral methods only to ask profound questions about the organization of underlying neural circuits. As a result of this pioneering research, many scientists then sought to connect the physiological aspects of the nervous and sensory systems to specific behaviors.

Since Adrian (1931, 1937) and Adrian and Matthews (1934), among others, drew attention to some evidence of similarity and, mainly, differences between invertebrates (insects) and mammals, little progress has been made in this field. Bullock (1945, 1974, 1983, 1984a, b) and Bullock and Horridge (1965) provided evidence both for widespread similarity among vertebrates, and general differences between them and invertebrates.

Many invertebrate ganglia are simple-structured nerve cell populations consisting of a relatively small number of cells. Lower level ganglia, analogous to spinal cord, plus the brains of a few less advanced invertebrates, consists of up to a few thousand neurons. The brains of most insects, lobsters and cephalopods have fairly complex structure and tens to hundreds of thousands of cells. The *Helix pomatia* snail is intermediate, probably of the order of  $> 10^4$ . The cat or human brain, a complex, three-dimensional network, is composed of an astronomical number of neurons (of the order of up to  $10^{12}$ ). The significance of studying an invertebrate CNS as a brain model may be supported by Bullock's (1988) observation:

“When ongoing compound field potentials in the brains of invertebrates and vertebrates are compared, the recorded differences between vertebrates and most invertebrates are not due to brain size, cell size, number or density, lamination, or single cell power spectrum, but are primarily due to assembly properties, i.e., to co-operativity”.

Therefore, the following questions have been addressed: (1) Are there some common components among the frequency characteristics of evoked potentials of the vertebrate and the invertebrate, representing different stages of evolution? (2) Are there changes of coherence in the neural tissue during the evolution of the species?

### 6.2. The relationship between the EEG of vertebrates and field potential fluctuations of invertebrates

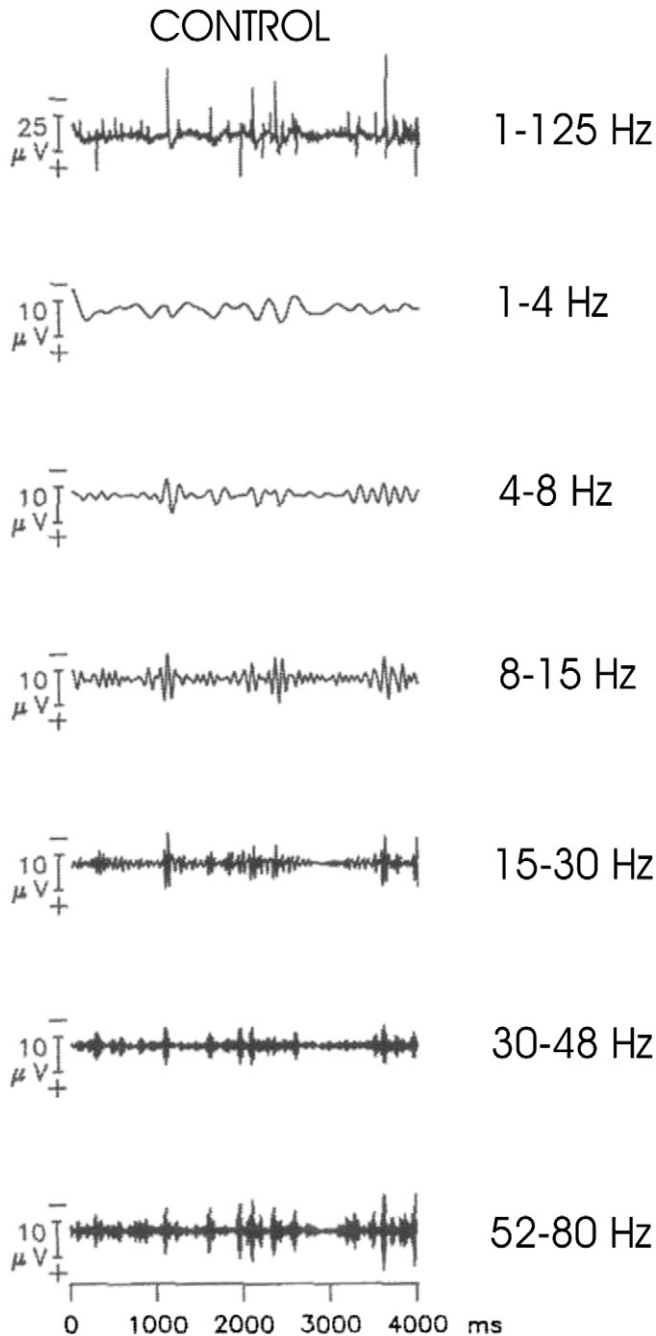
When comparing the slow, rhythmical potential fluctuations of the *Helix* and *Aplysia* ganglia with those of the higher vertebrates, it must be kept in mind that the CNS is totally disconnected from the peripheral organs, meaning that the sensory association fields no longer have exogenous inputs in natural forms. Nevertheless, distinct fluctuations are revealed in the low amplitude field potentials of the invertebrate ganglia when the signals are arbitrarily pass-band filtered: For *H. pomatia* in the 1–4 Hz, 4–8 Hz, 8–15 Hz, 15–30 Hz, 30–48 Hz and 52–125 Hz ranges (Röschke, 1988; Schütt et al., 1992) and for *Aplysia* in the 2–5 Hz, 5–10 Hz, 10–20 Hz and 40–80 Hz ranges (Bullock and Başar, 1988) (see Fig. 9 for all frequency windows). The different types of pass-band filters chosen for *Aplysia* and *Helix* are simply arbitrary and not due to any consistent, reproducible differences in fluctuations between species. These fluctuations are solely of the intrinsic cellular activities of small cell populations, independent of sensory modality.

The relative weakness of slow waves in most invertebrates might be due to relatively little synchrony among neurons. In contrast to *Aplysia*, and presumably most other invertebrates, vertebrates have a significant degree of synchronization of low-frequency components ( $< 25$  Hz), judging by the mean coherence between electrodes  $< 1$  mm apart. Another basic difference is that the power spectra of higher centers in arthropods and gastropods are much stronger (ranging from 50 to 500 Hz) than in the vertebrate higher centers, resembling the cerebellum and spinal cord (Bullock and Başar, 1988).

Evidence provided by these findings strongly implies that the 8–15 Hz activity (alpha band), which is known as one of the most important frequency components of mammalian brain activity, is also generated in the much smaller and less developed CNS such as the isolated invertebrate ganglia. Fig. 10 illustrates the 8–15 Hz apparent rhythms from both cerebral and visceral ganglia of *H. pomatia* superimposed on the wide-band (1–50 Hz) filtered time signals (Röschke, 1988; Schütt et al., 1992).

