

Are cognitive processes manifested in event-related gamma, alpha, theta and delta oscillations in the EEG?

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Abstract

Gamma oscillations, now widely regarded as functionally relevant signals of the brain, illustrate that the concept of event-related oscillations bridges the gap between single neurons and neural assemblies. Taking this concept further, we review experiments concerning oscillatory responses to events (in the alpha, theta and delta ranges) as possible correlates of sensory and cognitive functions. It is argued that selectively distributed delta, theta, alpha and gamma oscillatory systems act as resonant communication networks through large populations of neurons, with functional relations to memory and integrative functions. © 1999 Elsevier Science Ireland Ltd. All rights reserved

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‘During the ‘Decade of the Brain’ brain science is coming to terms with its ultimate problem: understanding the mechanisms by which the immense number of neurons in the human brain interact to produce the higher cognitive functions’ [18]. One of the candidate mechanisms, oscillatory neuroelectric activity has recently attracted much interest, mainly focused on synchronous gamma activity in spatially distributed cells. The present review has several aims, namely: (1) to survey functionally related findings in oscillatory brain activity between 0.5 and 100 Hz, i.e. by surpassing approaches centered on the gamma band. In particular, the alpha band, so far mostly neglected, deserves more interest; (2) to emphasize that oscillatory networks are selectively distributed and functionally related to sensory as well as cognitive processes. This view might help to reconsider several controversies; (3) to propose a new approach to the question of general communication proper-

ties in the brain. It is suggested that complex stimuli elicit superimposed oscillations of different frequencies, possibly serving as letters in an alphabet [4]; (4) to stress similarities between oscillations at the levels of single neurons, field potentials, electroencephalography (EEG) and magnetoencephalography (MEG).

Event-related oscillations (with a defined temporal relation to a sensory or cognitive event) are classified as ‘evoked’ or ‘induced’ oscillations (the former being phase-locked to the event, the latter not). A further axis of classification discerns these oscillations according to the ‘natural frequencies’ of the brain (alpha: 8–13 Hz, theta: 3.5–7 Hz, delta: 0.5–3.5 Hz and gamma: 30–70 Hz). The present paper will focus on evoked oscillations with only some examples of induced oscillations.

As for event-related gamma oscillations, the most prominent examples are oscillatory responses in the 40–60 Hz range occurring in synchrony within a functional column in the cat visual cortex [15,20]. Such induced oscillations have been suggested as a possible mechanism of feature

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linking in relation to the ‘binding problem’. This theory, however, does not fully explain the ‘ubiquity of gamma rhythms’ [13,32]. In this respect, it may be helpful to consider further empirical findings (partly going back to Adrian [1]), roughly classified into sensory (or obligatory) versus cognitive gamma responses. Concerning the former: (1) auditory and visual gamma responses are selectively distributed in different cortical and subcortical structures. They are phase-locked stable components of evoked potentials (EPs) in cortex, hippocampus, brain stem and cerebellum of cats occurring 100 ms after the sensory stimulation with a second window of approximately 300 ms latency [2,4,32]. (2) A phase-locked gamma oscillation is contained in the human auditory and visual response [2]. Several cognitive paradigms showed that the 40 Hz response in the first 100 ms after stimulation has a sensory origin, being independent of cognitive tasks [21]. The auditory MEG gamma response is similar to human EEG responses with a close relationship to the middle latency auditory evoked response [8,30]. (3) An early phase locked 40 Hz response was recorded in visceral ganglia of *Helix pomatia* using electrical stimulation [34]. For light-induced gamma responses in arthropods, see [22].

Several investigations dealt with cognitive processes related to gamma responses, some of them based on measuring the P300 wave. This positive deflection typically occurs in human event-related potentials (ERPs) in response to ‘oddball’ stimuli or omitted stimuli interspersed as ‘targets’ into a series of standard stimuli: (1) A 40 Hz response superimposed to a slow wave of 4 Hz (P300–40 Hz component) has been recorded as an induced oscillation (latency approximately 300 ms) in the cat hippocampus, reticular formation and cortex (in response to omitted auditory stimuli as targets) [9]. Preliminary data indicate similar P300–40 Hz responses to ‘oddball’ stimuli in humans [6]. However, a suppression of 40-Hz activity after target stimuli has also been reported [16]. (2) Attention-related 40 Hz responses were observed in humans (with frontal and central maxima) [37]. (3) Human frontal EEG gamma activity has been reported to increase by 50% during visual perception of reversible or ambiguous figures [11]. (4) The spatiotemporal magnetic field pattern of gamma band activity has been interpreted as a coherent rostrocaudal ‘sweep of activity’ [26].

This wide spectrum of experimental data is in accordance with a hypothetical ‘selectively distributed parallel processing gamma system’. Gamma oscillations might be important building-blocks of electrical activity of the brain, related to multiple functions (observable even in isolated invertebrate ganglia in response to electrical stimulation [34]). They may (1) occur in different and distant structures and (2) show phase locking, time locking or weak time locking [38]. Gamma oscillations possibly represent a universal code of central nervous system communication [3,4]. This view might also serve as a synthesis overcoming controversies in earlier reports.

