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A review of theta oscillation and its functional correlates

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A REVIEW OF THETA OSCILLATION AND ITS FUNCTIONAL CORRELATES

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**Abstract**

Theta is an extensively studied oscillation of the nervous system, but there is only a paucity of reviews on the subject. A review of specifically the cognitive-affective correlates of the theta oscillation is currently unavailable. The present review aims to fill this gap. This review shows that theta-based hippocampal binding brings together the environmentally triggered multimodal elements of episodes or scenes, make multimodal sensory/perceptual and motor processing, facilitatory and inhibitory attention, navigation and episodic memory possible. Hippocampus is centrally located in a selectively distributed theta network. The association between different sources of information and between oscillations of different frequency bands, the connectivity in the theta network and coherences between selected brain areas contribute to the synchrony and hypersynchrony in the human brain. The densely associated pool of information that are represented by the theta oscillation travel over this densely interconnected, and highly synchronized hippocampal-cortical system. In this network, the theta-based cortico-hippocampal interplay produces many cognitive-affective processes, chief one being memory with its encoding, consolidation and retrieval stages. The present review does not make a comparative evaluation of the theta over the evolutionary spectrum; it is focused on the hippocampal-cortical system, and does not consider the subcortical and brain stem structures of the theta network; and among the many different types of memory, treats specifically the episodic memory. Future theta reviews may choose to also treat these issues. Providing a concise exposition of the currently available empirical findings and theoretical formulations, this state-of-the art that review may stimulate research, make new conclusions available, and lead to creative syntheses, allowing a detailed understanding of the contribution of the theta oscillation to the whole-brain work and to the human mind.

**Keywords:** Theta oscillation, hippocampus, cortico-hippocampal interplay, connectivity, coherence, hypersynchrony, cognitive-affective correlates, memory

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*The necessity of a review paper on the theta oscillation was pointed out by the lately deceased Prof. Dr. Erol Başar. The choice of the subjects and their logical succession was our joint project. This was the last manuscript that Prof. Başar planned and, in his last days, evaluated.*

## **1. Introduction**

The goal of this article is to present a state-of-the-art review outlining the critical developments that have contributed to our current understanding of theta oscillation and its cognitive-affective correlates. The nature and the functional correlates of theta oscillations are currently described by a vast body of empirical findings and alternative theoretical formulations. The present paper is an attempt to synthesize and provide a concise summary of the empirical and theoretical studies, with the aim of stimulating research, new conclusions, and creative syntheses.

### **1.1. The Advent of Oscillatory Dynamics**

The history of the brain oscillations dates back to 1929, when Hans Berger recorded the spontaneous “Berger wave” (alpha wave) in humans. A high-frequency (beta) wave was spontaneously recorded when eyes were opened; in this state, the alpha wave was blocked. Berger (1929) concluded that the alpha wave represents relaxed wakefulness, and beta waves represent an attentive state or attentive wakefulness. Subsequently, Adrian (1942) identified gamma oscillations, this time in response to stimulation. Over the years that followed, the interest of the scientific community in brain oscillations fluctuated (for a review, see Karakaş and Barry, 2017). Nonetheless, by the 1990s, research had already been conducted on the neuro-oscillatory responses *in vitro* tissue of visceral organs (e.g., stomach, colon, vasculature) (Başar, 1976; Başar and Weiss, 1981), and *in vivo* brain tissue (Eckhorn, Bauer, Jordan, Brosch, Kruse, Munk and Reitboeck, 1988; Gray and Singer, 1989;

Jahnsen and Llinás, 1984). Direct recordings were made from the nervous system of invertebrates (e.g., *Helix pomatia*) and lower vertebrates (goldfish and ray), while deep recordings were obtained from higher vertebrates (e.g., cats, rats, and monkeys) (for reviews, see Başar, 1980, 2011; Green and Arduini, 1954; Lopes da Silva, 1992. Also see Dudkin, Glezer, Gauselman and Panin, 1978). In the beginning, studies on humans were largely on the oscillatory potentials obtained in response to sensory stimuli (for a review, see Başar, 1980; Green and Arduini, 1954; also see Galambos, Makeig and Talmachoff, 1981).