## 7. Alpha in the maturing brain

There are important changes in the structure and electrical activity of the human brain from the fetus to the brain of elderly subjects. How do these changes affect the transfer functions, i.e. communication processes, in the maturing brain? A two-year-old child does not have a full command of their native language and cannot solve mathematical problems; and neither does a two-year-old child does show alpha activity. Furthermore, the frontal lobes are not completely developed; synaptic organization is in the process of steady development. The present section includes measurements of three groups:

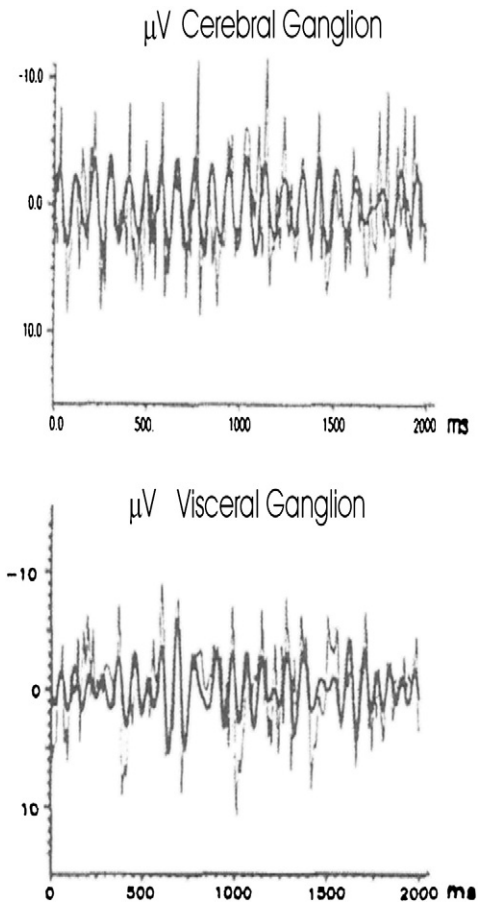


**Fig. 9.** *Helix pomatia*: A typical time signal (ca. 4 s) of the ongoing activity with a modest number of spikes in the neuropile of the isolated visceral ganglion; wideband (1–125 Hz) and pass band components (1–4, 4–8, 8–15, 15–30, 30–48 and 52–80 Hz). Modified from Schütt et al. (1999).

three-year-old children, adults and elderly people. In order to provide the basis of the ontogenesis of the maturing brain, the next section gives an anatomical description.

#### 7.1. Changes in structure and synaptic organization of the human brain

In ontogeny, similar to the evolution of the species, the neo-cortex develops much more in size and volume than any other neuronal structure of the brain. Also, in humans, from embryo to adult, the relative growth of the white matter, underlying the cortex with its connective structure, far surpasses that of white matter elsewhere in the central nervous system (CNS). In the human neocortex, neuron generation seems to be completed by the end of the second trimester



**Fig. 10.** *Helix pomatia*. The field potential fluctuations in different ganglia; a sample of 2 s each. Top: the cerebral ganglion; bottom: visceral ganglion; thin line: wide band component (1–50 Hz); thick line: narrow-band component (8–15 Hz). Note that occasional, regular 10-Hz oscillations of maximal 10 μV can be recorded. Modified from Schütt et al. (1999).

of gestation. Subsequently, however, cortical neurons continue to grow in size; even at the time the infant is born, some neurons are still developing and migrating to their final location. Synaptogenesis begins in the third trimester of the pregnancy and continues until the age of two years. According to Changeux (2004), in humans, about half of all adult synapses are formed after birth, and their number continues to change, rising and then falling, until death. In humans, the postnatal development of the brain lasts considerably longer than in other mammals. Cranial capacity in humans increases 4.3 times after birth. Moreover, cranial capacity reaches 70% of the adult human volume 3 years after birth. It is important to note that alpha activity in children starts 3 years after birth, almost parallel to the development of speech. In humans, the rapid phase of synaptic growth is shorter in a sensory area such as the visual cortex, where it continues to grow until two or three years after birth, than in association areas such as the prefrontal cortex, where it lasts up to 10 years from birth. Changeux (2004) further states that this observation has great importance from a functional point of view. The prefrontal cortex, which is very rich in neurons in layers two and three, plays a central role in cognitive functions (see also Fuster, 1995, 1997).

In their book, "The Brain and the Inner World", Solms and Turnbull (2002) indicate that the frontal cortex is crucial for the retrieval of memory. In this context, it is notable that the frontal cortex, no less than the hippocampus, is poorly developed in the first two years of life. There is a substantial growth spurt in the frontal cortex at around two years of age and then a second spurt at about five years. Further, the frontal cortical volume continues to expand throughout adolescence. In the first few

years, the organizational level of the frontal system may be considered so poor that the organized retrieval process is not available to the young child. The growth of volume and synaptic organization is seemingly accompanied by important changes of alpha activity in primary visual areas and crucial changes in frontal areas (association).

The age of the human subject is one of the most important factors influencing the amplitude and frequency of the EEG (Obrist, 1976; Katada et al., 1981; Dustman et al., 1993; Niedermeyer, 1993).

Most studies analyzing alpha frequency range during maturation have focused on the spontaneous “alpha rhythm”. In spontaneous EEG, a general decrease of spectral alpha power was reported, with this effect being most pronounced at parietal, temporal and occipital locations. Furthermore, slowing of alpha frequency and a shift in the distribution of spectral alpha power and alpha incidence from posterior to anterior locations were also reported (Babiloni et al., 2006; Fisch, 1991; Niedermeyer, 1997; Polich, 1997; Rossini et al., 2007).

Lindsley recorded the posterior dominant alpha rhythm in 75 healthy adults (Lindsley, 1938) and in 256 healthy children (Lindsley, 1939) aged from one month to 16 years. The author reported that the posterior dominant alpha rhythm was 10.2 Hz in adults; Children achieved posterior dominant alpha rhythm frequency of 10.2 Hz by the age of 11 years. A series of studies reported that the mean posterior dominant alpha rhythm is 9.8 at age 15 and 10.2 Hz at age 21 (Eeg-Olofsson, 1971; Petersen and Eeg-Olofsson, 1971). In a more recent study, Marcuse et al. (2008) showed that the maturation of posterior dominant alpha rhythm is nearly complete at the age of 16.

## 7.2. Spontaneous and evoked alpha activity at occipital sites in three age groups

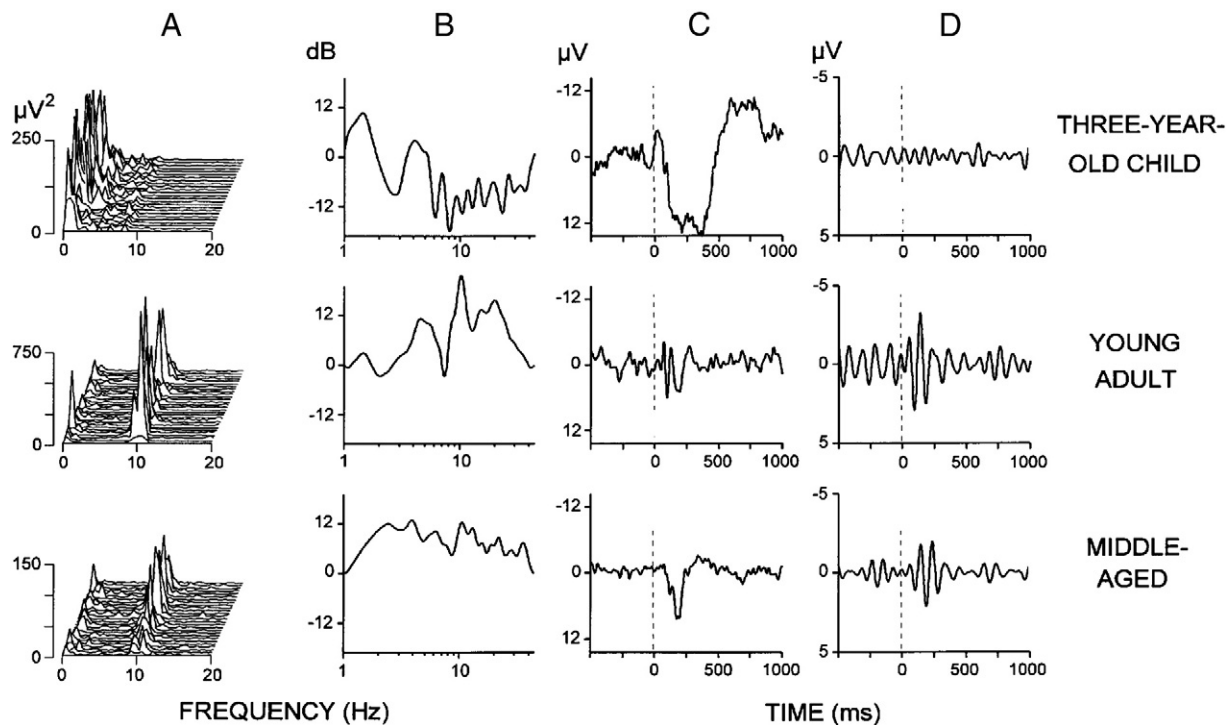
Fig. 11 illustrates the instantaneous power spectra at occipital recordings of three subjects from each of the three age groups: three-year-old child, young adult and middle-aged adult. As known from earlier studies

(Eeg-Olofsson, 1971; Petersen and Eeg-Olofsson, 1971; Niedermeyer, 1993), the EEG in three-year-old children does not, as a rule, have spontaneous activity in the 10-Hz frequency range; no 10-Hz activity was recorded in the EEG of the three-year-old child: In contrast to the results from children, young adults had distinct and ample 10 to 12-Hz activity in the occipital recording (Fig. 11A, middle panel).

