Alpha oscillations in brain functioning: an integrative theory

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Abstract

The old concept stating that EEG alpha (10-Hz) activity reflects passive or idling states of the brain is giving way to modern views of 10-Hz oscillations in relation to diverse brain functions comprising sensory, motor, and memory processes: (1) \textit{Spontaneous} alpha activity is not pure noise as shown by methods of chaos analysis. (2) \textit{Evoked} alpha oscillations patterns (precisely time-locked to a stimulus; duration approx. 200–300 ms) depend on the modality of stimulation and the recording site. (3) \textit{Induced} alpha oscillations are initiated by, but not closely time-locked to a stimulus. (4) 10-Hz oscillations are recorded in nervous systems of different complexities, from the human brain to isolated ganglia of invertebrates. The neural origins of 10-Hz oscillations are demonstrated by recordings at the cellular level. (5) Rather than trying to locate a unique alpha generator, it is preferable to assume that a ‘diffuse and distributed alpha system’ exists. A particular support for this hypothesis is given by stimulus-dependent hippocampal alpha responses in the cat brain. (6) The major physiological meaning of 10-Hz oscillations may be comparable to the putative universal role of gamma responses in brain signaling. © 1997 Elsevier Science B.V.

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\textit{If one understands the alpha rhythm, he will most probably understand the other EEG phenomena.}

Storm van Leeuwen (1979).

1. Aim of this special issue

Since the discovery of the alpha rhythms by Hans Berger, one of the biggest puzzles in electroencephalography has been the physiological understanding of their origin, their relation to sensory and cognitive functions of the brain, and not least their interactions as an indicator of the brain state. The common aim of the contributions to this special issue is to support a new theory stressing the functional significance of alpha activity (for a brief overview, see also Başar and Schürmann, 1996). The rationale of this type of approach is anchored to the following recent developments in the integrative neurosciences, and human electrophysiology.
1. The old concept stating that alpha activity reflects passive states of the central nervous system (CNS) or the idling of the brain is replaced now with modern views clearly demonstrating the existence of function-related 10-Hz oscillations, spontaneous, evoked, or induced.

2. Analysis with the methods of chaos analysis supports that 10-Hz activity is not pure noise, but probably a signal with quasi-deterministic properties.

3. 10-Hz spontaneous rhythms and evoked rhythms are distributed in the human brain. These oscillatory activities are also recorded in the brains of animals, even in the isolated ganglia of invertebrates. Accordingly we introduced the expression 'alphas' which is considered to be equivalent to the distributed 10-Hz oscillations in the brain. The present study will underline that alphas may be correlated with multifold functions.

4. Spontaneous and evoked 10-Hz oscillatory activities are also recorded at the cellular and/or membrane level, thus demonstrating that these oscillations have neural origins.

5. In the present volume several articles confirm, emphasize and extend the relevant findings and strong statements.

A review of all these reports together with the long-standing results of our research groups since the 1970s enables us to bring a new light on 10-Hz oscillations of the brain. The new theory, which is a synthesis reflecting fundamental properties of 10-Hz can be of considerable importance to an integrative understanding of brain functioning.

2. Emitted alpha rhythms in expectancy and memory states

By trying to establish the new theory we start with an introductory example: these experiments clearly demonstrate that: (1) the alpha activity is not noise; (2) it can be a manifestation of internally cognitive evoked potentials as signs of expectancy and short term memory; and (3) 10-Hz oscillations can be induced as repeatable patterns by the expectation of a cognitive target.

Our example of such rhythms — referred to as 'internally induced 10-Hz event-related rhythms' — is related to an experiment in which the pre-stimulus EEG becomes phase-locked to an expected target. The expression 'internally induced' requires some clarification: an external stimulus — e.g. a light flash eliciting 10-Hz enhancement — can effect the transition from a 'disordered' to an 'ordered' state of the brain (see Schürmann et al., 1997). At this point an important question is: can we find a way to put the brain in coherent states of EEG activity without external sensory stimulation? Can we find a sensory–cognitive task to produce coherent internal EPs, or better, internal event-related potentials?

Our task is related to the well-established tasks for 'P300' measurements. Such paradigms have frequently been used in order to correlate cognitive tasks and behaviour with slow waves of the brain. However, there are only a few reports which analyse pre-stimulus EEG activity during these tasks. As the following figures will show, we observed regular, phase-ordered pre-stimulus EEG-rhythms, which tend to form repeatable patterns preceding successful cognitive tasks.

Experiments were carried out with 16 volunteer healthy subjects, mostly students aged 19–21 years. The EEG was recorded from vertex, parietal and occipital locations against an ear lobe reference (vertex electrode Cz, parietal electrodes P3, P4 and occipital electrodes O1, O2 in the international 10–20 system; digital filtering procedure). The subjects sat in a sound-proof and echo-free room dimly illuminated. Tones of 2000 Hz, 80 dB, and 800 ms duration were applied with regular intervals of 2600 ms. Every third or fourth tone was omitted. The subjects were asked to predict and to mark mentally the time of occurrence of the omitted signals.

When subjects had learned and successfully followed the regular sequence of the tones including the cognitive target, they were usually able to increase their attention. Then, rhythmic pre-stimulus EEG patterns could be observed. Most of the subjects reported that at the beginning of
an experimental session with repetitive signals they had difficulty predicting the time of occurrence of the stimulus omission. Usually, in the second half of the experiment they were able to predict the time of occurrence of the stimulus omission. Accordingly, we selectively averaged approximately 10 pre-stimulus EEG epochs from the beginning of the experiment (‘first 10’) and 10 such epochs from the end of the experiment (‘last 10’). Fig. 1A illustrates comparatively the averages of the first and the last 10 pre-stimulus EEG epochs (digitally filtered: 1–25 Hz) which were recorded at the vertex of a subject who reported that at the beginning of the experiment he felt uncertain about stimulus timing. According to the subject’s report, his concentration increased towards the end of the experimental session, and so he performed his task much better. The average of the last 10 sweeps depicted a regular rhythmic behavior with large amplitudes. The same rhythmicity was observed in the average of the first 10 sweeps, being, however, less regular and of low amplitude.

In addition, the superposition of single sweeps demonstrates the formation of repeatable patterns. Fig. 1B,C shows approximately 10 pre-stimulus EEG epochs at the end (B) and at the beginning (C) of an experiment (vertex (Cz) recordings, digitally filtered: 7–13 Hz). At the end of the experiment repeatable patterns were observed whereas at the beginning no coherent state was attained. The superimposition shows that the amplitude increase observed in the average (Fig. 1A) is not only due to alpha amplitude increase in single trials but to increased synchronization of alpha waves.

These experiments and our earlier results (Başar et al., 1992) have shown that during cognitive tasks it is possible to measure almost reproducible EEG patterns in subjects expecting defined repetitive sensory stimuli. This was not only observed with omitted acoustical stimuli but also with omitted visual stimuli as shown in Fig. 2 for occipital recordings. ‘Cross modality experiments’ with respect to anticipatory alpha were also performed, e.g. by recording occipital EEG activity with auditory stimuli, some of them omitted as indicated above. In this condition, no large increases of 10-Hz waves were recorded. Preliminary results show that single sweeps were less congruent than with visual stimulation.

