

A NEURO-SYNAPTIC MODEL OF EEG RHYTHM FORMATION
IN THE THALAMO-CORTICAL SYSTEM

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Summary

A neuro-synaptic model of the thalamo-cortical system was presented on the basis of the interaction of the positive and negative cortical surface potentials generated by current source densities originating from excitatory postsynaptic potentials in order to analyze the mechanism of cortical rhythm formation, especially alpha waves with specific spatio-temporal pattern. In the case of one superimposed potential of two surface potentials, the increase in the relative amplitude of the negative potential also caused a shift in the DC level as well as in the amplitude of the fundamental wave. The model system with two superimposed surface potentials could simulate the generation of a sinusoid-like wave at the second harmonic frequency with no use of a nonlinear function.

1. Introduction

A number of studies on brain rhythm as a candidate for the command of neural timing in human behavior have appeared since Lashley (1951) proposed "The problem of serial order in behavior."¹⁾ Byers (1979), for example, analyzed the movements of three Eskimos in cooperative operation on a seal as well as the conversation between two Bushmen to conclude that normal human behavior is incooperated in interactional as well as internal synchrony²⁾. The fundamental rate of such synchronous timing for performance and perceptual grammar is said to be 5 to 10 Hz in normal situations, but to vary or rather to be fixed at a different on pathological conditions, e.g., 7 Hz in stuttering, 5 Hz in monotone, etc. (Shaffer, 1982)³⁾.

The cortical activities, which generate such human behavior, are difficult to observe in normal subjects, but this is possible in animals implanted with cortical electrodes. Beuyer, et al. (1983) observed the cortical rhythms during attentive and quiet wakefulness in a cat which showed cortical rhythms of 35-40 Hz at high vigilance, 14 Hz in quiet wakefulness, 14 and 8 Hz when drowsy, but with hemispheric asymmetries in spatio-temporal patterns⁴⁾. These animal cortical rhythms have been reported as having correlation with behavioral timing (Semba and Komisaruk, 1984)⁵⁾.

Electromagnetic signals derived from the scalp, e.g., electroencephalogram (EEG), magnetoencephalogram (MEG), etc., can produce some information on brain rhythms as neural timings, if such signals reflect cortical activities (Wood, et al., 1985)⁶⁾. The EEG/MEG also show a rhythmic pattern, which are divided into several frequency bands, i.e., delta band (1-3 Hz), theta band (3-7 Hz), alpha band (7-14 Hz), and beta band (14-28 Hz). In some EEGs, a slow (DC shift) component lower than delta band and a fast

component higher than beta component can be observed.

Such changes in the internal and external state influence the EEG, the transitive variances of which are named event-related potentials (ERPs), e.g., BP (Bereitschaftspotential) of readiness for voluntary movements, EP (evoked potential) for stimulation of sensory inputs (Deecke, et al., 1983)⁷⁾. Pfurtscheller (1981) combined data on rhythmic EEG activities and cortical functioning to investigate the correlation between human behavior and EEGs⁸⁾. He found that the alpha rhythm decreased about 4 sec prior to movement onset and recovered about 2 sec after movement offset. Such blocking was observed also in the beta band, but with a different time course. In another study, some rhythmic components even in the alpha band were found to be movement-resistant (Papakostroupos, 1980)⁹⁾.

Event-related changes in rhythmical EEGs during the cognitive mode were found by Storm van Leeuwen and Kamp (1980)¹⁰⁾. The higher alpha components as well as beta components increased with lower-theta enhancement, but the lower alpha and higher theta components were unchanged by presenting a number to be added in mental calculation to a number in memory. These event-related alpha and beta blocking/enhancement studies indicate the independence of the alpha and beta components.

Recent applications of multielectrodes to the cortex have made it possible to obtain "micro-EEGs" which can present information on cortical activities intermediate between single neuron firing and macro-EEGs (Petsche, et al., 1984)¹¹⁾. The micro-EEGs are related to current sourced densities (CSDs) which are volume-ensemble activities of microscopic currents in extracellular space. The CSDs are generated by action potentials of neurons as well as by synaptic activations, but the CSDs only from excitatory synapses are observed at the cortical surface as monopolar potentials. The surface potentials (SUPs) may be positive or negative according to the direction and number of pairs of CSD sources and sinks.

On these physiological data, various types of models of brain rhythmicity have been proposed such as periodic oscillation (Van Rotterdam and Lopes da Silva, 1982)¹²⁾, waveform generation (Freeman, 1980)¹³⁾, wave propagation in a volume (Nunetz, 1981)¹⁴⁾, etc.. In this paper, a neuro-synaptic model of the thalamo-cortical system will be presented on the basis of the interaction of the positive and negative SUPs generated by CSDs originating from excitatory postsynaptic potentials (EPSPs) in order to analyze the mechanism of cortical rhythm formation, especially alpha waves with specific spatio-temporal pattern.

2. The model

In this model, the process of rhythmic wave formation is performed as follows.

- 1) The SUPs derived from CSDs are assumed to be analogous to the CSD drivers, i.e., EPSPs.
- 2) The periodic oscillation is generated in the thalamic complex which consists of three mutually connected nuclei.
- 3) Two of the three nuclei project the periodic neural bursts at

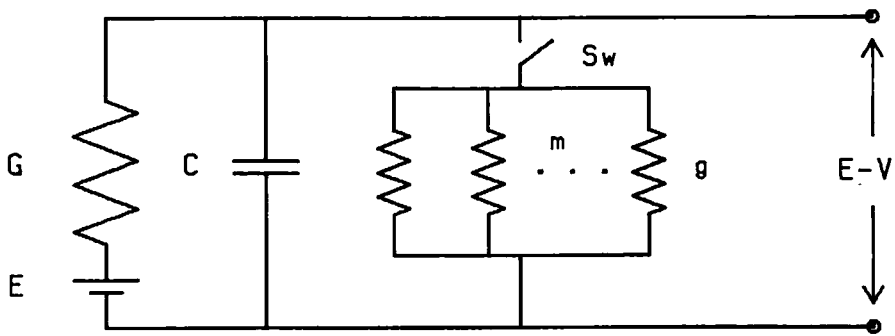


Fig.1. Electrical circuit model of the postsynaptic membrane. C: membrane capacitance; E: resting membrane potential; g: unit shunt conductance; G: resting membrane conductance; m: number of quanta transmitted by one pulse; Sw: switch of ion channel; V: postsynaptic potential (from Ref.16).