Results from experiments on middle-aged subjects showed a reduction in 10-Hz activity in the occipital areas. Fig. 11 (bottom) illustrates the power spectra of a 55-year-old subject. The 10-Hz activity of this subject is apparent in comparison with the three-year-old child, but drastically reduced in comparison with the young adult. Fig. 11B shows the amplitude–frequency characteristics (AFCs), and Fig. 11C displays the averaged evoked potentials upon visual stimulation for the three subjects. Fig. 11D illustrates the filtered average visual EP responses with band limits of 8–15 Hz. No alpha responses (defined as the oscillatory brain activity in the 8–15 Hz frequency range within approximately 200–300 ms following external stimulation) are recorded in the visual EPs of children. In young adults, the group mean amplitude of the peak-to-peak alpha responses in the averaged visual EPs was 4.5  $\mu\text{V}$ . In the visual EPs of middle-aged adults, the peak-to-peak alpha response was 3.1  $\mu\text{V}$ .

## 7.3. A comparative analysis of frontal versus occipital 10-Hz activity in young and middle-aged adults

Fig. 12A presents stack plots of power spectra of the spontaneous EEG of young and middle-aged adults to enable comparison between their frontal and occipital alpha activities. Although young adults generally showed low 10-Hz activity at the frontal site (or sometimes no activity), their posterior alpha had relatively high amplitude (in this example the young adult manifests alpha power at approximately 100  $\mu\text{V}^2$  for the frontal, and more than three times higher for the occipital recording). In the middle-aged adult, a most important



**Fig. 11.** (A) Instantaneous power spectra of consecutive 2 s duration EEG epochs; (B) amplitude–frequency characteristics of visual evoked potentials; (C) averaged VEPs; and (D) averaged VEPs of three representative subjects, filtered in the range of 8–15 Hz: three-year-old child, young adult, and middle-aged adult. All recordings are from the left occipital site  $O_1$ . Stimulus onset occurs at 0 ms. Modified from Başar et al. (1997c).



phenomenon was observed, in that the alpha power of the occipital recording ( $O_1$ ) was maximally  $20 \mu V^2$ , whereas at the frontal ( $F_3$ ) recording site alpha power was approximately  $80 \mu V^2$ .

A significant increase of frontal alpha amplitude was obtained for middle-aged subjects, as also revealed from the mean group RMS values in Fig. 12. In contrast, for the occipital recordings, lower RMS values were produced by the older subject.

Yordanova et al. (1998) assessed the effect of age on time and frequency components of auditory-evoked potentials in two groups of adults, young (18–30 years old) and middle-aged (50–55 years old). These authors showed that only at the frontal site was the alpha responses stronger in phase-locking and enhancement among middle-aged compared with young adults, despite the overall reduction of spontaneous alpha power in older subjects.

Kolev et al. (2002) analyzed visual evoked alpha oscillations and found a prominent effect of aging on frontal alpha (7–15 Hz) oscillations, whose amplitudes and phase-locking were significantly higher in middle-aged subjects. This finding was similar to previous results obtained with auditory stimulation by Başar et al. (1997b) and Yordanova et al. (1998). Furthermore these authors reported that fast alpha responses (10–15 Hz) and slow alpha responses (7–10 Hz) showed differential results.

Srinivasan (1999) analyzed spontaneous eyes-closed and eyes-open EEG in 20 children aged 6–11 years and 23 adults aged 18–23 years. The author used power and coherence to characterize the spatial structure of the alpha rhythm. It was reported that power at anterior electrodes was considerably lower in the children, than in the adults. Coherence between anterior and posterior electrodes was considerably lower in the children.

#### 7.4. Recent results on maturation

Krause et al. (2001, 2007) studied ERD/ERS responses of children while performing an auditory memory task. These authors reported results in the 8–10 Hz alpha frequency band. During retrieval, children exhibited lower magnitude and delayed ERD responses compared to those of adults and these differences were most prominent in the posterior and central electrodes. In the 10–12 Hz frequency band, the ERD/ERS responses in children did not differ significantly from those of the adults.

Maurits et al. (2006) analyzed the changes of event-related coherence with aging during an auditory oddball task. These authors reported that elderly subjects had increased short intra-hemispheric delta, theta and alpha coherences when compared to younger adults.

Schmiedt-Fehr et al. (2009) also analyzed the effect of aging on event-related alpha oscillations. In their study, early event-related synchronization (ERS, 0–250 ms) and late event-related desynchronization (ERD, 200–600 ms) of single-trial lower- and upper alpha were analyzed using poststimulus amplitude enhancement and inter-trial phase coherence measures upon application of visual evoked potential (VEP), a cued stimulus response (S-R) and a cued visual Go/No-Go task. These authors reported that there were no age-related differences in amplitude amplification or inter-trial coherence upon stimuli.

Doesburg et al. (2010) analyzed long-range synchronization and local desynchronization of alpha oscillations during visual short-term memory (STM) retention in children, reporting increased long-range alpha and beta band synchronization during STM retention in children age 6–10 years.

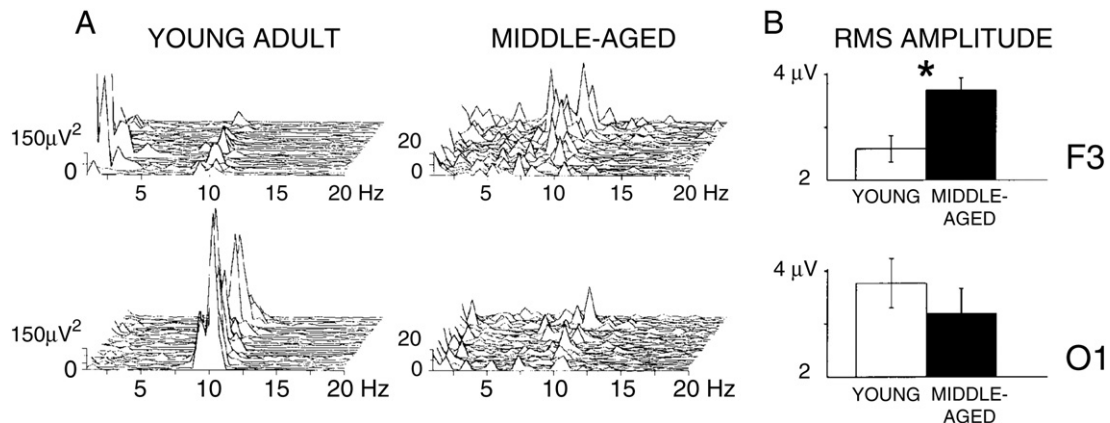
Spironelli and Angrilli (2010) analyzed the functional roles of several EEG bands across age by analyzing language hemispheric lateralization in linguistic tasks. They reported that children had higher alpha amplitude than middle-aged participants over both posterior sites during the orthographic task. Furthermore, children showed higher alpha in left-posterior locations during phonological and semantic processing.