We use the expression ‘quasi-deterministic EEG’ for the recurrently emitted EEG patterns. The occurrence of such EEG patterns — and possibly similar patterns in other frequency ranges — may be linked to a type of short-term memory process (Başar, 1988). This introductory example suggests that alpha rhythms are functionally relevant signals, far from being merely noise. This idea is central not only to this report, but to all contributions to the present volume.
3. Alphas and the alpha response

When a healthy adult relaxes, with eyes closed, rhythmic electric activity around 10 Hz can be recorded over the posterior scalp regions. Numerous attempts have been made to localize sources of the alpha rhythm and at finding functional correlates of the so-called spontaneous alpha rhythm (for an overview, see e.g. Niedermeyer, 1993). Niedermeyer’s (1993) statement that the EEG is a ‘phenomenon with important psychophysiological implications’ is supported by results obtained in the framework of non-linear dynamics: these results refute the view that the spontaneous EEG is merely ‘noise’ (for a collection of studies, see e.g. Başar, 1990).

3.1. Why the expression ‘alphas’?

In several chapters of the present book, the authors state that we confront the problem to record several types of alpha rhythms or alpha patterns. A pattern is essentially an arrangement which is characterized by the order of the elements of which it is made rather than by the intrinsic nature of these elements (Haken, 1992). It should be made clear that when calling a phenomenon an ‘alpha pattern’, this should be taken in a generic sense.

More than 40 years ago, Grey Walter (1950) pointed out that the alpha rhythm in one subject is composed of, and is the end product of many alpha rhythms. In 1964 he stated:

We have managed to check the alpha band rhythm with intra cerebral 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.

The ‘alpha states’, ‘alpha patterns’ or ‘alpha rhythms’ will be considered here as spontaneous
alpha (resulting from hidden sources in CNS), or induced alpha (external sensory induced, or internal proprioceptive, or internal cognitive induced alpha), taking into account a classification proposed by Galambos (1992).

Statements by G. Walter and Galambos clearly express the necessity for use of the expression ‘alphas’. Alphas, i.e. several and different alpha activities are related to brain functions. From the physiological viewpoint, the interest in ‘alpha activity’ has disappeared in most of the neuroscientists of the late 1960s. The resonance phenomena at the alpha frequency range on the cellular level as described by Llinás (1988), Silva et al. (1991), and Dinse et al. (1997) again open a new window for the interpretation of alpha processes.

3.2. 10-Hz oscillations in the brain — spontaneous, induced, evoked, emitted

For the alpha range, a variety of functional correlates have been found some of which appear in the following classification (extending a previous version by Galambos, 1992):

1. The alpha rhythm is more than just a spontaneous rhythm. It is the prototype of a spontaneous brain rhythms. According to Başar (1992) it is a prototype of a dynamic process which governs a large ensemble of integrative brain functions.
2. Alpha patterns can be induced, i.e. initiated by, but not closely time-locked to a stimulus (Başar et al., 1992).
3. Alpha patterns can be evoked, i.e. precisely time-locked to a stimulus (Başar et al., 1992).
4. Alpha patterns can be movement-related and also memory-related (Pfurtscheller and Klimesch, 1992).
5. Finally, alpha patterns can be emitted. Well trained subjects emitted time-locked bursts of alpha band energy for up to a full second before the delivery of an expected target. The alpha locking to the future moment, when a target will be delivered, is robust and statistically significant (Başar et al., 1992).

The dynamics of alpha processes (spontaneous, evoked, induced, emitted), which is related to memory, movement and sensation (often as parallel processes), provides an outstanding prototype for discovering universal building blocks in CNS functions. The interrelated, parallel or cognitive processes demonstrate the significant role of the dynamic approach to the understanding of integrative brain functions. Additionally, the 10-Hz oscillations, which can be measured at the cellular level, may bridge the gap between different levels of analysis thus increasing our knowledge in integrative neuroscience. Results from non-linear dynamics support the hypothesis that alpha activity is not simple ‘noise’ but a deterministic-chaotic signal rather than an idling process of the brain (for a collection of studies see e.g. Başar, 1990).

3.3. Alpha response susceptibility: evoked alpha

From the very start of our group’s activities in brain research (Başar, 1972), an important view of Galilei has been a governing principle:

First of all one must observe that each pendulum has its own time of vibration, so definite and determinate, that it is not possible to make it move with any other period than that which nature has given it. On the other hand one can confer motion upon a heavy pendulum which is at rest by simply blowing against it. By repeating these blasts with a frequency which is the same as that of the pendulum one can impart considerable motion.

G. Galilei, Discorsi a Due Nuove Scienze (1638)

Our group considers the 10-Hz activity to be one of the natural frequencies of the brain. In this case excitation of the brain should put this 10-Hz activity to a resonance state. Indeed, we had 10-Hz enhancements upon application of sensory stimulation in all areas of the brain. We have called this type of 10-Hz activity during the 300 ms after stimulation the ‘evoked alpha’ (this expression was already used by several scientists ranging from Adrian to Bishop and Andersson — for examples, see Schürmann et al., 1997). In this respect, two issues are remarkable:

1. It is well-known that in children younger than 3 years no ‘spontaneous’ 10-Hz activity is
present in the EEG. These children usually have no 10-Hz activity upon application of sensory stimulation (Başar-Eroğlu et al., 1994; Kolev et al., 1994). In this case — according to the resonance principle of Galilei — 10-Hz activity does not belong to natural brain frequencies.

2. We also have shown that the 10-Hz activity prior to sensory stimulation has a big influence on the evoked potentials. In the case of high amplitude 10-Hz activity preceding the stimulation, evoked potential amplitudes are reduced by 30%.

These are also examples showing that 10-Hz activity cannot be considered just a noise to be eliminated from recordings or from evoked potentials. In fact, the alpha activity is strongly related to the system's response. In this case also, the evoked potential so-obtained would contain the alpha coding.

3.4. A new survey of evoked and induced alpha activity

Başar (1972a) reviewed further 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 a state of excitation, either by means of sensory stimulation or cognitive tasks, it can generate induced alpha rhythms. The last ones are not the alpha states fitting in the conventional description of the alpha activity. On the contrary, if the brain is excited by a sensory stimulation it shows short oscillatory behavior with a duration of approximately 300 ms upon stimulation. If this oscillation is in the alpha range it is referred to as the alpha response. Now, all these results are also confirmed by wavelet analysis (Başar et al., in press).

Further results of Başar et al. (1979a,b) demonstrated that if a cat has been stimulated with a sensory stimulation (light or sound), an increased coherence in the 10-Hz range between all structures in the visual pathway, hippocampus and reticular formation was observable for all pairs of recordings in the visual and auditory pathways (Başar, 1972a). We repeat here again: we have assumed that a central or a common mechanism could put all these various centers into a state of alpha rhythmicity, i.e. upon application of sensory stimulation various structures in the cat brain generate evoked rhythms of 10 Hz in all structures at the same time (Başar, 1972a). Here, it should be emphasized that phase spectra between all pairs of studied structures did not show any phase shift in the 10-Hz frequency range.