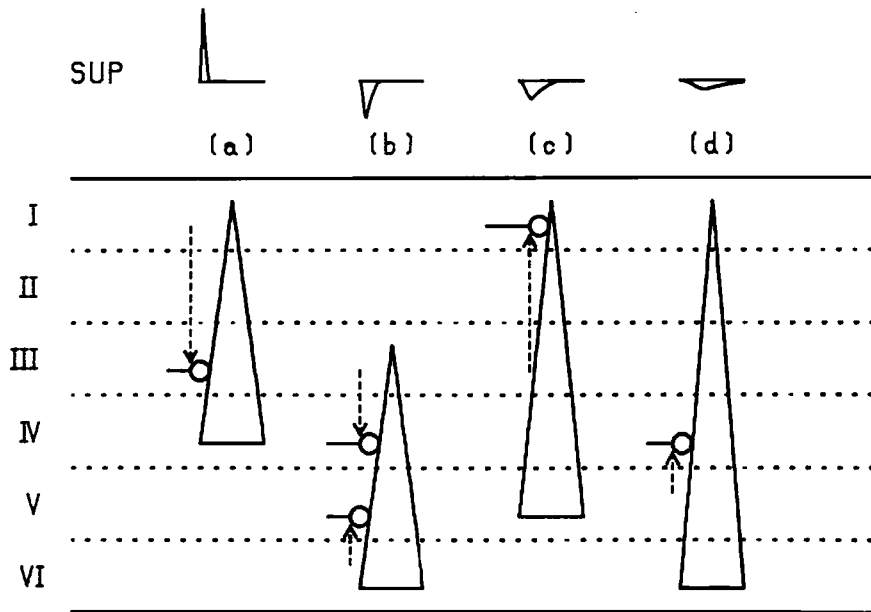


Fig.2. Current source densities (CSDs) and surface potentials (SUPs) evoked by EPSPs in cortical layers. SUP: surface potential; I-IV: cortical layers; Triangles: neurons; Circles: excitatory synapses; Arrows: CSDs (modified from Ref.15).

different layers in the cortex.

- 4) A burst in any layer generates EPSPs with intensity proportional to the density of the burst.
- 5) The CSDs from the EPSPs evoke positive or negative SUPs.
- 6) Some neurons activated by the EPSPs generate secondary EPSPs with a proper delay in the same or other layers.
- 7) The train of isolated events which emerge from the above process forms a "rhythmic EEG phenomena" (Mitzdorf, 1985)¹⁵⁾.

The EPSP can be modelled by an equivalent circuit composed of resting membrane potential (E), resistance (1/G), and capacitance (C) as shown in Fig.1. With a conductance change in post-synaptic membrane, the EPSP, $v(t)$ is described by

$$dv/dt + (G+mg)v/C - mgE/C = 0 \quad (1)$$

after conductance change ceases,

$$dv/dt + G/C = 0 \quad (2)$$

where mg is a shunt conductance and G/C is the resting membrane time constant. Using an approximation of the conductance change with a composite curve of cosine and sine waves with the same frequency but with different amplitudes, the time course unit for EPSPs, $V(t)$ is simplified as follows,

$$V(t) = \begin{cases} (1 - \cos(2\pi t/2T_c))/2 & (0 \leq t < T_c) \\ \exp(-(t-T_c)/\tau) & (T_c \leq t) \end{cases} \quad (3)$$

where T_c is the duration of the conductance change and τ is the discharging time constant.

When the EPSP is generated repetitively, the EPSP is

$$V(t) = \begin{cases} (1 - \cos(2\pi t/2T_c))/2 & (0 \leq t < T_c) \\ (\exp(-(t-T_c)/\tau) - V_0)/(1 - V_0) & (T_c \leq t < T) \end{cases} \quad (4)$$

$$V_0 = \exp(-(T-T_c)/\tau) \quad (5)$$

$$V(t+T) = V(t) \quad (6)$$

where T is the period of the repetitive stimuli (Itoh, 1984).

The SUPs are specified by the layer of the generated EPSPs as in Fig.2. If the SUP generated by the EPSPs in the i th layer is $V_i(t)$, the superimposed SUP, $S(t)$ is

$$S(t) = \sum a_i V_i(t - \delta_i) \quad (7)$$

where a_i and δ_i are the amplitude and delay of V_i .

In the case where the secondary EPSPs are activated, the summed SUP of the first and second superimposed SUPs, $U(t)$ is

$$U(t) = \sum m_j S_j(t - d_j) \quad (8)$$

where m_j and d_j are the amplitude and event delay of the j th superimposed SUP.

The model system, as given in Fig.3, consists of a set of six neuronal assemblies layered in cortex and a group of thalamic nuclei, i.e., specific relay nucleus (ST), reticularis thalami nucleus (RT), and central thalamic complex (CT). The reciprocal connection between the ST and RT generates a train of periodic bursts, which are projected to the fourth and first layers in the cortex through the ST and RT, respectively. The corticothalamic