According to Yordanova and Kolev (2009), the differences between the EROs in children and adults suggest that the theta and alpha response systems in 6–10-year-old children operate differently than in adults, such that adults produce responses lower in amplitude and more strongly synchronized. Further, subject age was found to have differing effects on ERO phase-locking and ERO amplitude, suggesting that a mechanism of phase reordering might operate independently of mechanisms regulating the spontaneous power and the magnitude of the response.

#### 7.5. Comments on the parallelism of alpha activity during maturation of the human brain and the evolution of the species

Does a child have a different type of cognitive performance compared with an adult? Does an elderly subject have a different type of experience and “different type of mind” in comparison to young adults? The findings emphasize the need for a “categorization at different levels” for the comparison of cognitive processes in babies, young adults and elderly subjects.

It is intriguing to observe that, during the evolution of the species and during the maturation of the human brain, the alpha activity increases in amplitude (Section 7). Further, as humans age, the high amplitude alpha activity moves from the posterior brain to the frontal brain. Bullock et al. (1995) showed that the coherence in the human cortex is higher in comparison to lower animals. Since, in the brain of the young child, alpha activity is not found in frontal areas, it would



**Fig. 12.** (A) Instantaneous power spectra of EEG epochs in one representative young and one representative middle-aged adult recorded from the left frontal ( $F_3$ ) and left occipital ( $O_1$ ) electrode locations; (B) group mean values  $\pm 1$  standard error of the RMS amplitudes measured in the pre-stimulus epoch from the same electrode locations; significance of difference is \*  $p < .05$ .

Modified from Başar et al. (1997c).

be not possible to find high coherences. Altogether, it seems that the existence of mature alpha activity is of major importance for the development of associative behavior of human brain structures.

During the maturation of the child brain to the adult brain, an increase in the alpha activity is observed. Moreover, in the brains of elderly subjects, the alpha activity shifts from the posterior areas to the frontal cortex. In terms of evolutionary theory, this can be tentatively considered as a *mutation* of alpha activity in the human brain. With the development of cognitive processes and semantic experience of the maturing brain, the frontal alpha activity is becoming richer. The same situation is observed during the evolution of the species: The 10-Hz oscillations in invertebrates have small amplitudes and no coherent activity is observed in the isolated ganglia; in the human brain, the alpha activity shows high amplitudes and regular waveforms. Are there parallels in the evolution of the species and the maturing brain? This is a very important question related to a type of maturation of alpha activity during evolution of species. Is the increase of alpha activity a sign of augmentation of cognitive processes?

## 8. Relationship between prestimulus alpha and evoked alpha response

### 8.1. Event-related desynchronization (ERD)

An important property of the alpha activity is the phenomenon of “alpha blocking”, first described in the early days of EEG research. Opening the eyes blocks the existent alpha-activity; a simple light stimulation triggers the same effect. One of the first demonstrations related to the possibility of functional effect was provided by interesting measurements of Creutzfeldt (1993), who showed that, during mental arithmetic operations, the alpha activity of subjects was blocked, whereas beta activity was increased.

A detailed description of measurements of ERD can be found in Pfurtscheller and Lopes da Silva (1999). According to these authors, the term ERD is only meaningful if the baseline (alpha activity), measured some seconds before the event, represent a rhythmicity, seen as a clear peak in the prestimulus power spectrum. Pfurtscheller and Lopes da Silva (1999) further state that ERO (event-related oscillations) only have meaning if the event results in the case of an oscillatory response component not detected in the prestimulus event. The last statement is, however, somewhat contradictory, since event-related oscillations can be also detected in the presence of alpha activity.

### 8.2. Prestimulus EEG and alpha response

It is also fundamental to emphasize that an inverse relationship exists in all frequency windows between the amplitudes of prestimulus oscillations and event-related responses. This basic phenomenon was analyzed in the last thirty years by several groups (Başar, 1980; Rahn and Başar, 1993a,b; Stampfer and Başar, 1985; Brandt, 1997; Busch et al., 2009; Mathewson et al., 2009; Hanslmayr et al., 2007).

The studies by Jansen and Brandt (1991) are among the most systematic. We also refer to relevant work of Barry et al. (2006), mentioning the importance of preparatory rhythms and preferred states. According to the above-mentioned publications, any statement related to the final functional interpretation of alpha ERD should be pronounced only after examination of the relationship between EROs and prestimulus alpha.

The concept of “evoked alpha” was already developed half a century ago, as stated in Section 1. Studies by Dinse et al. (1991, 1997) and Dudkin et al. (1978) confirmed the existence of the “alpha response” at the cellular level. Later, cross-modality experiments demonstrated that sensory alpha responses are dependent of sensory stimulation and recording site (Section 4).

The amplitude, time course, and frequency contents of evoked potentials (especially N100–P200 wave complexes) strongly depend on the amplitude of alpha activity prior to a sensory stimulation. Publications

by Brandt and Jansen (1991) and Brandt (1997) confirmed not only the findings of Başar (1980), regarding the inverse relationship between evoked potentials and prestimulus EEG; but these authors also described a model presenting evidence that the generation of spontaneous EEG activity can acquire the waveforms of EPs when pulse-like signals serve as input. Further, these authors described a marked correlation between N100 amplitude and prestimulus EEG. The data of Jansen and coworkers supported the hypothesis that spontaneous 10-Hz activity and visual evoked potentials are generated by some of the same neural structures, and that the visual-evoked potentials are due to distributed action rather than dipolar sources.

Hanslmayr et al. (2007) investigated the differences in the prestimulus EEG between subjects who were able to discriminate between four shortly presented stimuli and subjects who were not. Their results showed that perceivers exhibited lower prestimulus alpha than non-perceivers. Furthermore, their analysis of the prestimulus EEG between perceived and unperceived trials revealed that perception of a stimulus is related to low phase coupling in the alpha frequency range. Busch et al. (2009) investigated the effect of prestimulus oscillations on visual perception. These authors presented visual stimuli near threshold, and they have reported that the detection of visual stimuli was strongly dependent on phase of spontaneous EEG oscillations in the low alpha band just before stimulus onset. Mathewson et al. (2009) demonstrated that alpha power and phase differences contribute to conscious target detection. These authors suggested that the oscillatory nature of alpha oscillates between cortical excitability and inhibition. Accordingly, these authors proposed “pulsed inhibition” framework.

Assuming that several 10-Hz generators are distributed in the brain, and further supposing that these activities act as nonlinear clocks (as hypothesized by Norbert Wiener, 1948), then we are confronted with the question of whether 10-Hz processes may facilitate overall association mechanisms in the brain. 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 communication signal “*par excellence*” between different structures (see also results in the volume edited by Başar et al. (1997b)).

### 8.3. Extended results related to the relationship between prestimulus alpha and alpha response

Rahn and Başar (1993a,b) showed a substantial increase in both auditory and visual N1–P2 amplitudes, when stimuli are presented, only during low amplitude alpha and theta EEG states. Furthermore, Schürmann and Başar (1994) and Başar and Schürmann (1994) demonstrated the topographic and modality-dependent EP differences in alpha and theta responses to visual and auditory stimulation resulting from non-linear resonance phenomena.

According to Barry et al. (2004), “averaging” is generally used to increase the signal:noise ratio of the small stimulus-related response hidden in the background EEG activity. These authors state that the resultant ERP is simply an average, which may not be truly representative of the actual response from any single event. There is increasing evidence to suggest that the average does not provide a good estimate of the trial-to-trial response, which appears to be highly variable (Anderson et al., 1991; Başar, 1980; Ford et al., 1994; Stampfer and Başar, 1985). Recognition of these limitations of conventional ERP extraction methods has led researchers to explore new methods of examining and interpreting the ERP (Jasiukaitis and Hakerem, 1998; Price, 1997; Rahn and Başar, 1993b).