As to the alpha range, a ‘renaissance of functional alphas’ is under way. The interpretation of alpha rhythms as an ‘idling rhythm’ rests on observations such as blocking of ‘spontaneous’ occipital alpha oscillations upon opening of the eyes or blocking of central mu rhythm upon movement onset [25] (‘event-related desynchronization’ [31]). A reverse effect (increase of mu rhythms during visual information processing, ‘event-related synchronization’ [24,31]) has also been reported. However, co-existing with these well-known phenomena and in relationship with Adrian’s ‘evoked alpha’ [1], several forms of ‘functional alpha’ have been observed during sensory and cognitive processes [3–5,7]: (1) in the auditory and visual pathways in cats, adequate stimuli elicit alpha responses (damped 10 Hz oscillations of approximately 300 ms), which are visible without filtering [2–4] (for confirmation by wavelet analysis, see [3]). Human alpha responses similar to those in the cat brain were also described [4]. Multiple sclerosis patients with optic neuritis show reduced alpha responses to visual stimuli, in consistence with a sensory function to the alpha response [3]. (2) Thalamo-cortical circuits are not unique in generating alpha responses. Hippocampal and reticular 10 Hz responses are relatively modality-independent, hinting at possible supra-modal functions. (3) Cognitive targets significantly influence the alpha responses in P300: using an oddball paradigm, prolonged event-related alpha oscillations up to 400 ms were observed [3,4]. (4) Memory related event-related alpha oscillations can be observed in well-trained subjects 1 s before an expected target. New results [5,23] demonstrate that alpha activity is strongly correlated with working memory and probably with long-term memory engrams. (5) Alpha activity is not unique to mammals: spontaneous and electrically evoked 10 Hz oscillations in isolated ganglia of *Helix pomatia* and *Aplysia* [4,12,34] serve as an example.

In parallel to the gamma band, these results are consistent with a hypothetical selectively distributed alpha system. Event-related alpha oscillations may facilitate association mechanisms in the following way: when a sensory or cognitive input elicits ‘10 Hz wave-trains’ in several brain structures then it can be expected that this general activity can serve as a resonating signal.

The co-existence of evoked alpha oscillations with alpha-blocking and event-related desynchronization [31] hints at multiple processes being reflected in alpha oscillations. An example of such co-existence are earlier measurements where high amplitude spontaneous alpha activity coincided with alpha-blocking while low amplitude alpha preceded EPs of high amplitude [3].

Again, parallel observations at the cellular level are noteworthy: evoked oscillations in the 8–10 Hz frequency range in visual cortex neurons upon visual stimulation suggest a relation to scalp-recordable alpha responses [14,35]. The sum of these observations permits a tentative interpretation of alpha as a functional and communicative signal with multiple functions. This interpretation of 10 Hz oscillations

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

Experimental data suggests that event-related theta oscillations are related to cognitive processing and cortico-hippocampal interaction [4,23,28]: (1) theta is the most stable component of the cat P300-like response [3,4]. (2) Bimodal sensory stimulation induces large increases in frontal theta response, thus demonstrating that complex events require frontal processing [4]. (3) Event-related theta oscillations are prolonged and/or have a second time window approximately 300 ms after target stimuli in oddball experiments. Prolongation of theta is interpreted as being correlated with selective attention [10]. (4) Event-related theta oscillations are also observed after an inadequate stimulation (in contrast with event-related alpha oscillations). Thus, the associative character of event-related theta oscillations might be more pronounced than for higher frequency event-related oscillations [4]. (5) 'Orienting' - a coordinated response indicating alertness, arousal or readiness, is related to theta oscillations during exploration, searching and motor behavior [3,4].

Thus, event-related theta oscillations can be considered as important building-blocks of functional signaling.

As to delta oscillations, experimental data hint at functional correlates roughly similar to those mentioned for theta oscillations, i.e. mainly in cognitive processing: (1) delta responses to visual oddballs are largest in parietal locations, whereas for auditory target stimuli the highest delta response amplitudes are observed in central and frontal areas [3,4,33]. (2) The delta response is considerably increased during oddball experiments. Accordingly, it was concluded that the delta response is related to signal detection and decision making [10]. (3) In response to stimuli at the hearing threshold delta oscillations are observed in human subjects, in consistence with the hypothetical relation to signal detection and decision making [4]. (4) A waveform observed in response to deviant stimuli not attended by the subject, the mismatch negativity [29] is shaped by a delayed delta response superimposed with a theta response. (5) Phase-locked delta responses are observed in the sleeping cat and human brain [2].

The topographic distribution of such delta oscillations is again consistent with a distributed response system.

It is suggested that event-related oscillations might help to understand Fessard's 'transfer functions of multiunit homogeneous messages during their progression through neuronal networks' [17]. The transfer function (mathematically represented in the frequency characteristics [3]) describes the ability of a network to increase or impede transmission of signals in resonant frequency channels. Empirical findings of similar frequency characteristics in distributed networks imply the existence of such general transfer functions [3,4]. Further experiments are needed to find such subsystems tuned in 'common frequency modes'. The results reviewed above, however, hint at function-

related frequency selectivities in selectively distributed oscillatory networks. According to models, cognitive and memory processes involve the formation of specific templates as selectively distributed processing in anatomically differentiated localization's [19,27]. Thus, analysis of the hypothetical distributed oscillatory systems may lead to fundamental functional mapping of the brain, complementary to morphological studies.

In conclusion, results from several laboratories imply that it is impossible to assign a single function to a given type of oscillatory activity. These oscillations have multifold functions and may act as universal operators or codes. Besides frequency and site of oscillations, several other parameters are dependent on specific functions, namely amplitude enhancement, time locking, phase locking, delay and duration of oscillations. Our hypothesis is that complex and integrative brain functions are manifested in the superposition of several oscillations. In reply to Stryker's question 'Is grandmother an oscillation?' [36], we suggest that complex stimuli (such as a picture of 'grandmother') elicit multiple oscillations (in delta, theta, alpha and gamma ranges) in selectively distributed networks.

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