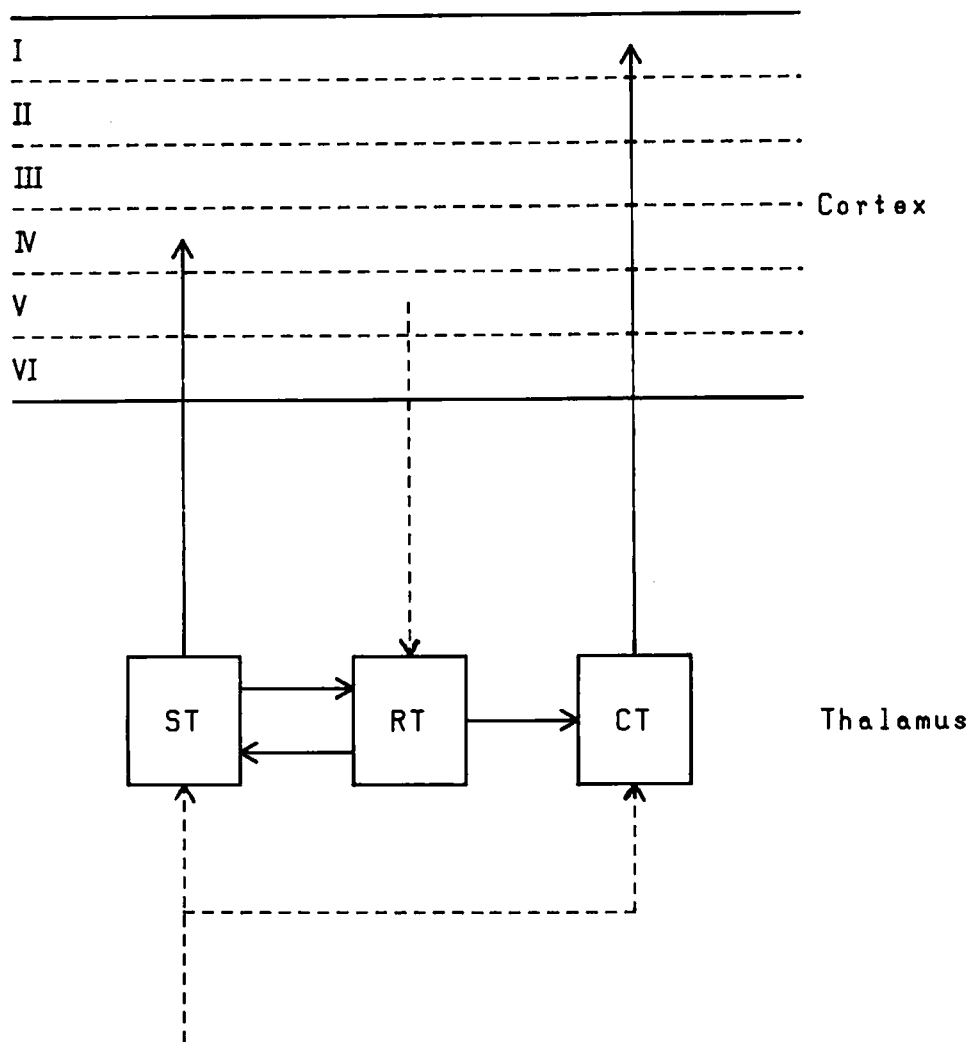


Fig.3. Block diagram of the thalamocortical system. CT: central thalamic complex; RT: reticularis thalami nucleus; ST: specific relay nucleus; I-VI: cortical layers. Solid lines: connections necessary for thalamic oscillation; Broken lines: pathways not involved in thalamic oscillation (modified from Ref.17).

efferent and sensory afferent on the thalamus (broken lines) are excluded because of no contribution to thalamic oscillation (Striade and Deschenes, 1984)¹⁷⁾.

3. Simulation

Figure 4 shows a result of the simulated rhythmic waves in the case of only two SUPs from layer I and IV with various relative amplitudes ($a_4/a_1=0$ to 2). Two components in the repetitive superimposed SUP, i.e., a DC level and sinusoidal wave of fundamental frequency (ALPHA) were extracted by spectral analysis. The model system could simulate the phase shift of a rhythmic wave by controlling the V_4 amplitude, but showed a reversed direction of phase shift for a long delayed V_1 potential in Fig.4c compared to short one in Fig.4a.

Figure 5 shows a result of the summated SUP of two superimposed SUPs as in Fig.4 but with various delays between the first and second superimposed SUPs ($d_2-d_1=0$ to 360°). The model system could simulate a sinusoid-like wave of second harmonic frequency ($d_2-d_1=180^\circ$) as well as of fundamental frequency ($d_2-d_1=90^\circ$ and 270°).

4. Discussion

In the neuro-synaptic model of the thalamo-cortical system, a simple superimposed surface potential of only two surface potentials with the same charging duration as well as a simple summated potential of two superimposed potentials with the same components were adopted to explain the amplitude and phase shifts in EEG rhythmic waves on scalp. In the case of only one superimposed potential, the increase in the relative amplitude of the fourth surface potential also caused a shift in the DC level as well as in the amplitude of the fundamental wave. Thus, the model system in this case could not determine the phase and amplitude of the wave independently.

As described in the introduction, there exist two or more components in the alpha band. Such rhythmic waves with multiple components in the alpha band (Itoh, 1982)¹⁸⁾ as well as in the slow band (Grozinger et al., 1980)¹⁹⁾ can be obtained also during the preparatory period for utterances. Schoppa et al. (1980) found two components with different coherence in promotion alpha waves with frequencies of 9 and 11 Hz, respectively²⁰⁾.

The model system with two superimposed SUPs could simulate the generation of a sinusoid-like wave at the second harmonic frequency with no use of a nonlinear function. The wave corresponds to a beta wave when the repetitive frequency of the thalamic bursts is in the alpha band and also to an alpha wave when the frequency is in the theta band. Jansen and Llinas (1984) investigated the electrophysiological properties of guinea-pig thalamic neurons to observe the firing patterns in two modes with frequencies of 5 and 10 Hz, respectively²¹⁾. However, the alpha as well as beta waves have different spatio-temporal patterns on the scalp (Pfurtscheller and Aranibar, 1978)²²⁾. It is now difficult to ex-