Başar and Stampfer (1985) observed a phase reordering or ‘preferred phase angle’ in the delta (0.5–3.5 Hz) frequency range to produce maximal negativity at the time of stimulus onset. Phase alignment was also observable in the alpha range (the focus of this study). Further evidence for preferred (dynamic) EEG frequency phase alignment has been reported by Barry et al. (2003), Pleydell-Pearce (1994), and Rockstroh et al. (1989).

In more recent studies, Becker et al. (2008) insist that, for stages of low pre-stimulus alpha activity recorded at the vertex, an enhancement of the N1–P2 peak-to-peak amplitude (100–250 ms) was demonstrated in fronto-central areas. Also, Barry et al. (2000) showed convincing evidence from auditory oddball data, that a direct relationship between prestimulus alpha activity and EP component amplitude (as proposed by Brandt and Jansen, 1991) is compatible with the existence of an inverse relationship between pre-stimulus alpha and the mentioned “EP enhancement factor” (as proposed by Başar, 1980). These studies imply that the reported inverse correlation allows manifold interpretations of the relationship between EP amplitude and ongoing alpha amplitude. Actually, any relationship that is weaker than directly proportional, even a clear independence of EP and ongoing alpha amplitude, yields such an inverse correlation. Barry et al. (2000) described that the results of Başar’s and Brandt’s studies on the “EP enhancement factor” do not contradict but rather support the evoked theory and its implications. However, at least a strict phase reset can be excluded, since such a behavior would prevent the consistently reported inverse relationship between prestimulus and post-stimulus alpha enhancement. In contrast to the results of Başar’s group on early EP components, Brandt and Jansen (1991) reported a positive enhancement of eyes-closed early VEP components for higher pre-stimulus alpha activity. Again, for comparison, Brandt and Jansen had analyzed sets of averages of 40 trials each and maximum peak-to-peak amplitudes were individually determined for each such average. This analysis is susceptible to systematic confounding effects of residual alpha activity being superimposed on the evoked potential, because estimated peak-to-peak amplitudes with variable latencies are particularly affected by strong residual ongoing alpha activity. In the study by Barry et al. (2003), the analysis approach was to average a large number of trials ( $n \sim 750$ ) pooled over subjects, and analyzed the grand average EPs with fixed latencies. Thus, residual effects of ongoing alpha activity were canceled out more effectively. For this analysis method, the mentioned early EP-enhancing effect disappeared.

The results of Ben-Simon et al. (2008) also suggest that the human alpha rhythm represents at least two simultaneously occurring processes, which characterize the ‘resting brain’; one is related to expected change in sensory information, while the other is endogenous and independent of stimulus change. These findings support the earlier claim made by Walter (1950), that the scalp-recorded alpha is the end product of many alpha rhythms that are spatially averaged over the scalp. A similar idea was expressed more recently by Nunez et al. (2001) who stated: “the human alpha band contains multiple rhythms that apparently interact to varying degrees in different brain states”. Barry et al. (2006) examined relationships between stimulus intensity, the phase of narrow-band EEG activity at stimulus onset, and the resultant event-related potentials (ERPs) in a passive auditory oddball task, using a novel conceptualization of orthogonal phase effects (cortical negativity vs. positivity; negative driving vs. positive driving; waxing vs. waning). EEG responses to the standard stimuli (50 vs. 80 dB, varied between subjects) were analyzed. Prestimulus narrow-band EEG activity (in 1-Hz bands, from 1 to 13 Hz) at Cz was assessed for each trial by digital filtering. For each frequency, the cycle at stimulus onset was used to sort trials into four phases, for which ERPs were derived from both the filtered and unfiltered EEG activity at Fz, Cz and Pz. Preferred brain states at various frequencies were indicated by 16–34% differential occurrence within the orthogonal phase dimensions explored. The results indicate that, even in paradigms with a slightly varying interstimulus interval, brain dynamics provide preferred brain states at the moment of stimulus presentation, which differentially affect the EEG correlates of stimulus processing.

Barry et al. (2006) further describe that an important dimension of the prestimulus EEG, its phase at stimulus onset, was explored in early work, which showed that shorter reaction times are more likely to result from stimuli presented at negative peaks of the alpha cycle (Callaway and Yeager, 1960; Trimble and Potts, 1975). Rémond and Lesèvre (1967) noted enhancement of ERP components when stimuli were presented at the maximum and, to a lesser

degree, the positive-going zero crossing of the alpha wave. Jansen and Brandt (1991) found that N1 was maximal when stimulus onset was near the positive-going zero crossing, with smaller effects in P2. Further evidence for such dynamic phase-alignment of EEG with regular stimuli has been reported by Başar et al. (1984), Rockstroh et al. (1989) and Pleydell-Pearce (1994). Barry et al. (2003) used narrow band (1-Hz bandwidth) digital filtering to investigate the occurrence of different phases of EEG activity at stimulus onset in a fixed interstimulus interval auditory oddball task, and their effects on the amplitude of ERP components in the response to non-target stimuli.

The work of Fingelkurts et al. (2003), on the dynamics of alpha processes in relation to memory, supports the hypothesis that alpha oscillations may be the “building blocks” of brain functions rather than idling states of the brain, as earlier claimed by Başar (1980), Schürmann et al. (1997) and Lehmann (1989).

According to Min and Herrmann (2007), the relationship between prestimulus alpha and poststimulus performance implies that the prestimulus alpha, which prepares the subsequent task, seems to predict the post stimulus responses. Ishii et al. (2009) analyzed oddball tasks by means of MEG and found prolonged alpha responses, and also positive correlations between prestimulus theta/alpha spectral power and P300 amplitude.

According to Harris (2003), “prediction”, “expectancy” and “motor preparation” are manifested with changes of alpha activity.

Silvanto et al. (2008) stated that the impact of any external stimulus is dependent not only on the properties of that stimulus, but also on the initial state of the stimulated system. *State dependency* is an important factor in understanding the mechanisms through which brain stimulation modulates neural activity and behavior.

## 9. Selectively distributed alpha responses and alpha coherences in the whole brain

Ross Adey’s (1960) group undertook pioneering work on the theta rhythms of the limbic system of the cat brain during conditioning. These authors were the first to use spectral and coherence functions, performing relevant experiments demonstrating that rhythmic field potentials of the cat brain are related to behavior (see also Elazar and Adey, 1967; Miller, 1991).

The use of the coherence function in comparing EEG activity between various nuclei of the brain was useful in refuting the view that “EEG is an epiphenomenon” (Adey, 1989). The identification of induced theta rhythm and the “task-relevant coherence” in the limbic system of the cat brain are milestones in EEG research. During these experiments, the cat hippocampal activity exhibits a transition from irregular activity to coherent, induced rhythms. (For resonance phenomena in the hippocampus, see also Miller, 1991).