Electroencephalography was acknowledged as a scientific phenomenon at a forum in 1937 (Karakaş and Barry, 2017). At the end of the 20<sup>th</sup> century, Mountcastle (1992) stated: “Rather suddenly, a paradigm shift is upon us, for the proposition that slow wave events are active ingredients for signal transmission stands as a testable hypothesis.” The ensuing decades witnessed the accumulation of an immense amount of data on neuro-oscillatory dynamics (Bernat, Malone, Williams, Patrick and Iacono, 2007; Besle, Schevon, Mehta, Lakatos, Goodman, McKhann et al., 2011; Cravo, Rohenkohl, Wyart and Nobre, 2013; Gomez-Ramirez, Kelly, Molholm, Sehatpour, Schwartz and Foxe, 2011; Henry and Obleser, 2012; Ishii, Canuet, Herdman, Gunji, Iwase, Takahashi et al., 2009; Jones, Porjesz, Chorlian, Rangaswamy, Kamarajan, Panabhapillai et al., 2006; Kösem, Gramfort and Wassenhove, 2014; Stefanics, Hangya, Hernádi, Winkler, Lakatos and Ulbert, 2010). Brain oscillations became a conceptual tool for understanding cognitive-affective processes (for reviews, see Karakaş and Başar, 2006a, 2006b; Mountcastle, 1998). The transfer of environmental stimuli (presentations) to the cognitive-affective processes (re-presentations) was explained through frequency-encoding mechanisms (Pribram, 1980). These findings led to generalizations; the experimentally tested generalizations then led to principles that describe the way the universe operates, and these eventually led to theories, which explain why the universe operates as it does (Başar 1976, 1980, 1998, 1999, 2011; for a review, see Karakaş and Başar, 2006b).

Using various frequency decomposition techniques, oscillatory components and their subcomponents were identified. The major oscillatory components and their conventionally accepted frequency ranges were defined as follows: delta (0.5-3.5 Hz), theta (4.0-7.5 Hz), alpha (8.0-13.5 Hz), beta (14.0-29.0 Hz), and gamma (30.0-70.0 Hz). Four of these components (delta, alpha, beta, and gamma), and their functional correlates were extensively addressed in different review articles and/or treated in some critical papers (Berger, 1929; Adrian, 1942; Başar, Özesmi and Urgan, 1973; Demiralp, Yordanova, Kolev, Ademoğlu, Devrim and Samar, 1999; Güntekin and Başar, 2007, 2009, 2010, 2014; Karakaş and Başar, 1998. For recent reviews, see Başar, 2012, 2013; Başar and Güntekin, 2012, 2013; Buzsaki and Wang, 2012; Güntekin and Başar, 2014, 2016; Harmony, 2013; Karakaş, Başar-Eroğlu, Özesmi, Kafadar and Erzenin, 2001; Klimesch, 2012; Knyazev, 2012).

### **1.2. The Need for a Review Paper on Theta Oscillation**

The first hippocampal recordings of theta band activity were obtained from rabbits by Jung and Kornmüller (1938). Theta was acknowledged to be the largest, best synchronized, and most sinusoidal rhythm of the brain that is mainly generated from the cells of the hippocampal formation (Kowalczyk, Bocian and Konopacki, 2013; Kowalczyk, Caban and Bocian, 2013). Surprisingly, there are only a few review articles on theta oscillation. The earliest articles are by Green and Arduini (1954) and Stumpf (1965). The first article discusses studies on the electrophysiology of theta response; describes the basic properties of the hippocampal theta in cats, rats, rabbits, and monkeys; and considers the relevance of the hippocampal theta to the arousal response. The second article discusses the effects of pharmacological agents on hippocampal electrical activity. At this early period, functional correlates of theta oscillation had not aroused the interest of the scientific community (Schacter, 1977).

By the 20<sup>th</sup> century, Klimesch (1999) reviewed the findings largely obtained by his research group on memory-related oscillations in humans, and concluded that event-related theta synchronization represents encoding of new information, and

event-related upper alpha desynchronization represents semantic memory. The author suggested that hippocampal-cortical feedback loops underlie the event-related theta, and that thalamocortical feedback loops underlie the event-related alpha. In a later review, Klimesch and colleagues (Klimesch, Freunberger, Sauseng and Gruber, 2008) proposed the following hypothesis: theta and upper alpha oscillations reflect top-down processing whereby working memory (WM) and long-term memory access and manipulate stored information. A subsequent review (Colgin, 2013) focused on the neuronal mechanisms underlying theta oscillations in lower mammals, specifically rats.