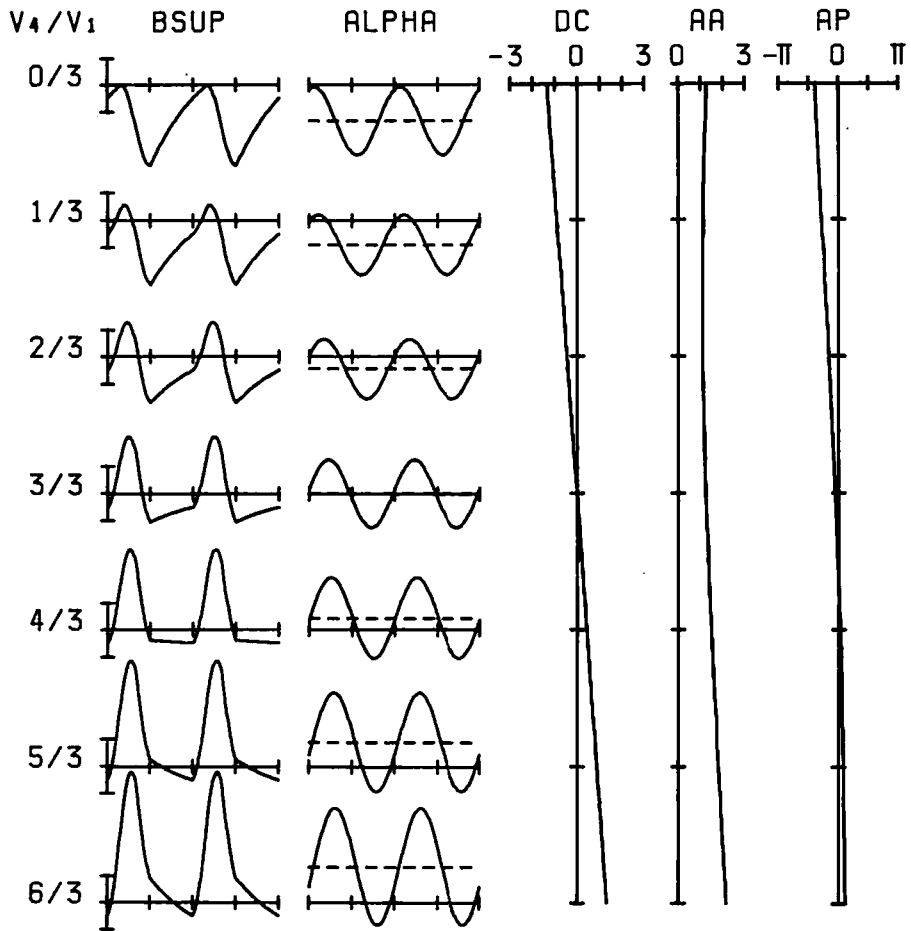


Fig.4. Rhythmic response of the system with the PSP charging duration $T_c=T/3$ (T : period of thalamic burst train) and discharging time constant $\tau=2T_c$. V_4/V_1 : ratio of positive SUP (by layer IV) and negative SUP (by layer I) amplitudes; BSUP: superimposed biphasic potential of the positive and negative SUPs; ALPHA: DC level (broken line) and rhythmic fundamental wave (solid line) extracted from the superimposed SUP (data for two periods); DC: DC component in superimposed SUP; AA: amplitude of fundamental rhythmic wave; AP: phase of the wave ((a): $\delta_4-\delta_1=T/6$; (b): $\delta_4-\delta_1=T/3$; (c): $\delta_4-\delta_1=T/2$). (See (7))

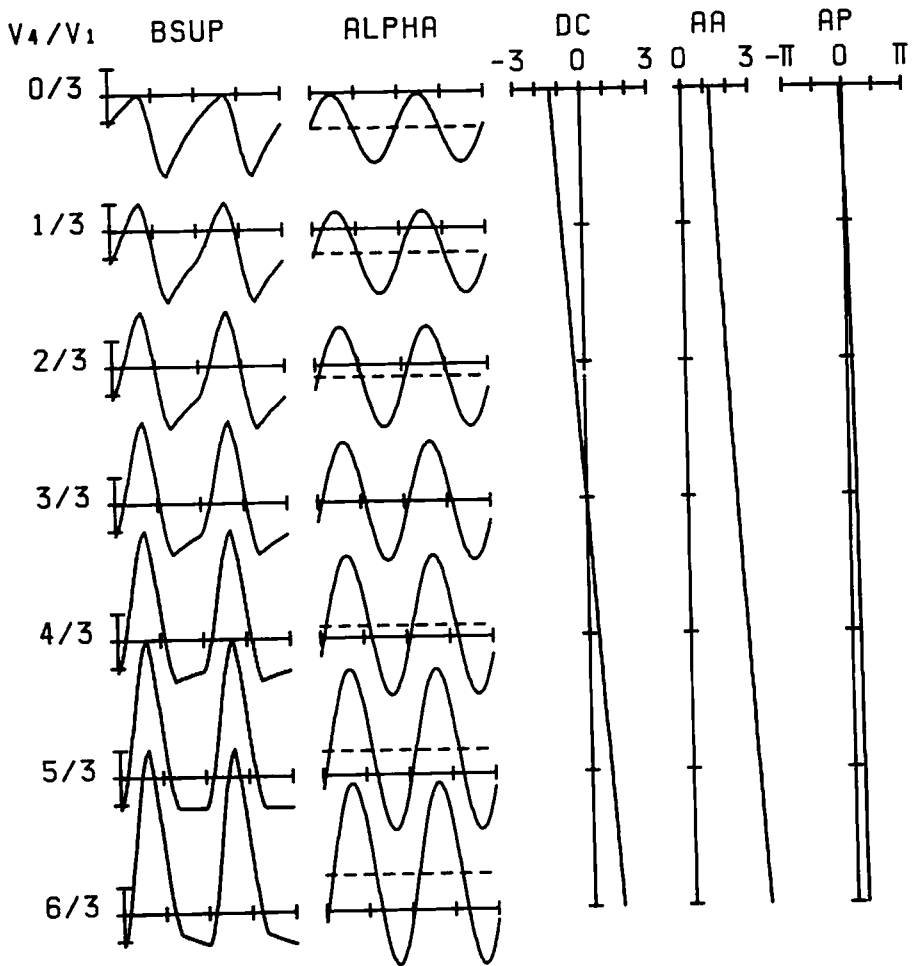


Fig. 4b. $\delta_4 - \delta_1 = T/3$.