### 9.1. Sensory-evoked coherences in substructures of the cat brain

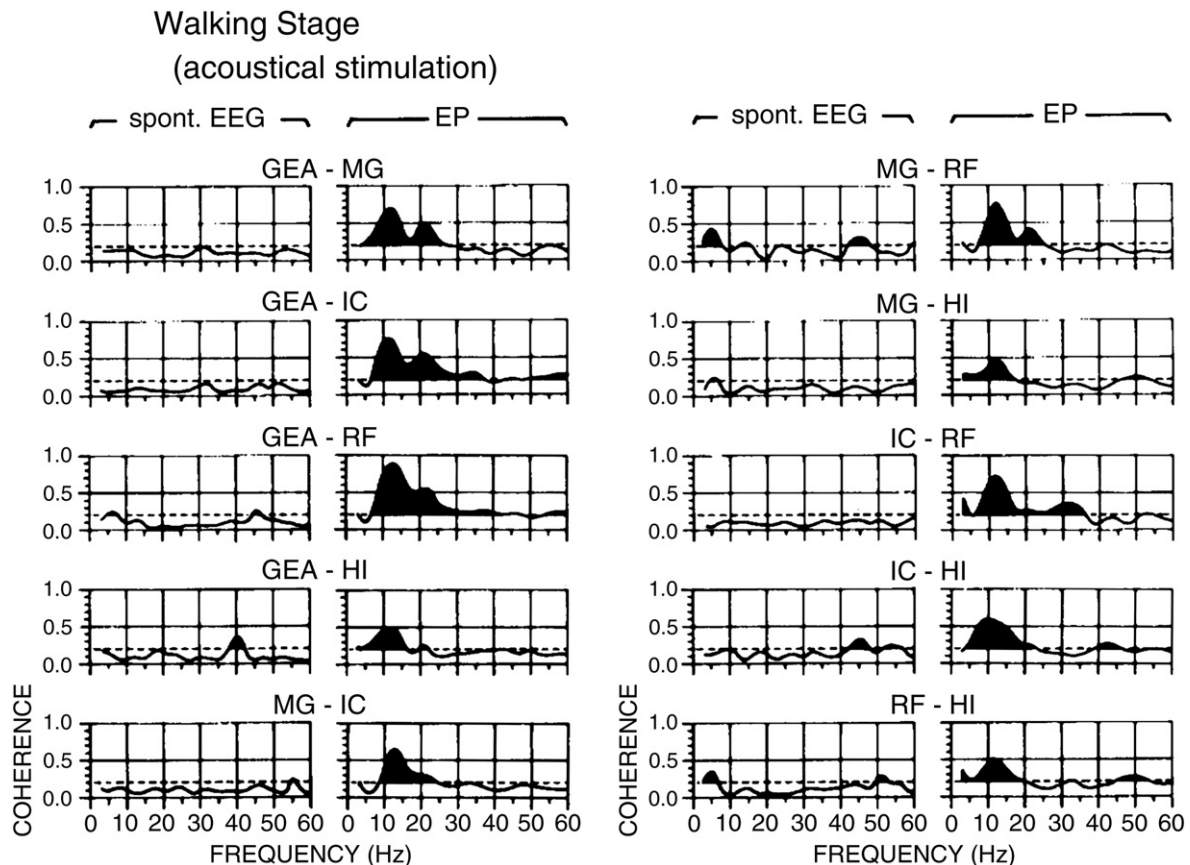
The description of integration necessitates morphological and functional interrelation in defined durations in the time space; the degree of interaction between two signals can be measured by coherence (von Stein and Sarnthein, 2000). Coherence is a statistical measure; the value of coherence depends on the extent of repeated correlations between events in the frequency domain. The phase relationship between the two signals is less relevant; however, it must be stable. Since the signal at each electrode site mostly reflects the network activity beneath the electrode, coherence between two electrodes should measure interactions between two neural populations. The statistical nature of coherence helps to differentiate them from noise if they repeat consistently (von Stein and Sarnthein, 2000). If two brain locations are coherent, one of the locations drives the other or they reciprocally cooperate; they can be also be coherently activated by a common driver (Bullock and Mc Clune, 1989).



Başar (1980) and Başar et al. (1979a,b) measured long distance coherences in the alpha, beta, theta and delta frequency ranges in structures such as sensory cortices, hippocampus and brain stem, in waking and freely-moving or sleeping cats. The strength of coherence depends on stimulation modality and recording sites. During the waking stage, the coupling (and/or synchronization) of resonant responses from various nuclei in the alpha and beta frequency ranges can also be demonstrated by using the coherence functions between all possible pairings of spontaneous and evoked activities in the structures as GEA, MG, IC, RF and HI. Fig. 13 presents the results of a typical experiment, illustrating the coherences in a frequency range of 3–60 Hz for spontaneous activities and evoked potentials of all possible pairings of the studied brain structures. Due to the reasonably large number of single sweeps included in the computation of averages, and due to the spectral window used, the auto- and cross-spectral amplitudes have been adequately smoothed and a significance value of 0.2 was attained for all the curves. Therefore, the area under the coherence function is shaded only if the curve surpasses this value, in order to emphasize those parts of the curves above the significance level. It is immediately recognizable that, in the alpha (8–14 Hz) and beta (14–25 Hz) frequency ranges, the coherence usually has high values, between 0.5 and 0.9, for evoked responses. However, the coherence between spontaneous activities of the same pairings of nuclei definitely has lower values. In the alpha and beta frequency ranges, the coherence of the spontaneous activity barely reaches 0.3 in a few cases. In other words, there exists an important coherence increase upon stimulation. During slow-wave sleep stages, the evoked coherences between all brain structures were shifted to a slower delta

frequency range (Başar, 1980; Başar et al., 1979b). Fig. 14 presents the coherences to visual stimuli in the cat brain.

In search of experimental support for the hypothesized distributed alpha response system, (Ungan, 1974) measured EEG responses to visual stimuli in the cat brain (with intracranial electrodes in cortical, thalamic and hippocampal sites, see Fig. 14). Alpha responses (10–Hz oscillations of 200–300 ms duration) were observed not only in occipital cortex and thalamus, but also in the hippocampus. Remarkably, hippocampal alpha showed higher amplitude than at thalamic sites, and the coherence of hippocampus-cortex was higher than the evoked coherence between thalamus and cortex (Schürmann et al., 2000). It was found that (1) coherences increased significantly upon visual stimulation in delta, alpha, beta and gamma frequency ranges; (2) hippocampal-cortical coherences were significantly higher than thalamo-cortical coherences for the alpha (HI-OC: 0.28 vs. LG-OC: 0.15), beta and gamma frequency ranges; (3) the effect of the interaction of channel and experiment factors, which refers to the differences in coherence changes upon stimulation between the two electrode pairs, was only significant in alpha and beta frequency ranges. Upon visual stimulation, the alpha coherence HI-OC increased to 0.41, whereas, the coherence LG-OC increased only to 0.18. These findings also demonstrated that, during sensory stimulation, the recordings between various structures showed *varied degrees of coherence*, thus indicating the interaction between two structures (Kocsis et al., 2001; Schürmann et al., 2000). The “varied degrees of coherences” reported by several authors lead to the concept of selectively coherent oscillatory networks. The important role of functional integration and frequency response of long-range interactions within the alpha and theta ranges in



**Fig. 13.** A typical set of coherence functions computed from the spontaneous activities and EPs of all possible pairings of the studied brain structures during the waking stage. The scale is indicated at the bottom. The frequency, from 0 Hz to 60 Hz, is along the abscissa; the coherence, between 0 and 1, is along the ordinate. The horizontal broken lines indicate the significance level (0.2 for all plots). The area under the coherence function is shaded only if the curve surpasses the significance level. In order to facilitate comparison between the coherence values computed from spontaneous and evoked parts of the EEG-EP epochs, the respective coherence functions are presented adjacently for all paired recording electrodes.

From Başar et al. (1979b).

processing of the mental context is also emphasized by Başar (1980, 1999), and von Stein and Sarnthein (2000). In the gamma frequency range, coherences between different spatial locations of the brain vary, as these areas are activated by different classes of stimuli (haptic and visual) in an associative learning task (Miltner et al., 1999).

### 9.2. Sensory evoked coherence and event-related coherence in human subjects

In the present section, *spontaneous, evoked and event-related coherences* in healthy subjects and subjects with cognitive impairment will be presented together, since such analyses remain rare. In this and the following section, we do not present the responses in healthy subjects and pathology separately. Namely, comparative studies including evoked and event-related coherences are, in general, rare. It is possible that the combination of all these analyses may open, in the near future, an important window for biomarkers related to a wide range of cognitive processes, and to the impairment of cognitive processes.