Now the survey by Başar (1972a) will be extended by a survey considering the new results of alpha responses and related rhythms. The classification of sensory or cognitive evoked or induced alphas given in this section is a restricted one, since more examples can be found in the literature concerning alpha oscillatory components. This only serves to give an idea of the richness of functionally related alpha components:

1. Alpha response at human occipital electrodes by sine-wave modulated light stimulation (Van der Tweel and Verduyn Luynel, 1965; Regan, 1966; Spekreijse, 1966)
2. Alpha after-discharge. Enhanced alpha component with 500–600 ms latency (following alpha-blocking) at human scalp electrodes (Barlow and Estrin, 1971; Lansing and Barlow, 1972; Nogawa et al., 1976)
3. Strong alpha resonance in the auditory cortex, thalamus, reticular formation, inferior colliculus, hippocampus and cerebellar cortex of the cat upon acoustic stimulation (Başar et al., 1975b,c, and Başar et al., 1976a,b; see also Schürmann et al., 1997). 'Strong alpha resonances' are manifold with the enhanced 10-Hz band oscillation following the stimulation. The duration of the oscillation is 250–300 ms, and the enhancement factors reach values higher than 1.5
4. Strong resonant alpha responses of 12 Hz upon light stimulation in the visual pathway, reticular formation and hippocampus of the cat (Başar et al., 1977a; Başar, 1972a; see below — Fig. 3 — for an example)
5. Perfect time-locking in the alpha channel during spindle sleep in the cat cortex fol-
Hippocampus visual stimulus

0.3 - 45 Hz

8 - 15 Hz

single trials (0.3 - 45 Hz)

average (0.3 - 45 Hz)

Fig. 3. Responses to visual stimulation recorded from the cat hippocampus (see Başar-Eroğlu et al., 1991 for methodological details). Above, single trial EPs, selected according to enhancement factor (Başar, 1980); below, averaged EP. Left column: wide-band filtered responses (0.3–45 Hz), right column: responses filtered in the alpha range (8–15 Hz). Note the distinct alpha responses in the first 200 ms after stimulation which are visible in the averaged EP as well as in the single trials. Such alpha responses are even visible in the wide-band filtered responses in the left column.

6. Time locking in the alpha frequency range at scalp electrodes of human subjects with closed eyes upon auditory stimulation (Başar et al., 1976b). This is the time-locked, but not enhanced response to inadequate stimulation
7. Time-locking and after-discharge with 500–600 ms latency at scalp electrodes of human subjects with closed eyes upon auditory stimulation (Başar et al., 1976b)

8. Enhancement and perfect time-locking in the alpha frequency channel at scalp electrodes upon acoustic stimulation of human subjects with open eyes (Başar et al., 1976b)

9. Enhancement and time-locked alpha response with 50–150 ms latency at scalp electrodes of human subjects sitting in a dimly illuminated room upon photic stimulation (Başar et al., 1977b)

10. Strong resonant alpha responses in various brain structures such as the auditory cortex, medial geniculate nucleus, inferior colliculus, reticular formation and hippocampus of the cat during slow wave sleep stage (Özesmi and Başar, 1974; Başar et al., 1975c, 1979b)

11. Induced 10-Hz rhythm without a physical stimulation. Anticipatory 10-Hz oscillations which are phase locked to the moment of a cognitive target (for review see Başar et al., 1989; for examples see above)

12. Prolonged alpha response component of the P300 response (Stamper and Başar, 1985; Başar-Eroğlu et al., 1991). In experiments with certain cognitive tasks, induced EEG rhythmicities show an event-related prolongation. This was observed by comparing EPs obtained in the following paradigms:


   (ii) In ‘cognitive’ sessions, the same stimuli were applied, but subjects had been instructed to wait for deviant tones of 1500-Hz frequency.

For data analysis, we combined digital filtering (Başar and Ungal, 1973) and a single sweep wave identification method (Kolev and Daskalova, 1990). The time-locking of single sweeps was prolonged in ‘cognitive’ sessions. Prolonged responses were observed both in the theta (4–7 Hz) and in the alpha (7–13 Hz) ranges. It was hypothesized that the prolonged endogenous ERP components may be due to induced rhythmicities trig-

gered by additional information processing when a high degree of certainty has to be resolved during the ‘cognitive’ session (Kolev and Schürmann, 1992)

13. Event-related synchronization and desynchronization. The terms ‘event-related desynchronization’, or ERD, and ‘event-related synchronization’, or ERS, are used by Pfurtscheller and Klimesch (1992) to describe the ability of neural structures to generate more or less coherent oscillating potentials. ERD describes the attenuation or blocking and ERS is the enhancement of oscillating potentials within the alpha and beta frequency bands. ERD was observed during visual stimulation (Aranibar and Pfurtscheller, 1978), voluntary movement (Pfurtscheller and Aranibar, 1979; Pfurtscheller and Berghold, 1989) and cognitive activity (Sergeant et al., 1987; Klimesch et al., 1990).

ERS and ERD in the alpha frequency range can be observed within the same time interval on different locations on the scalp. For example, during a reading task, ERD is dominant over the posterior region. The magnitude and area of ERD depends on, besides other factors, the frequency band (upper or lower alpha band) chosen. ERS, however, was strictly localized to the central electrodes C3 and C4 overlying the sensorimotor cortex. The ERS pattern showed a high degree of bilateral symmetry and was dominant in the upper alpha band (Klimesch et al., 1988, 1990; Pfurtscheller and Klimesch, 1989).

It is of interest to note that the enhancement of central localized alpha band rhythms is inversely related to the attenuation of central localized mu rhythms found during voluntary finger movements (Pfurtscheller and Berghold, 1989). Since the localization and form of the alpha power enhancement pattern during reading and the alpha power attenuation pattern during movement are quite similar, it can be speculated that the mu rhythm is desynchronized or blocked during planning or execution of motor acts.
and becomes synchronized during visual processing and immobility. Our results concerning alpha responses (Başar, 1972a; Başar and Schürmann, 1996; Schürmann et al., 1997) are not in contradiction with results of the Pfurtscheller group. Sensory alpha enhancements can be elicited only if the amplitude of the pre-stimulus alpha activity is low and the stimulation signal is adequate regarding the recording site. The enhanced or sensory alpha responses have usually a duration of 250–300 ms and are time-locked to stimulation. The alpha oscillations prior to cognitive targets are also different from the phenomena described by Pfurtscheller’s group. Thus, it becomes clear that there are several ways to elicit 10-Hz synchronization and desynchronizations (see above for Grey Walter’s [1950] comments on the variety of alpha rhythms).

14. Evoked alphas in invertebrate ganglia. Further evidence shows that alpha activity cannot be attributed to generators only in the thalamus or cortex. Experiments performed with the cerebral ganglion of aplysia and also with isolated ganglia of Helix pomatia gave evidence that such 10-Hz generators can be spontaneously recorded or electrically induced in vitro in this small neural population consisting only of approximately 2000 neurons. Although the amplitudes of 10-Hz activity are fairly low and cannot reach the higher amplitude synchronized states, which can be measured in the mammalian cortex, there is some good synchrony. Furthermore, amplitudes of spontaneous and induced alpha rhythms can be modulated by using pharmacological agents (Schütz et al., 1992; Schütz and Başar, 1992).