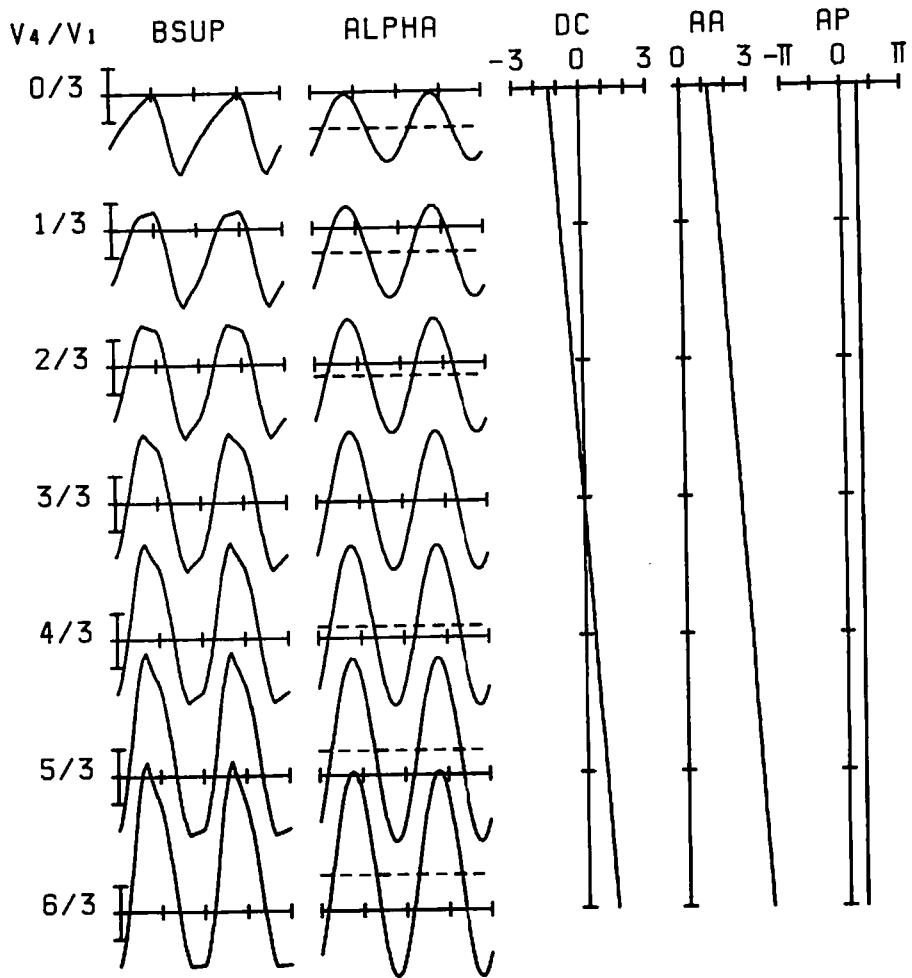


Fig. 4c. $\delta_4 - \delta_1 = T/2$.

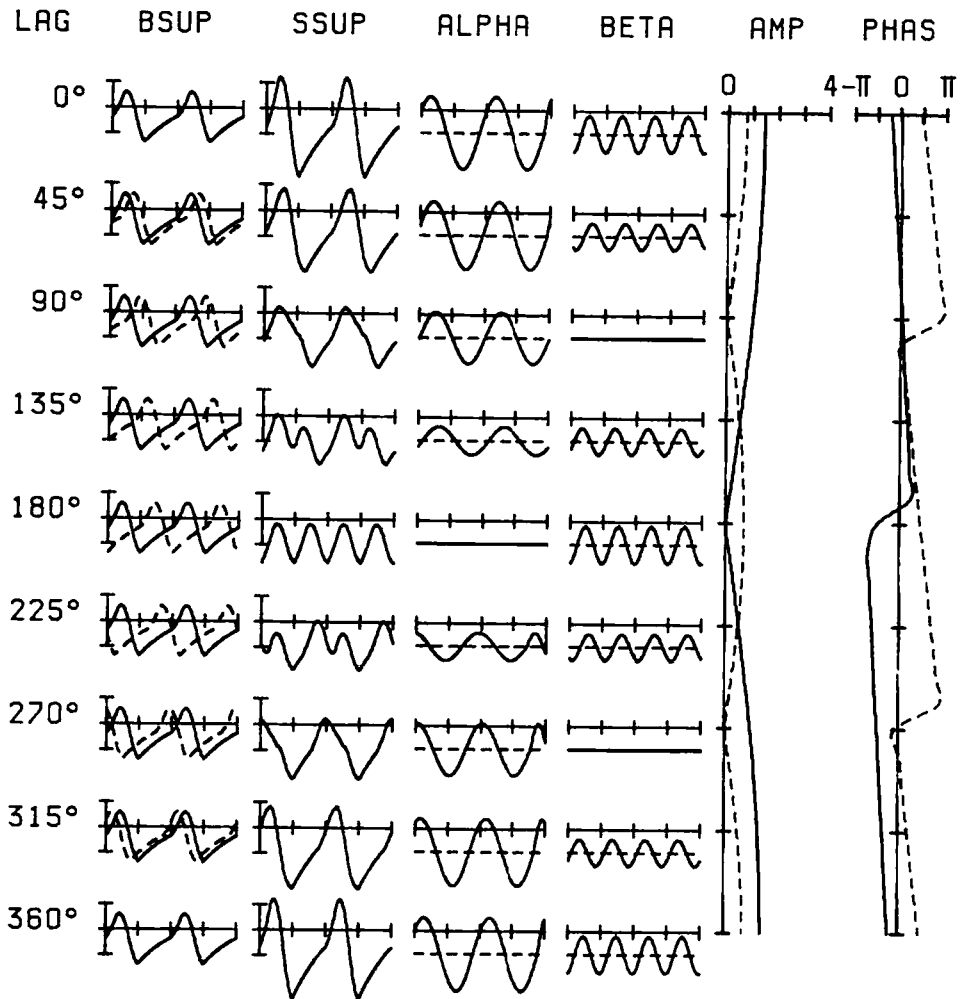


Fig.5. Rhythmic response of the system with two superimposed SUPs as in Fig.4. BSUP: biphasic superimposed SUP; SSUP: summated SUP of two BSUPs with event delay (LAG) of 0 to 360°; ALPHA: DC level (broken line) and rhythmic fundamental wave (solid line) extracted from SSUP; BETA: DC level (broken line) and rhythmic second harmonic wave (solid line) extracted from SSUP; AMP: amplitudes of fundamental wave (solid line) and second harmonic wave (broken line); PHAS: phases of fundamental wave (solid line) and second harmonic wave (broken line) ((a): $a_4/a_1 = 1/2$ and $\delta_4 - \delta_1 = T/6$; (b): $a_4/a_1 = 1/2$ and $\delta_4 - \delta_1 = T/3$; (c): $a_4/a_1 = 1/2$ and $\delta_4 - \delta_1 = T/2$; (d): $a_4/a_1 = 1/1$ and $\delta_4 - \delta_1 = T/3$; (e): $a_4/a_1 = 2/1$ and $\delta_4 - \delta_1 = T/3$ but $m_1/m_2 = 1.0/0.5$).