At this point, it is vital to emphasize that there are important functional differences between “EEG coherence”, “Evoked Coherence” and “Cognitive Response Coherence”: EEG analysis can only measure sporadically occurring coherences from hidden sources; Sensory Evoked Coherences reflect the property of sensory networks activated by a sensory stimulation; Event-related (or cognitive) coherences manifest coherent activity of sensory and cognitive networks triggered by a cognitive task. Accordingly, the cognitive response coherences comprehend activation of a greater number of neural networks that are most possibly not activated, or less activated, in the EEG and sensory

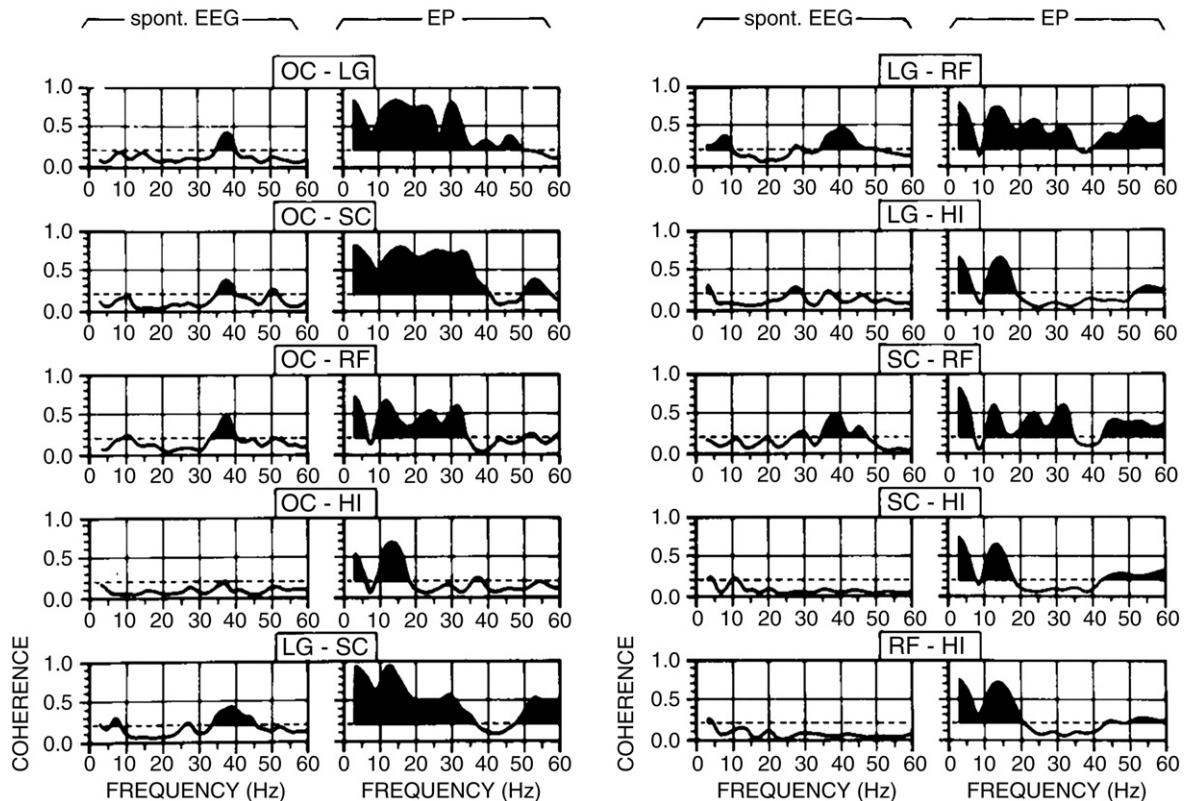
evoked coherences. Therefore, *event-related coherence* merits special attention. It is particularly relevant to analyze whether medical treatment (drug application) in AD patients with strong cognitive impairment acts selectively upon sensory and cognitive networks manifested in topologically different areas and in different frequency windows. Such an observation may provide, in the future, a deeper understanding of the physiology of distributed functional networks and, in turn, the possibility of determining biomarkers for medical treatment. According to the statements above, there are new steps and emerging questions in neuro-physiological and clinical studies.

Locatelli et al. (1998) studied EEG coherence in patients affected by probable Alzheimer's disease (AD) and reported that alpha-band coherence was decreased in the AD group compared with the control group, more evidently between electrodes over the temporo-parietal regions. The decrease was more accentuated for the inter-hemispheric coherences of the posterior regions.

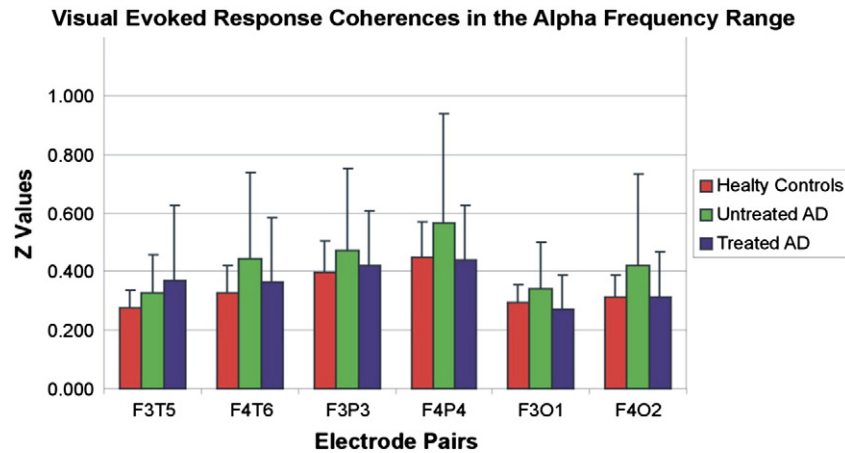
The decrease of alpha coherence was more relevant in more cognitively impaired patients. Furthermore, inter-hemispheric delta and theta coherences tended to increase in almost all the analyzed pairs of electrodes with the exception of F<sub>7</sub>–F<sub>8</sub> and T<sub>5</sub>–T<sub>6</sub>.

Van der Hiele et al. (2007) investigated the relationship between EEG measures and performance in tests of global cognition, memory, language and executive functioning, and found that alpha coherence did not differ between AD and control groups and was unrelated to cognition. The most common observation in all these studies is of decreased alpha and beta band coherences between distant structures (Adler et al., 2003; Besthorn et al., 1994; Dunkin et al., 1994; Leuchter et al., 1987; Locatelli et al., 1998; Zheng-yan, 2005).

## Visual



**Fig. 14.** A typical set of coherence functions computed from the spontaneous and visual evoked potentials of all possible pairings of the studied brain structures. The scale is indicated at the bottom. The frequency, from 0 to 60 Hz, is along the abscissa; coherency, between 0 and 1, is along the ordinate. The horizontal broken lines indicate the significance level (0.2 for all plots). The area under the coherence function is shaded only if the curve surpasses the significance level. In order to facilitate a comparison between the coherence values computed from spontaneous and evoked parts of the EEG-EP epochs, the respective coherence functions are presented adjacently for all paired recording electrodes. Modified from Ungan (1974).



**Fig. 15.** Mean Z values of healthy control, treated AD and untreated AD subjects for alpha frequency range upon “simple light” stimuli. Red bars represent the mean Z values for healthy subjects, green bars represent the mean Z values for untreated AD subjects and blue bars represent the mean Z values for treated AD subjects (Başar et al., 2010).

Relatively few studies have analyzed the evoked coherence differences between AD patients and healthy controls upon the application of different memory paradigms. Zheng-yan (2005) stated that, during photic stimulation, the inter- and intrahemispheric EEG coherences of AD patients showed lower values in the alpha (9.5–10.5 Hz) band than those of controls.