To our knowledge, an up-to-date review of the various cognitive-affective correlates of the theta oscillation is presently lacking. The present article aims to present a concise exposition of theta oscillation and its functional correlates, particularly from a cognitive neuroscience perspective.

## **2. Hippocampal Theta and Its Functional Correlates**

The pioneers of studies on the cognitive-affective correlates of the hippocampus and the relationship between cognitive functions and the theta rhythm are Grastyan and colleagues. They showed the relevance of theta oscillation to the development of conditioned reflexes (Grastyan, Lissak, Madarasz and Donhoffer, 1959) and to homeostatic regulation of motivation (Grastyani, Karmos, Vereczkey and Kellenyi, 1966). Other studies reported the cognitive-affective correlates of hippocampal theta in instrumental conditioning (Aleksanov, Vainstein and Preobrashenskaya, 1986), delayed conditional reflexes (Karmos and Grastyan, 1962), orientation reaction (Karmos, Grastyan, Losoczy, Vereczkey and Grosz, 1965; Sokolov, 1963), appetitive and aversive conditioning (Buzsaki, Haubenreiser, Grastyan, Czopf and Kellenyi, 1981).

By the 20<sup>th</sup> century, theta had become the most studied hippocampal rhythm (for a review, see O'Keefe, 2007; Miller, 1991a and c). The theta oscillation corresponding to spontaneous activity in the electroencephalogram (EEG) resonates upon

stimulation. Sensory stimuli trigger evoked oscillations (EOs), while cognitive-affective stimuli produce event-related oscillations (EROs). The following decades were focused on assessing the effect of cognitive-affective manipulations on theta band oscillations in EEG, EOs and ERPs. The text below provides a concise exposition of the findings and the theoretical formulations for the hippocampal theta and the selectively distributed theta network. Figure 1 is a simplified representation of brain's theta network and the role that it plays in neurocognitive functions.

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Please insert Figure 1 about here.

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### **2.1. Theta in Sensory/Perceptual and Motor Processing**

*Sensory/Perceptual Processing.* These were the earliest functional correlates of the hippocampus to be studied. The initial studies noted prolonged hippocampal activity following click stimulation, nociceptive stimulation, electrical stimulation of the sciatic nerve and the optic nerve (Gerard, Marshall and Saul, 1936; Liberson and Cadilhaci, 1953; Jung and Kornmüller, 1938; MacLean, Horwitz and Robinson, 1952). In an early study, Başar and Özesmi (1972) demonstrated auditory EOs in freely moving cats via electrodes that were implanted in the right dorsal hippocampus. Later studies with multiple intracranial electrodes displayed theta responses in the auditory EOs from the various hippocampal layers (CA1, CA3 and CA4), from the structures on the auditory pathway, and the reticular formation (Başar, Gönder, Özesmi and Ugan, 1975a; Başar and Ugan, 1973; Başar-Eroğlu, Başar and Schmielau, 1991; Demiralp, Başar-Eroğlu, Rahn and Başar, 1994). The relevance of the theta response to sensory processing was also demonstrated in simple organisms such as *Helix pomatia*. Odorous stimulation evoked a prolonged theta response in the pedal ganglion of this species (Schütt, Bullock and Başar, 2000).

*Motor Processing.* The background research on motoric theta dates back to the 1930-1950 period, when studies were mainly conducted on rodents with implanted

intracranial electrodes (for a review, see Green and Arduini, 1954). The two types of response-related hippocampal theta were discovered during this period. The first type of motoric theta occurs in active periods, when rodents are engaged in voluntary movements such as walking, running, jumping, bar-pressing or exploratory sniffing. Theta associated with voluntary movement is very strong and can continue for many seconds, hence the name “rhythmic slow activity” (RSA). The second type of motoric theta occurs in inactive periods, when rodents groom, eat or sleep. In these functional states, RSA is replaced by large and irregular theta waves (LIR) (Vanderwolf, 1969).