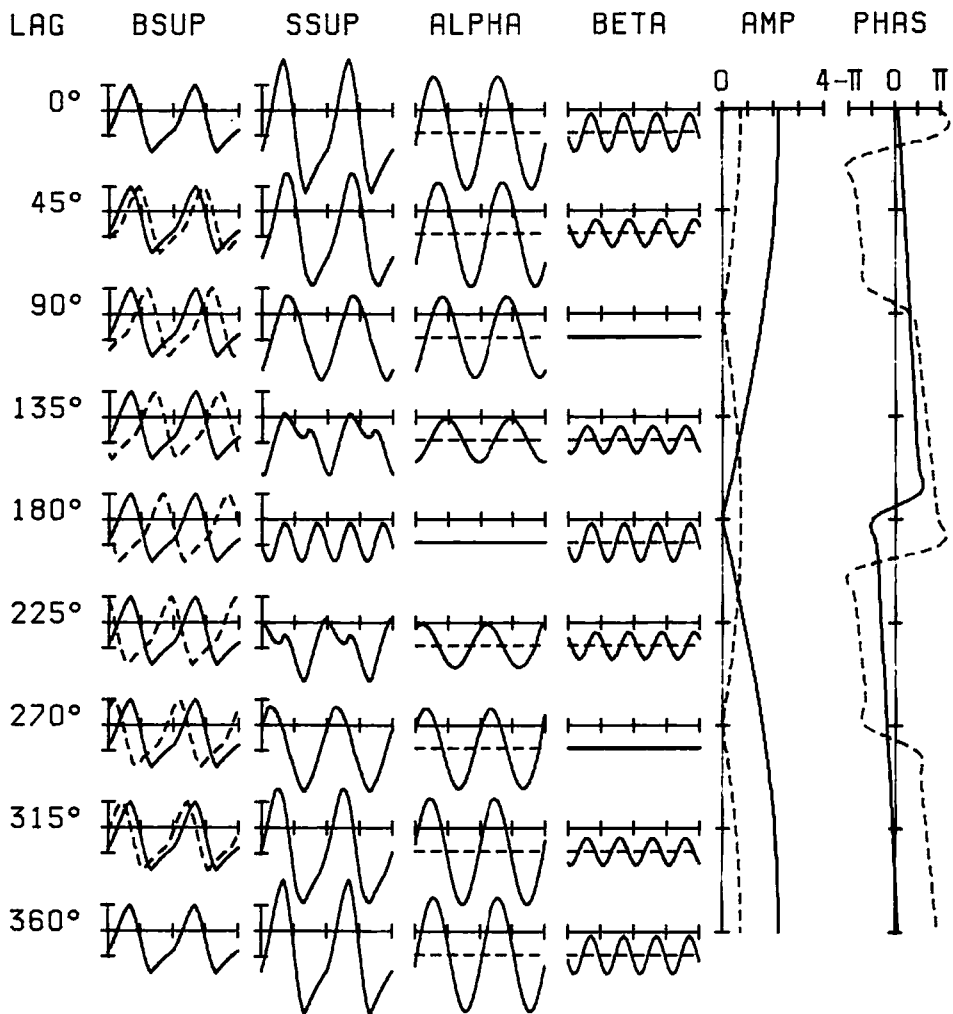


Fig.5b. $a_4/a_1=1/2$ and $\delta_4-\delta_1=T/3$.

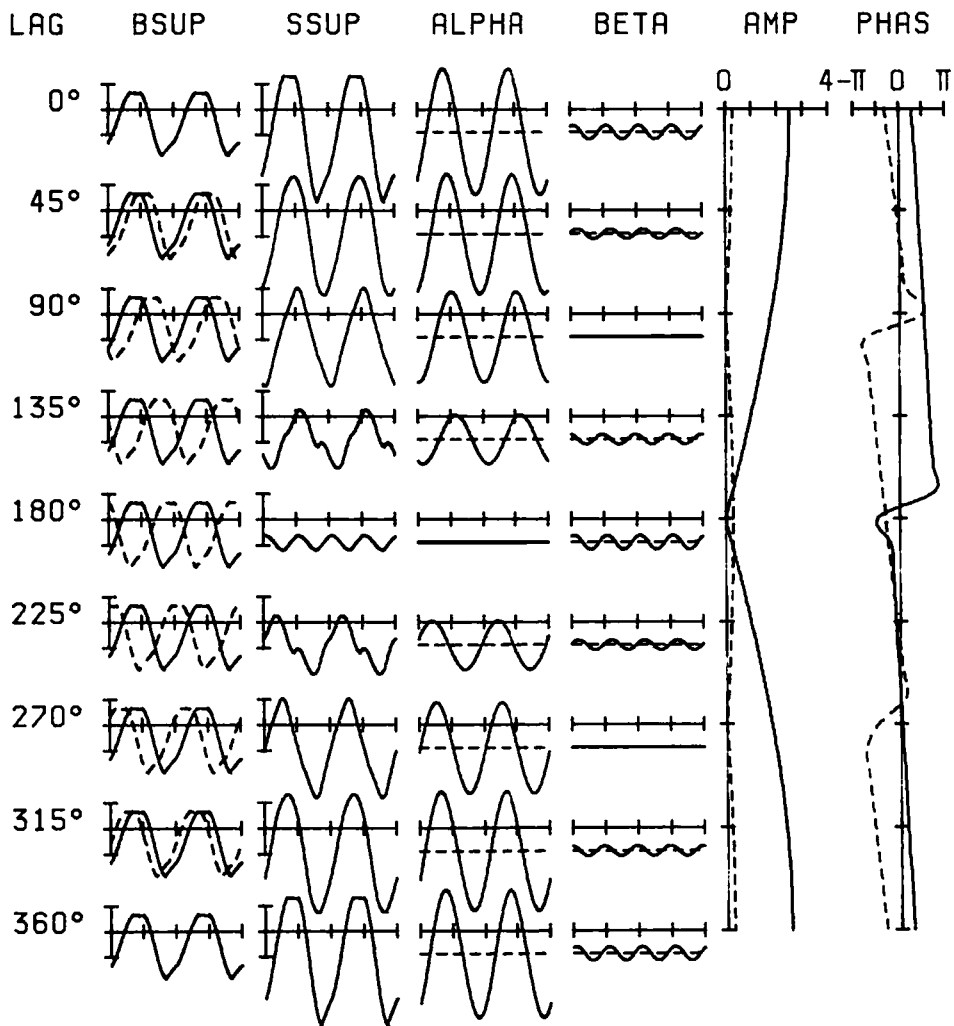


Fig.5c. $a_4/a_1 = 1/2$ and $\delta_4 - \delta_1 = \pi/2$.