15. With respect to the relation between evoked potentials, e.g. the N1 component, and evoked alpha activity, a new model has been presented by Karakaş (1997). Such models are very promising for future understanding of oscillatory brain dynamics, taking into account the temporal organization of brain responses.

3.4.1. Secondary alpha response or alpha response with delay

As stated by Başar et al. (1991) and Schürmann et al. (1997) inadequate stimuli could not generate significant and time-locked cortical alpha enhancements in the first 300 ms after stimulation. The occipital cortex of the cat brain does not oscillate with enhanced 10-Hz if the stimulation is an auditory one (i.e. inadequate stimulation). However, even with inadequate stimulation a small 10-Hz enhancement can be recognized in the post-stimulus interval between 250 and 300 ms. The time-locking is weak in comparison to results with adequate stimuli. Therefore, although single sweeps may contain fairly high 10-Hz amplitudes, the responses are not perfectly phase-locked and delayed. These types of responses are also obtained in the auditory cortex by means of visual stimulation (inadequate stimulation) as well as emitted alpha waves following the omitted stimuli in the cortex of the cat brain (Başar-Eroğlu et al., 1991).

These ‘secondary’ or ‘delayed’ 10-Hz responses were also recorded from human brains during cross modality experiments with EEG as well as with magnetoencephalographic recordings (Schürmann et al., 1997). This means that this type of delayed 10-Hz response was encountered in various types of experimental recordings. What can be the cause of this delayed oscillatory 10-Hz activity which we call now secondary alpha enhancements? We will point out the possible role of a gating mechanism related to the thalamic nuclei which may act as follows: thalamic 10-Hz enhancement is only recorded if the stimulation is an adequate one. This means the medial geniculate nucleus depicts alpha enhancement only if auditory stimulation has been applied, but it does not react, upon visual stimulation, with an immediate alpha enhancement (i.e. within the first 200 ms). On the contrary, the hippocampus reacts always with an ample 10-Hz oscillatory behavior upon stimulation. This oscillatory response of the hippocampus is around 9–10 Hz upon auditory stimulation and approximately 12 Hz upon visual stimulation. An example is given in Fig. 3. It seems that gates open to every type of sensory stimulation in the hippocampus and that this
structure merits the expression ‘supramodal-gate par excellence’ as described by Swanson (1981).

Taking into account a further model presented by Miller (1991) the following mechanism is conceivable: if hippocampus generates an oscillatory alpha pattern upon every stimulation mode, and if hippocampus transmits this signal to other association areas, the primary sensory areas would receive information in the region of 150–200 ms following the application of the stimulation. Accordingly, it can be hypothesized that the secondary alpha oscillations recorded in the primary visual or auditory areas have their pacemaker source in the hippocampus. At least our data may demonstrate that such a transfer of information in the 10-Hz frequency range from hippocampus to cortex is possible. The hippocampus itself receives signals from brain stem structures such as the reticular formation.

If an auditory stimulation generates 10-Hz activity in reticular formation, this signal can be hypothetically transferred to hippocampus and from there to pre-frontal cortex and non-limbic association cortex. In this case there is the possibility that the signal can reach the primary sensory areas, too, via the non-limbic association cortex, as recorded in the cortical potentials.

In this way specific afferents from sense organs do not only reach the primary cortical areas, but the same sensory information will be partly sent to association areas of the cortex via the limbic system (hippocampus). On the other hand, the sensory input reaches mesencephalic reticular formation. As stated by the theory of Hernandez-Peon et al. (1960) the reticular formation acts as a filter and is also a gate structure par excellence, controlling the information flow to primary sensory areas of the limbic system as well as to polymodal association areas of the cortex.

The 10-Hz response recorded in the reticular formation has also marked enhancements similar to those in the hippocampus. The information flow over mesencephalic reticular formation also produces ‘delayed signals’. This signal transmission over reticular formation can also be considered as an additional system acting parallel to the prolongation of the 10-Hz activity. If we follow the same scheme used for the hippocampus, the delay of signals through the reticular formation would be again in the range of 200–300 ms. Provided that the described signal transfer does in fact occur, further experiments are needed to establish the significance or use of this type of signal transfer.

4. Chaos in alpha activity

As already shown by the introductory example of internally induced alpha rhythms (Başar, 1972a), we must not always consider the spontaneous oscillations in brain electrical activity as a background noise. On the contrary, in the aforementioned approach on field potentials, we assumed that the EEG must be considered as one of the most important oscillations affecting the production and conduction of signalling in the brain.

This view is strongly supported by results obtained with methods of non-linear dynamics (chaos analysis). These investigations lead to the tentative assumption that the EEG has a strange attractor (Başar, 1983a,b). This new trend in brain research is mainly based on evaluations of the correlation dimension $D_2$ of the EEG. Babloyantz et al. (1985) computed this parameter for the EEG during slow wave sleep (SWS). Shortly afterwards, the same was done for some pathological cases. Following the most important pioneering work by Babloyantz et al. (1985); Röschke and Başar (1985) published results on the strange attractors in several intracranial structures of the cat brain during SWS and confirmed in a general way the results of Babloyantz et al. Further, Rapp et al. (1985) interpreted the waking EEG as chaotic behavior. This has become the most widely used measure to describe chaotic behavior. A valuable first step in the study of dynamical behavior, particularly when chaos is present, is measuring its dimension and investigating how the dimensionality can change under different operational circumstances.

The trajectory is a mathematical description of the sequence of values taken by a state variable in going from an initial or starting condition to an attractor or through a sequence of attractors.
(Abraham and Shaw, 1983). Transition from one attractor to another is called a state change or bifurcation. Attractors can be periodic, quasiperiodic or chaotic; the latter are called strange attractors.

A rigorous review of correlation dimensions is given in several papers (Grassberger and Procaccia, 1983; Lützenberger, 1997; Pritchard and Duke, 1997; Röschke et al., 1997). Less rigorously stated, it can be said that the correlation dimension of a system’s behavior is the minimum number of dimensions of a space that can contain the trajectories generated by the system. As expressed by Rapp et al. (1985), the dimension of a system is its number of degrees of freedom. This definition is restricted but simple and useful. It is important to compare systems only by referring to the same quantity, usually the correlation dimension ($D_2$). A system is periodic if its $D_2$ is a whole number (e.g. 2.0, 3.0, 4.0) and chaotic if $D_2$ is ‘fractal’ (e.g. 2.1, 3.9, 4.5).

4.1. Correlation dimension of alpha activity — brain alpha attractors

The description of dimensionality of the human EEG shows enormous fluctuations in studies by several authors (see also Table 4, Başar, 1990). Babloyantz (1989) mentioned that according to the length of time series, values as low as $D_2 = 2.6$ and as high as $D_2 = 6.6$ may be found. Layne et al., 1986 have estimated occipital and central alpha dimensionality during the waking stage from 5.5 to 6.6 (central) and 6.5 to 7.7 (occipital). Dvorak and Siska (1986) estimated the alpha activity as being between 3.8 and 5.4. Saermark indicated that the alpha activity (magnetic field activity) could reach dimensions up to 11 (Saermark et al., 1989). Rapp et al. (1986) have described the correlation dimension during two different conditions of measurement, eyes closed and relaxed and eyes closed and chaotic. They have published correlation dimensions which are much lower ranging from 2.4 to 3. In these reports, however, there are usually no spectral descriptions showing the qualitative changes in the alpha activity and also depicting the ‘noisy state’.