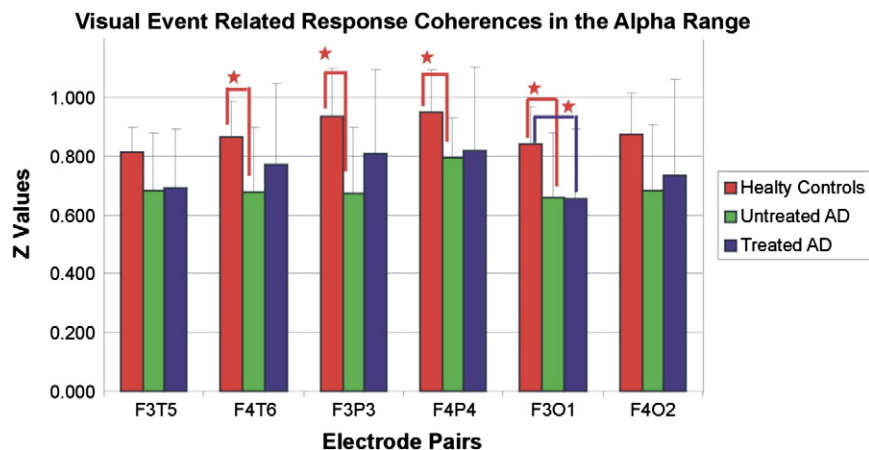
Hogan et al. (2003) examined memory-related EEG power and coherence over temporal and central recording sites in patients with early AD and normal controls. While the behavioral performance of very mild AD patients did not differ significantly from that of normal controls, the AD patients had reduced upper alpha coherence between the central and right temporal cortex.

In the most recent studies, Başar et al. (2010) compared sensory evoked coherences and event-related coherences between healthy subjects and AD patients. Fig. 15 illustrates mean Z values for the alpha frequency range upon application of “simple light” stimuli for all electrode pairs. Fig. 16 illustrates mean Z values for the alpha frequency range upon application of “target” stimuli, for all electrode pairs. Fig. 16 shows that the healthy subjects had higher alpha response coherence compared to both untreated and treated AD subjects upon application of target stimuli for almost all electrode pairs. The mean Z value of healthy subjects was 25%–38% higher than AD patients in most of the electrode pairs upon application of “target” stimuli. The comparison of Figs. 15 and 16 shows that the evoked alpha coherence upon “simple light” is not high. Further, no differences were recorded between

healthy and AD subjects. In contrast, the event-related coherences are much higher than in sensory coherences.

The target response of the applied P300 oddball paradigm is activated by four basic cognitive functions: “perception”, “focused attention”, “learning” and “working memory” (Rektor et al., 2004; Başar-Eroğlu and Başar, 1991; Halgren et al., 2002; Klimesch et al., 2006). The “response coherence” is defined as the coherence of an evoked/event-related coherence, which is different from the spontaneous coherence (or the coherence in the unfiltered EEG).

It is worthwhile to further discuss the differentiation of evoked coherence and event-related (cognitive) coherence. The evoked coherence mostly reflects the augmentation or strengthening of links between various neural networks upon application of pure sensory signals, whereas the event-related coherence reflects the strengthening of links (or neural connections) of neural networks upon stimulation by a sensory signal loaded with a cognitive task. Accordingly, upon application of a signal loaded with cognitive task (in this case the oddball paradigm), it is most possible that extended neural assemblies are activated; in turn, a recorded increase of coherence in a given frequency channel reflects the strengthening of links and amplification of electrical signal flow between the brain areas under examination. This increased coherence is a function of the applied cognitive task. In the present case, the increased coherence observed between left frontal and left parietal areas logically reflects the role of connectivity in the alpha oscillations during tasks of focused attention, learning and working memory.



**Fig. 16.** Mean Z values of healthy control, treated AD and untreated AD subjects for alpha frequency range upon target stimuli (\* represents  $p < 0.01$ ). Red bars represent the mean Z values for healthy subjects, green bars represent the mean Z values for untreated AD subjects and blue bars represent the mean Z values for treated AD subjects (Başar et al., 2010).



### 9.3. General remarks related to alpha machineries

- (1) Alpha rhythms at the cellular level. Spontaneous or evoked 10-Hz oscillations are also measured at the cellular level, thus 10-Hz activity reflects basic physiological properties of the brain.
- (2) "Spontaneous alphas are not noise but probably quasi-deterministic signals". As demonstrated by the results of several studies, the 10-Hz oscillations of the brain are not pure noise: The best examples are the analysis of correlation dimension and phase-locked and reproducible 10-Hz rhythms preceding a cognitive target. This topic is not reviewed in the present study; for reviews, see Lehnartz and Elger (2000) and Stam (2006).
- (3) Alpha does not generally reflect "passive states" or "idling of the brain". Moreover, it is possible that passive states or idling are components of some states of the brain, the causalities of which are yet unknown (hidden causality).
- (4) Relationship between EEG and evoked/event-related oscillations. The inverse relationship between alpha and EPs is not only valid for alpha; but a theory of inhibitions should be also valid for all other frequencies.
- (5) Rémond and Lesevre's (1967) observation on phase-relation of the alpha responsiveness, which was partly demonstrated by Jansen and Brandt (1991), might serve as one of the causal factors of alpha blockade or desynchronization.
- (6) Selectively distributed alpha system. Rather than trying to locate a unique alpha generator, it is preferable to formulate the existence of a "selectively distributed alpha system" (Başar and Schürmann, 1996). The following physiological results concerning *l* alpha responses illustrate this proposition:
  - (i) Auditory and visual stimulations elicit strong and stable alpha responses in cat hippocampus and reticular formation (10-Hz oscillations of approx. 300 ms), which are also visible without filtering.
  - (ii) Sensory cortical and sensory thalamic 10-Hz responses can be elicited only by stimulations that are adequate for the respective area.  
The auditory cortex and medial geniculate nucleus depict alpha responsiveness only upon *auditory* stimulation, whereas visual cortex and lateral geniculate nucleus depict alpha responsiveness only upon *visual* stimulation. In contrast, *hippocampal* 10-Hz responses are present in all types of stimulations (Figs. 4A and B, 5, 6, 7).
  - (iii) Selectively distributed 10-Hz generators in the whole brain. Among coherence functions computed from visual evoked responses, the hippocampo-cortical coherence is significantly larger than the thalamo-cortical coherence (the latter being extremely low following inadequate stimulation). Thus, thalamo-cortical circuits are not unique in generating alpha responses; the reticular formation and hippocampus may even have a more general significance (Section 4, Figs. 6 and 7). Accordingly, the empirical findings indicate the existence of selectively distributed alpha networks in the whole brain. Although the facultative pacemaker theory has been a good step to launch the existence of pacemakers in the brain, the concept of selectively distributed pacemakers should replace that of solely thalamo-cortical networks.
- (7) Brain in evolution of species: connectivity between brain structures. Changes of spontaneous alpha in the maturing brain. Studies by Bullock and co-workers (Section 7) showed that, during evolution of species, from *H. pomatia* upwards, connectivity (coherence) does increase. The development and changes of alpha activity during maturation must be taken into account in the analysis of cognitive functions and

the genesis of alpha oscillations. Accordingly, alpha coherences can also be considered as a sign of cognitive ability. (That is also valid for other frequencies). At that point, Bullock's discovery is crucial. There are differences in human babies, adults and in *Aplysia*. It may be possible to use decreased coherences in cognitive impairment as clinical biomarkers.

- (8) Need for standardization of ERD. ERD merits important attention from the viewpoint of neurophysiology. Several researchers expressed the utility of ERD in search of cognitive function. However, standardization is recommended, taking into account topology, aging, type of subjects and the relationship between ERD and prestimulus EEG.
- (9) The studies of the group of Gebber and Barman on the role of alpha in whole-brain-body function indicate the necessity to integrate the alpha machineries in the vegetative system and also the brain and cerebellum. It is clear that drastic changes in the vegetative system can have considerable influences on cognitive processes. However, the development of such an integrated model will be a long process.

A more comprehensive description of function related to "alpha" is included in the companion report (Başar and Güntekin, 2012).

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