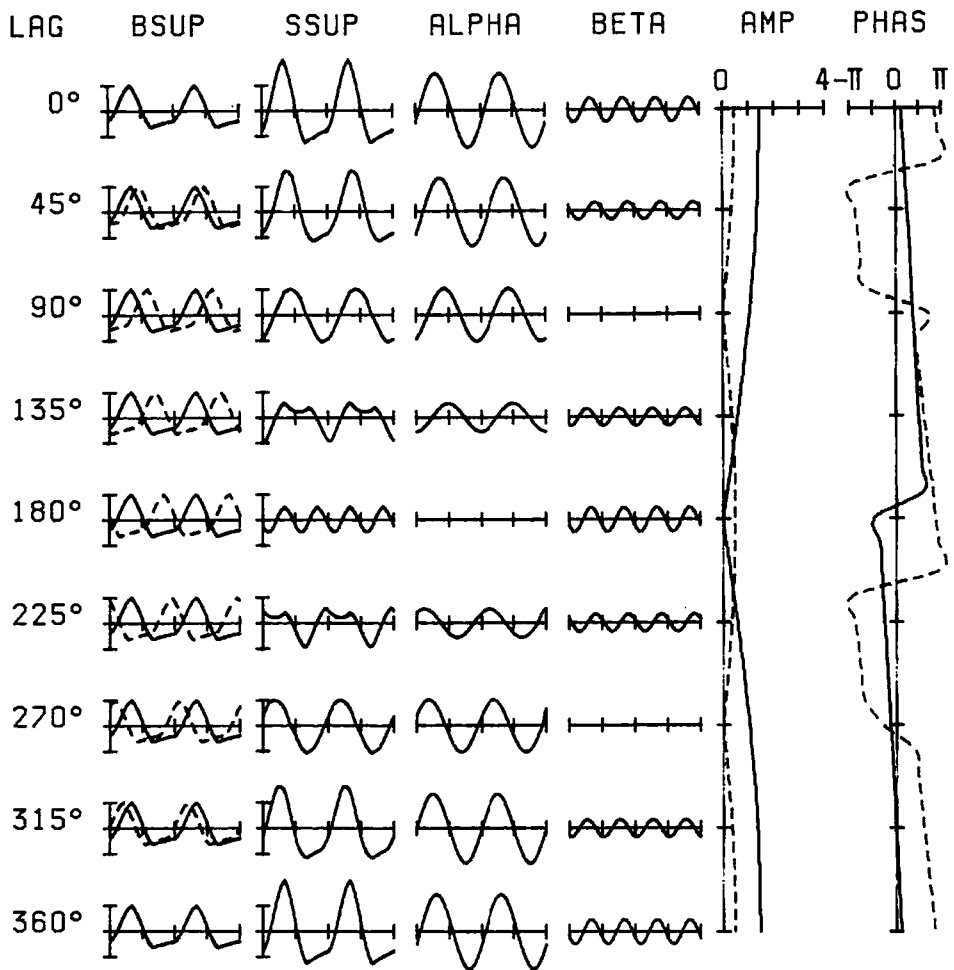


Fig. 5d. $a_4/a_1=1/1$ and $\delta_4-\delta_1=T/3$.

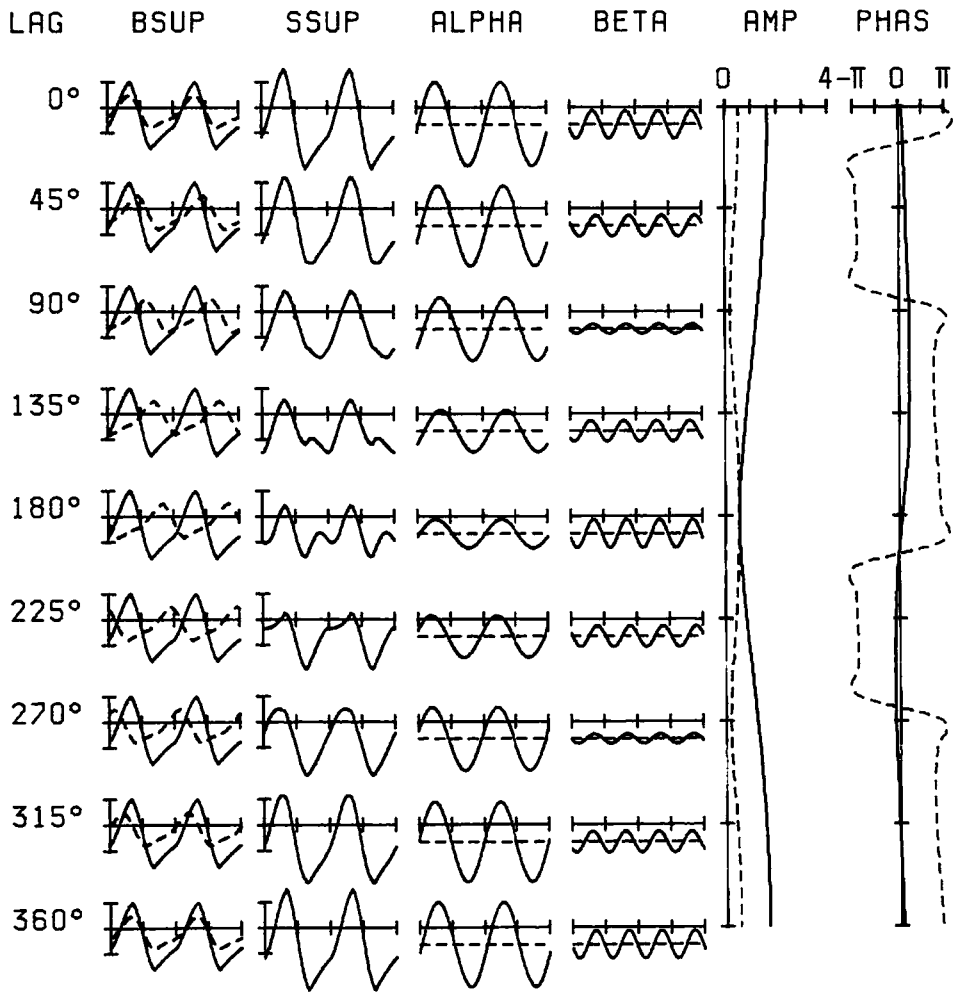


Fig.5e. $a_4/a_1=1/2$ and $\delta_4-\delta_1=T/3$ but $m_1/m_2=1.0/0.5$.

plain the generation of both waves by use of only one thalamic burst train.