Such spectral descriptions were included in the investigation by Röschke and Başar (1989) and Başar et al. (1990). In order to take into account changes in the brain alpha state, the computations of the correlation dimension comprise long sessions. The results show that $D_2$: (1) is dependent on the recording site; and (2) varies during the course of the measurement.

The evaluations were done on EEG segments the power spectra of which are shown in Fig. 4. Four different locations were investigated simultaneously (vertex, parietal, occipital and frontal) during the waking stage of a subject with eyes closed. In the central electrode (vertex) the power was usually centered between 7 and 10 Hz with large peakings 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 had usually lower amplitudes; high amplitude activities were mostly centered to lower frequencies including the theta band.

The correlation dimensions $D_2$ computed from the respective EEG segments are also given during corresponding time segments. For evaluation of $D_2$, EEG segments of the duration of 3 min (number of points $N = 16384$) were used. The sampling frequency was $f_s = 100$ Hz and the frequency resolution $D_f = 0.006$ Hz (before computing the correlation dimension of the EEG, the data were digitally filtered in the frequency range between 5 and 15 Hz). The correlation dimension $D_3$ of the occipital region showed fluctuations between 5.5 and 7.8. Only during a short period of measurement does the correlation dimension not reach any saturation, i.e. EEG activity during this period cannot be distinguished from ‘noise’.

It is important to note that: (1) the correlation dimensions do not vary in the same way in all locations; and, that: (2) left and right hemispheres may show considerable differences.

Fig. 5 shows an EEG of another subject who did not show any relevant alpha activity during the periods ‘eyes closed’ especially in the frontal region. In this case, as the illustration clearly shows, there are seldom time periods where the EEG shows a finite correlation, as it usually shows noisy behavior. The important message coming
from Figs. 4 and 5 is that two different locations in the brain may show completely different behaviors. In this case, during a long period of time, no finite correlation dimension (no saturation) was observed in the frontal region, whereas the occipital region simultaneously recorded showed the finite correlation dimensions in almost all segments.
There are large fluctuations in the dimensionality of alpha waves. This means that in this frequency range the brain has two types of behavior: noisy behavior and strange attractor behavior. Başar et al. (1990) concluded that the problem of the dimensionality of alpha waves or even whether the alpha activity presents a strange attractor behavior should be considered from a functional viewpoint. This means that the design of the experiment and expected results should also be taken into account in the interpretation of $D_2$.

Note the close relationship between the results of chaos analysis and the experiments in the introductory example: ‘internally induced alpha rhythms’ may be regarded as a sign of the strange attractor showing ‘reproducible patterns’, if initial conditions could be kept constant. Thus, the view that alpha rhythms are not simple noise rests on two foundations:

1. the existence of a convergent dimension $D_2$ of filtered alpha
2. the reproducible alpha activity (without physical stimulation) during a state of expectation.

Several contributions to the present volume deal with the EEG as a chaotic signal. Transitions of alpha waves accompanied by changes in correlation dimensions were mentioned by several authors and also by some of the descriptions in the present volume.

1. Röschke et al. (1997) differentiated in a well-founded manner between theta and alpha dynamics by also including the computation of Lyapunov exponents. These authors conclude that the dynamics of the alpha rhythm appear to be different at various lead positions. According to these authors it appears justified to state that the dynamics of the frontal alpha activity is functionally different from the alpha activity recorded at other locations.
2. For an interesting method separating alpha and beta band and for a differentiation of results in subjects we strongly recommend the reading of the analysis of Pritchard and Duke (1997). Groups of subjects with a very broad range of alpha power, or subjects with small alpha power have fundamentally different dynamical properties.


Differentiation of recording sites, differentiation of individual frequency contents of the EEG and application of tasks during measurements will in future probably open new avenues to use the dimensionality of the brain waves as an efficient mathematical tool, together with spectral analysis and wavelet analysis. If we take into consideration the trends for standardization proposed by Hari (panel discussion in this volume) and discussed by Niedermeyer (panel discussion in this volume) it is evident that frontal or occipital or temporal dynamics are different from the viewpoint of analysis of non-linear dynamics. However, we have to mention that middle-aged subjects show rich frontal alpha activity (Yordanava et al., 1996). Therefore we propose the use the expression 10-Hz oscillations for the ensemble of rhythms around 10 Hz.

5. Alpha rhythms as elementary signals in nervous systems

5.1. 10-Hz oscillations at the cellular level

Advances in measuring 10-Hz oscillations at the cellular level imply that it is merely a question of time for us to be more precisely able to correlate between neuron and neuron-population. Among the most recent publications are the following:

1. Dinse et al. (1997) recorded action potential sequences in cats and observed low-frequency oscillations in post-stimulus time histograms (showing the action potentials after stimulation according to their latency). Transformation of these histograms to the frequency domain showed a peak in the 6–8-Hz frequency range for auditory cortex neurons with
auditory stimulation. A respective peak in the 8–10-Hz frequency range was observed for visual cortex neurons with visual stimulation. Given the time-locked nature of these action potential sequences, the authors suggest a relation to scalp-recordable EPs (note that the modality-dependent difference of frequency maxima corresponds very well to similar differences for scalp-recorded auditory vs. visual EPs as reported by Schürmann and Başar, 1994).

2. Luhmann et al. (1995), Connors and Gutnick (1990), and Silva et al. (1991) observed neuronal discharge patterns in the 5–12-Hz frequency range in layer V of the neocortex (investigations performed on adult rat neocortical slices). According to Llinás (1988) thalamic neurons may generate action potentials at frequencies of 6 Hz or 10 Hz. All these phenomena are attributed to intrinsic membrane properties rather than synaptic interaction.

3. Schanze and Eckhorn (1997) observed phase correlation for slow frequencies (alpha, beta) in addition to previously observed phase correlations in the gamma range. For the gamma range, synchronization only extends over a few millimetres whereas synchronization for slower frequencies might serve for binding phenomena involving widely separated cortical areas.

In addition to these measurements at the cellular level, 10-Hz oscillations have been observed in isolated invertebrate ganglia (Bullock and Başar, 1988; Schütz et al., 1992; Schütz and Başar, 1992). In summary, we witness a parallel advance of knowledge about functional alpha rhythms at the cellular and at the EEG/MEG level (note that the renewed interest in gamma rhythms as developed over the last years was also triggered by results at the cellular level).

5.2. Alpha and alpha response revisited — theories on alpha generation

Since the first discovery of the alpha rhythm research, scientists have been confronted by the important question: where are the alpha activities generated? Do several alpha generators exist, and is it possible to find a pacemaker for the alpha rhythm in the brain?

The facultative pacemaker theory by Andersen and Andersson (1968) is based on the possibility of a central pacemaker mechanism in thalamic nuclei. The study of Lopes da Silva et al. (1973a,b) stating that thalamo-cortical coherences are usually lower than the cortico-cortical ones has contradicted the possibility of unique pacemakers in the thalamus. Steriade et al. (1990), Steriade (1993), and the group of Llinás re-emphasized thalamic pacemakers of the alpha activity. Our studies showed experimentally that resonant alpha generators are distributed in a diffuse way throughout the brain (Başar et al., 1975a–c; Başar, 1972a; Schürmann et al., 1997). Details concerning some of these theories are given below:

5.2.1. The facultative pacemaker theory

Andersen and Andersson (1968) advanced the hypothesis that facultative pacemakers in the thalamus influence activity in the corresponding cortical areas. Rhythm generation is assumed to occur at many independent thalamic locations. Via the specific thalamo-cortical fibers, the burst discharges of the thalamic rhythmic entity are imposed on a cortical area. Each thalamic burst will induce neuronal activity in the cortex, thus giving a correspondence between thalamic and cortical rhythmicity. Since each thalamic rhythm generator may act as an independent unit, the same individuality in rhythmical activity will occur also at the cortical level.

Andersen and Andersson (1968) noticed that the high degree of synchrony of rhythmical activity usually found in thalamic and cortical areas indicates that the activity of individual generators of the rhythm is coordinated into larger units. Experiments with decorticated preparations induced Andersen and Manson (1971) to assume that an intrathalamic mechanism in the thalamus operates giving a widespread synchronization of individual rhythm-generators, thus coordinating rhythmical activity in large cortical areas. We should mention here that the use of barbiturate spindles as a simplified model for spontaneous
rhythmical EEG activity was justified by Andersen and Andersson.

Başar et al. (1975a–c) and Başar (1972a) commented that the idea of alpha pacemakers and a transmission possibility between thalamus and cortex is useful; however, pacemaker hypotheses should be extended to other structures including brainstem and hippocampus and also to the other frequency bands.

5.2.2. Alpha rhythms generated in the cortex?

Contrary to the viewpoint of Andersen and Andersson (1968), Lopes da Silva et al. (1973b) did not assume a priori, that all rhythmic activities falling within the alpha range should be considered equivalent. The latter authors recorded the spontaneous alpha rhythms and barbiturate spindles in dogs from the same recording site. The alpha rhythms were found to differ from barbiturate spindles regarding 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 anaesthesia. Furthermore, the thalamic pacemaker hypothesis was tested by studying particularly the relationships between alpha rhythms recorded in the lateral geniculate nucleus and visual cortex. Although significant thalamo-cortical coherences were found, cortico-cortical coherences were generally higher than the highest thalamo-cortical coherences.

As we pointed out in several earlier reports (see above) various types of 10-Hz activities can be found in the human scalp records. Moreover, auditory and visual pathways have different types of alpha resonances. The hippocampus, a ‘supramodal association center’, shows a type of alpha plasticity depending on the modality of sensory stimulation.

5.2.3. Distributed alpha systems in the brain

Further, it is possible that in some structures of the brain, for example in the occipital cortex, the number of alpha generators is higher or that they are more densely distributed in comparison to other structures. On the contrary, the frontal cortex does not generate spontaneous or induced alpha activity as strongly as the occipital loops. (see Figs. 4 and 5). Furthermore, if we consider the data presented in this volume, the observations of alpha rhythms in other structures than the frontal or occipital cortex, e.g. in the cerebellum, cannot be explained by volume conduction. EPs and ERPs recorded from the cat hippocampus showed strong amplitude and frequency changes between different electrodes with an inter-electrode distance of only 1 mm. This makes volume conduction an improbable cause of alpha rhythms being observed in widely separated locations.

Distributed generators may explain the results observed better than the assumption of volume conduction. This view is also supported by the ‘cross modality’ experiments in the cat brain (Schürmann et al., 1997). The significant and stimulus-locked enhancements of the alpha response occur only when the cat has been excited by visual stimulation in the visual cortex and not auditory stimulation. Accordingly, there is no significant volume conduction between auditory and occipital cortex.

Another important experimental finding is the following: Polysensory structures, such as the reticular formation and the supramodal center, hippocampus, generate enhanced alpha responses to visual and auditory stimulation modalities. The question, ‘Why does the hippocampus generate an enhancement of 12 Hz by visual stimulation and an enhancement of 9–10 Hz by auditory stimulation’ is also a central point in understanding functional alpha activities. If the experimenters stimulate the cat brain with an auditory stimulation only the medial geniculate nucleus reacts with an alpha enhancement. In contrast, the lateral geniculate nucleus does not show enhanced, induced alpha rhythms. This is a typical and very important case to show that in the brain of a freely moving and non-anesthetized animal the enhancement of alpha activity can occur in the hippocampus independent of the modality of sensory stimulation. In other words, hippocampus is a gate ‘par excellence’ for the alpha signal transfer to several cortical locations. Our electrodes were implanted in various layers of the hippocampus and they all responded with enhanced alpha
rhythms. The same structures in hippocampus show a type of plasticity in alpha responsiveness by generating 10-Hz or 12-Hz rhythms depending on the sensory modality. The thalamus cannot work in this way; either it does not resonate, or it responds only to 10 Hz or 12 Hz. Accordingly, the thalamo-cortical alpha-circuit strongly emphasized by several investigators cannot be the only generating site of the alphas.

5.2.4. The neurophysiological basis of evoked alpha activity

"A particular feature of the thalamic relay nuclei is their ability to convert a single afferent volley to a series of rhythmic discharges along the thalamo-cortical fibers. Adrian (1941) discovered that a single tactile stimulus elicited a series of waves in the thalamus, which he called thalamic after-discharges. Similar rhythmic activity was found by Bremer and Bonnet (1950) in the medial geniculate nucleus in response to a click. All these authors noted that the frequency of the evoked activity was around 10/s, i.e. similar to that of the spontaneous rhythmic cortical waves. Adrian (1941) maintained that the after-discharges consisted of bursts of spikes separated by slow waves. A peripheral stimulus elicited a series of 3–7 such cycles. By recording from the white matter below the cortex, Adrian showed that the rhythmic discharge occurred in the thalamo-cortical fibers, indicating the thalamic origin of the after-discharges. Due to this rhythmic discharge in response to a single afferent volley, a series of waves are initiated in the cortex, appearing at a frequency of about 10/s (Bartley and Bishop, 1933; Bishop, 1933; Jarcho, 1949; Bishop et al., 1953).

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 that cortical area to which the thalamo-cortical fibers project. In 1951 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 the more recent observations by Adrian (1951) who critically tested the cortico-thalamic reverberating hypothesis, and by Galambos et al. (1952) (Andersen and Andersson, 1968).

6. 'Alphas' diffusely distributed in the brain

In various sections of the present report we have described functional correlates of the spontaneous, induced, cognitive, and sensory alpha activity. It was indicated that the visual cortex does react to sensory stimulation with short lasting 12-Hz oscillations, whereas the same structure does not respond to auditory stimuli. We have seen the same behavior of the auditory cortex which seems to generate oscillatory 10-Hz wave forms only upon auditory stimulation. A strong enhancement was also recorded in the hippocampus although this structure is especially known to generate regular theta activity.