Hobson (1981) proposed a reciprocal interaction model of sleep-cycle control using mutually connected units with respective positive and negative self-feedbacks²³. The model could generate "Lofka-Volterra" oscillation. The frequency of oscillation is known to be determined by long-lasting hyperpolarization after burst firing. In the present model, the thalamic have similar connections, which can also generate Lofka-Volterra oscillation but with a long-lasting hyperpolarization which is not produced by inhibitory inputs but by an intrinsic increase in membrane permeability of K^+ controlled by certain neurotransmitters (Roy et al., 1984)²⁴.

There are other neuro-synaptic circuits showing temporal rhythmic activities within the brain, e.g., the septo-hippocampal system (Leung, 1981)²⁵, the striato-motor system (Rolls et al., 1980)²⁶. For the further analysis of the rhythmic waves relating to the human behavior, the interaction among these multiple generators with different rhythmic patterns must be applied to the model.

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References

1. Lashley, K.S. (1951) The problem of serial order in behavior. In L.P. Jeffress (ed.) Cerebral mechanisms of behavior: The Hixon Symposium, Wiley: New York.
2. Byers, P. (1979) Biological rhythms as information channels in interpersonal communication behavior. In S. Weitz (ed.) Nonverbal communication (second ed.), Oxford Univ. Press: New York.
3. Shaffer, L.H. (1982) Rhythm and timing in skill. Psychol. Rev. 89, 109-122.
4. Bouyer, J.J., C. Tilquin, and A. Rougeul (1983) Thalamic rhythms in cat during quiet wakefulness and immobility. Electroenceph Clin. Neurophysiol. 55, 180-187.
5. Semba, K. and B.R. Komisaruk (1984) Neural substrates of two different rhythmical vibrissal movements in the rat. Neuroscience 12, 761-774.
6. Wood, C.C., D. Cohen, B.N. Cuffin, M. Yarita, and T. Allison (1985) Electrical sources in human somatosensory cortex: identification by combined magnetic and potential recordings. Science 227, 1051-1053.
7. Deecke, L., J. Boshert, H. Weinberg, and P. Brickett (1983) Magnetic fields of the human brain (Bereitschaftsmagnetfeld) preceding voluntary foot and toe movements. Exp. Brain Res. 52, 81-83.
8. Pfurtscheller, G. (1981) Central beta rhythm during sensori-

- motor activities in man. *Electroenceph. Clin. Neurophysiol.* 51, 253-264.
9. Papakostoroupos, D. (1980) The Bereitschaftspotential in left and right-handed subjects. *Prog. Brain Res.* 54, 742-747.
 10. Storm van Leeuwen, W. and A. Kamp (1973) Occurrence of beta bursts in frontal cortex during CNV paradigm. *Electroenceph. Clin. Neurophysiol.* S33, 95-97.
 11. Petsche, H., H. Pockberger, and P. Pappelsberger (1984) On the search for the sources of electroencephalogram. *Neuroscience* 11, 1-27.
 12. Van Rotterdam, A. and F.H. Lopes da Silva (1982) A model of the spatio-temporal characteristics of the alpha rhythm. *Bull. Math. Biol.* 44, 283-305.
 13. Freeman, W.J. (1980) A software lens for image reconstruction of the EEG. *Prog. Brain Res.* 54, 123-127.
 14. Nunetz, P.L. (1981) A study of origins of the time dependencies of scalp EEG: I - theoretical basis. *IEEE Trans. BME-28*, 271-280.
 15. Mitzdorf, U. (1985) Current source density method and application in cat cerebral cortex: investigation of evoked potentials and EEG phenomena. *Physiol. Rev.* 65, 37-100.
 16. Itoh, K. (1984) A neuro-synaptic model of bilateral interaction in auditory nervous system. *Trans. IECE Jap.* E67, 12-18.
 17. Striade, M. and M. Deschenes (1984) The thalamus as a neuronal oscillator. *Brain Res. Rev.* 8, 1-63.
 18. Itoh, K. (1982) Analysis of speech related rhythmic EEG activities in normal verbal behavior. *Proc. World Cong. Med. Physics and Biomed. Eng.* 18, 13.
 19. Grözinger, B., H.H. Kornhuber, J. Kriebel (1977) Human cerebral potentials preceding speech production, phonation, and movements of the mouth and tongue, with reference to respiratory and extracerebral potentials. *Prog. Clin. Neurophysiol.* 3, 87-103.
 20. Schoppenhorst, M., F. Brauer, G. Freund, and S.T. Kubicki (1983) Coherence estimates in determining central alpha and mu activities. In G. Pfurtscheller, P. Buser, and F.H. Lopes da Silva (eds.) *Rhythmic EEG activities and cortical functioning*, Elsevier: Amsterdam.
 21. Jahnsen, H. and R. Llinas (1984) Electrophysiological properties of guinea pig thalamic neurones: an vitro study. *J. physiol.* 349, 205-226.
 22. Pfurtscheller, G. and A. Aranibar (1980) Voluntary movement ERD: normative studies. In G. Pfurtscheller, P. Buser, and F.H. Lopes da Silva (eds.) *Rhythmic EEG activities and cortical functioning*, Elsevier: Amsterdam.
 23. Hobson, J.A. (1981) The reciprocal interaction model of sleep cycle control: a discussion in the light of Giuseppe Moruzzi's concepts. In O. Pompeiano and C.A. Marsan (eds.) *Brain mechanisms and perceptual awareness*, Raven Press: New York.
 24. Roy, J.P., M. Clerc, M. Striade, and M. Deschenes (1984) Electrophysiology of neurons of lateral thalamic nuclei in cat: mechanisms of long-lasting hyperpolarizations. *J. Neurophysiol.* 51, 1220-1225.
 25. Leung, L.S. (1981) Model of behavioral modulation of the hippocampal CA1 region of the rat. *Brain Res.* 205, 194-199.

26. Rolls, E.T., S.J. Thorpe, M. Boytim, I. Szabo, and D.I. Perrett (1984) Responses of striatal neurons in the behaving monkey. 3. Effects of iontophoretically applied dopamine on normal responsiveness. *Neuroscience* 12, 1201-1212.
27. Itoh, K. (1985) Simulated rhythmic EEG activities in a neuro-synaptic model of thalamo-cortical system. *Proc. XIV ICMBE/VII ICMP* (in press).