The distributed nature of evoked alpha rhythms is also supported by the following findings: the amplitude, time course, and frequency content of evoked potentials (especially N100-P200 wave complexes) strongly depend on the amplitude of alpha activity prior to a sensory stimulation. Recent publications by Brandt and Jansen (see Brandt, 1997) did not only confirm the findings of Başar (1972a) regarding the inverse relationship between evoked potentials and pre-stimulus EEG, but these authors also describe a model presenting evidence that the generation of spontaneous EEG activity can produce visual-EP-like wave forms when pulse-like signals serve as input. In particular, these authors describe a large correlation between N100 amplitude and pre-stimulus EEG. The data of Brandt and Jansen (see Brandt, 1997) provide support for the hypothesis that the 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.

We must also emphasize the 10-Hz spontaneous and enhanced activity of the snail ganglia (Schütt et al., 1992; Schütt and Başar, 1992). If we put together all these functional correlates it is possible to make a mental effort by postulating that these 10-Hz oscillations of 300 ms duration are sometimes longer and are involved in every type of brain function. If this is not an important enhancement of 10-Hz activity in the auditory pathway to a visual stimulation, then the limbic system and association cortex are highly involved with 10-Hz frequencies.

In accordance with these considerations it is plausible that alpha networks are distributed in the brain in a diffuse way. These networks do exist in the brain stem, in cerebellum, in thalamus, in the limbic system, in sensory and association and motor areas of the cortex. The alpha oscillatory behavior enters the process or to a cognitive or sensory input depending on tasks in adequate circuits of the brain. These experimentally established working types of the alphas might play an essential role in sensory and cognitive communication in the brain. We postulate that the combination or entering into action of the various alpha networks is a powerful dynamic property of the brain.

7. Synopsis on functions of ‘alphas’

‘Physiological alpha rhythms are likely to have closer relationships to ‘events’ than one might have thought earlier’ Niedermeyer (1997)

After Berger’s discovery of the EEG (1929) an explosion in research activity in this area quickly followed. Studies were made of the brain waves in every conceivable behavioral state, ranging from normal human subjects to those with psychoses or epilepsy to state changes such as the sleep–wakefulness phases. Berger believed that alpha waves reflect mostly passive states of consciousness. He had possibly opened the most important research area for the understanding of dynamics of brain function. However, his interpretation regarding alpha activity probably was a restrained explanation.

Adrian (1941) introduced the expression of induced rhythms. His experiments could clearly show various types of induced rhythms ranging from 5 to 10 Hz and also to 40 Hz known as the gamma band. Grey Walter published important contributions on EEG recording. The use of electroencephalography in the study of basic brain mechanisms reached a peak in the 1940–1950s; thereafter such studies plateaued and ceased to be attractive to most experimental neuroscientists. At the beginning of the 1960s neurophysiologists preferred to work on the single cell level in the belief of discovering most important brain functions by using spike activity. However, as Mountcastle (1992) recently stated, ‘...rather suddenly [...], a paradigm change is upon us, for the proposition that slow wave events are active agents for signal transmission now stands as a testable hypothesis with some evidence to support it’. Such a radical change has not occurred by chance. It is due to the development of new theories and concepts, new methods of data collection and analysis: to be found also in various contributions to this special issue. A number of investigators have performed experiments with highly significant functional correlations of the brain with alpha activity.

1. Williamson (Williamson and Kaufman, 1989; Williamson et al., 1997) states that changes in ongoing alpha activity provide a new dimension of alpha activity. This author described carefully functional aspects of alpha suppression, mental imagery and visual imagery by means of neuromagnetic studies. He further takes the viewpoint that by exploiting magnetic source images (as given in his examples) it may be possible to characterize the detailed evolution of cortical activity throughout the period when a subject is engaged in a cognitive task. This means that functional correlates of alpha activity should be differentiated both in time space and in topological space. This statement is also in accordance with analyzes of the dimensionality. We suggest also comparing the expres-
sion ‘alphon’ used by Williamson and ‘microstates as building blocks or atoms of thought’ as used by Lehmann (1989).

2. Lehmann and Koenig (1997) state that: (1) alpha strength is more sensitive to visualizing than to abstract mentation; (2) different alpha frequencies execute different brain functions; (3) alpha is inhomogeneous over time, consisting of building blocks (‘building blocks of mentation, the atoms of thought’); and (4) different modes of mentation are associated with different brain electric microstates.

3. The studies by Klimesch (1997), Lebedev (1980) and Malteva and Maslovaev (1997) and the results of my research group show evidence that the alpha activity is involved in short-time and long-time memory processes.

4. Petsche et al. (1997) emphasize the possible role for cognition even in different frequency bands within the alpha range. Visual perception, imagery and silent reading induced distinct differences between alpha 1 and alpha 2.

5. Geissler (1997) predicts with his model nine different alpha components.

6. Rougeul-Buser and Buser (1997) investigated the relationship between alpha rhythms and expectancy states in cats.

7. Physiological rhythmic activity in the 8–13-Hz range is observed not only as the posterior alpha rhythm. The sensory motor mu rhythm over the Rolandic region and now the third rhythm described by Niedermeyer (1993, 1997) gains important consideration.

8. Now, the measurements by means of magnetoencephalography will probably help us more precisely with regard to dynamics and topography of the alpha activity. As Hari et al. (1997) published recently, we have a new window (or a new tool, Hari, 1993) using magnetoencephalography. Although our group is not maximally experienced with regard to magnetoencephalography, some years ago in Saermark’s laboratories we observed ‘sharp’ 10-Hz responses in temporal brain areas or other types of induced rhythms without even the use of filtering (Saermark et al., 1992). For discussions on temporal spontaneous or induced rhythms and their possible functional correlates (Tihonen et al., 1992; Niedermeyer, 1993), see e.g. the panel discussion in this volume. In particular, functional correlates of magnetoencephalographic alpha rhythms have been investigated by Narici et al. (1990) and Narici (1997).

9. By studying several functional correlates of alpha it would be wise to take very carefully into account the model of Lopes da Silva et al. (1973, 1973, 1997) who hypothesized the existence of distributed alpha networks with similar design in the brain.

10. The role of alpha activity prior to stimulation for evoked potentials and for event related potentials were studied by Brandt (1997) and Polich (1997). Polich’s studies are relevant in relation to the discussion above: the alpha activity is related to cognitive states of individual subjects under study. However, the 10-Hz oscillations also have an indirect influence on cognitive processes. The P300 response is influenced by the alpha activity of the spontaneous EEG. The pioneering findings of Polich (1997) support the hypothesis that individual variation in background EEG alpha activity is associated with P300 amplitude and latency variability. Given that P300 measurements are used to assess cognitive capability for clinical purposes, investigations on how the EEG alpha activity is related to ERP generation may turn out to be particularly useful. The topographic distribution of alpha activity is a further parameter of interest for psychophysiological studies (Burgess and Gruzelier, 1997).

11. Samson-Dollfus et al. (1997) has, for years, published studies on the modification of alpha rhythms in children. In order to learn about alphas we also learn about its development (see also Yordanova and Kolev, 1997).

12. One of the pioneers, having first applied computational methods to the analysis of alpha waves and also having made important discoveries on alpha blocking, Barlow (1997)
now deals with models of coupled oscillators.

8. Functional correlates of ‘alphas’

We will group results and interpretations of functions of alpha generators into several categories:

8.1. Memory mechanisms and alpha

Klimesch et al. (1993) and Klimesch (1997) claims that the vast majority of experiments studying alpha correlations with cognitive performance are not concerned with memory processes. The general view here is that in comparison with a resting period, task demands tend to attenuate or desynchronize alpha rhythms (Berger, 1929; Creutzfeldt et al., 1966, 1969). As compared to the abundance of experiments dealing with alpha power measurements, relatively few studies focused on task related shifts in alpha frequency. The experiments by Osaka (1984) showed that only for difficult but not for easy tasks, alpha frequency increases selectively in the hemisphere which is dominant for a particular task. Clear evidence for a positive relationship between dynamic memory performance and increase in synchronized alpha activity was clearly demonstrated by Başar et al. (1989). Again, clear evidence for a positive relationship between memory performance and mean alpha was reported by Klimesch et al. (1990).

In an experiment involving a memory-search paradigm, the subject’s memory performance had a strong effect on individual alpha frequency. As compared to a resting period, the difference in individual alpha frequency between age-matched good and bad memory performers reached a maximum when subjects were actually retrieving information from their memory. During retrieval, the alpha frequency of good performers is 1.25 Hz higher than for bad performers. The results of amplitude analyses demonstrate further that during retrieval, alpha desynchronization is more pronounced for bad performers than for good performers. The results of Klimesch and the dynamic memory model of Başar et al. (1989) demonstrate that alpha activity is strongly correlated with short term memory, working memory and probably with long term memory engrams. A review of induced alpha rhythms has been given above, where these rhythms were considered as internally evoked potentials during periods of expectation of a visual or auditory target. Note that in this case the alpha activity should not be considered as a correlate of mental imagery most typical for occipital areas. The central cortical areas (vertex) can also develop such alpha rhythms (Başar, 1988; Başar et al., 1989).

8.2. Alpha as sensory response

Since the days of Adrian ‘evoked alpha’ was assigned to be the response (reactiveness) of the CNS to sensory stimuli. Sensory evoked 10-Hz responses were recorded in several cortical and intracortical structures (see Schürmann et al., 1997). It has been emphasized above that sensory stimulation can evoke 10-Hz rhythmic behavior at the cellular level.

8.3. Alpha and motor processes

Llinás (1988) assigned oscillations and resonances in the central nervous system to diverse functional roles. This author assumed that oscillations play a role for determining global functional states, for example: (1) sleep–wakefulness or attention; and (2) timing in motor co-ordination. These examples and the results of Pfurtscheller et al. (1997) show how the alpha activity is involved during movements.

8.4. The distributed nature of alpha rhythms and their putative role in general mechanisms of the brain

In a series of publications Wiener (1955, 1956, 1957) advanced the concept that the alpha rhythm might give a reflection of a relatively stable clocking mechanism of the brain, to serve a gating function. Wiener ascribed the hypothesized clocking mechanism to mutual entrainment of an ensemble of non-linear alpha rhythm generators.
such as the frequencies of individual members of the ensemble which would have a tendency to be pulled towards a central frequency, in a manner analogous to that in which large numbers of some species of fireflies flash synchronously.

Several induced, evoked, and spontaneous 10-Hz rhythms with slight frequency shifts, recorded in distributed cortical and intracranial structures led definitely to the conclusion of the correlation of alpha with movements, memory, sensory processing, attention and last but not least with general association mechanisms. The immediate question which arises now is as follows: are different alphas as distributed generators involved in general mechanisms of the brain and not just indeterministic signals coming from hidden or undefined sources, in a random manner? The answer which is obtained on strong empiricism, is 'yes'.

The message which comes from the ensemble of findings reviewed in this report is that a brain research scientist is advised to take very seriously into account the 10-Hz processes by studying the results of sensory, movement-related and cognitive processes. Depending on the site of recording and on the cognitive paradigm or strategies used, the alpha code for a given brain structure may enter the analyzed function in an appropriate way.

The articles in this volume show that in general a unique frequency component is, in general, not sufficient to find the exact electrical correlation of brain function. The most important point emerging is the fact that the experimenter has to pay attention to 10-Hz components or several alphas ranging from 7 to 13 Hz in his experimental strategy or design.

8.4.1. Associative networks

Assuming that several 10-Hz generators are distributed in the brain and further supposing that these activities act as non-linear clocks (as hypothesized by Wiener) then we are confronted with the question whether 10-Hz processes may facilitate, generally, 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.

From the viewpoint of energy conservation the central nervous system can facilitate the communication if there is a main frequency and some other minor frequency shifts in the same band. Such facilitatory networks do already exist in international telephone communication. The country codes, the area or city codes do not facilitate only information transfer but they also increase the capacity of the working memory of persons who are in search of a given phone-number. Accordingly, the distributed 10-Hz network might facilitate the sensory-cognitive communication in the brain.

9. An integrative view of alphas

1. Different 10-Hz oscillations (alphas) can be recorded from various areas of the human scalp and intracranial structures of the cat brain. They are related to diverse sensory and/or cognitive functions.

2. 'Spontaneous' alphas are not noise but probably quasi-deterministic signals. 10-Hz oscillations of the brain are not pure noise as demonstrated by several results: Best examples are the analysis of correlation dimension and phase-locked and reproducible 10-Hz rhythms preceding a cognitive target.

3a. Evoked 10-Hz oscillations can be generated in several structures of the brain simultaneously. The damped oscillations (of approximately 200–300 ms duration) after sensory stimulation are sensitive to the modality of stimulation and the recording site.

3b. When subjects are given a cognitive task, event-related alpha rhythms may be prolonged (cognitive components).

4a. Alpha does not necessarily reflect 'passive states' or 'idling' of the brain. This is a consequence of 3a,b. Moreover, it is possible that passive states or idling are components of general states of the brain, their causality being yet unknown (hidden causality).

4b. Alphas have multifold functional correlates. 10-Hz rhythms have important functional
correlates including sensory, motor and memory functions.

5. **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.

6. **Distributed alpha system.** Rather than trying to locate a unique alpha generator, it is preferable to formulate the existence of a 'diffuse and distributed alpha system' (Başar and Schürmann, 1996). The following physiological results concerning hippocampal alpha responses illustrate this proposition:
   
   (i) Auditory and visual stimulations elicit in cat hippocampus strong and stable alpha responses (10-Hz oscillations of approx. 300 ms), which are visible without filtering.

   (ii) Cortical and thalamic 10-Hz responses can be elicited only by stimulations that are adequate for the respective area. In contrast, hippocampal 10-Hz responses are present in all types of stimulations.

   (iii) In coherence functions computed from visual evoked responses, the hippocampo-cortical coherence is significantly larger than the thalamo-cortical coherence (the latter one being extremely low following inadequate stimulation).

Thus, thalamo-cortical circuits are not unique in generating alpha responses; the hippocampus may even have a more general significance.

7. **Alpha as a universal code or universal operator.** The results mentioned above underline the major physiological meaning of 10-Hz oscillations which may be comparable to the putative universal role of gamma responses in brain signalling.

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