There are two types of RSAs (Kramis, Vanderwolf and Bland, 1975). Type 1 RSA has a frequency of 8 Hz in the rat and 4-6 Hz in the cat and rabbit. It is not affected by Ach antagonists and is atropine-resistant. Behaviorally, it occurs during active states, as in voluntary responding. Type 1 theta originates from extra-hippocampal areas or is the result of the interaction of several neurotransmitters at receptor sites (Konopacki, Bland and Roth, 1988).

Type 2 RSA has a frequency between 4 and 7 Hz. It is observed in rabbits, cats, and guinea pigs but rarely in rats (Robinson, 1980; Sainsbury, Heynen and Montoya, 1987). It is blocked by acetylcholine (Ach) antagonists, and is atropine-sensitive. Evidence for cholinergically (muscarine) mediated Type 2 theta has also been obtained using *in vitro* slices of the rabbit hippocampus (Konopacki, 1996; Konopacki, 1998; Konopacki, Maciver, Bland and Roth, 1987). Behaviorally, Type 2 RSA occurs during inactive states, as in extended periods of immobility (freezing), motionless alertness, and rapid eye movement (REM) sleep. It also occurs when there is an intention to move or a preparation for movement: in these functional states, theta is of a brief duration (Robinson, 1980; Sainsbury, Heynen and Montoya, 1987; Whishaw and Vanderwolf, 1973). In macaques and squirrel monkeys, Type 2 RSA also occurs under anesthesia (Stewart and Fox, 1990).

Schütt, Başar, and Bullock (1992) found Ach-induced theta response in the visceral ganglion of *Helix pomatia*. The Ach effect was robust and produced a long-lasting theta oscillation (4-6 min). Only a transitory effect was observed in all the other bands. Konopacki and colleagues (Konopacki, 1996; Konopacki, 1998; Konopacki, Maciver, Bland and Roth, 1987) found theta-like oscillations in the rabbit by performing bath-perfusion of hippocampal *in vitro* slices with cholinergic agonists; the oscillation was antagonized with atropine. Generation of the theta rhythm was described by Vinogradova (2001) during extracellular recording of neuronal activity in the anesthetized rabbit. Subsequent research demonstrated that the cholinergically induced *in vitro* theta-like activity replicated the physiological and pharmacological properties of the theta rhythm observed *in vivo* (Konopacki, Golebiewski, Eckersdorf, Kowalczyk and Bocian, 2000; Kowalczyk, Bocian and Konopacki, 2013). A secondary advantage of these studies was that they provided justification for using *in vitro* slices when investigating theta oscillation in intact organisms.

The association between Type 1 RSA and voluntary movement develops via a chain of events (Ledberg and Robbe, 2011). When rats run at a certain speed (50-100 cm/s), their heads show vertical oscillations. The locomotor dynamics of the voluntary movement interact with the theta rhythm (Type 1 RSA) of the hippocampus (Vanderwolf, 1969). Theta oscillations are a function of the running speed: as speed increases, theta frequencies increase within the 6.5-9 Hz theta range. There is also a phase relationship between the input from the head oscillations and hippocampal theta such that the amplitude of the theta becomes greatest when the input from the head oscillation is in phase with the hippocampal theta. Thus, there is a positive correlation between running speed (or head oscillations) and theta. The interaction between locomotor dynamics and hippocampal theta makes the latter stronger and faster.

On the basis of the previously described information, theta oscillation is involved with both sensory/perceptual and motor processing. Early work on cat hippocampi

showed that experimental manipulations produced similar theta increases in CA3 (and CA4) and the motor cortex (Başar, Demir, Gönder and Urgan, 1979; Başar and Urgan, 1973; Başar-Eroğlu, Başar and Schmielau, 1991; Demiralp, Başar-Eroğlu, Rahn and Başar, 1994). The close involvement of hippocampal theta with not only multimodal sensory/perceptual processing but also motor processing led to the idea that the theta oscillation of the hippocampus is responsible for multimodal sensorimotor integration (Vanderwolf, 1969).

*A Clinical Model.* Alzheimer's disease (AD) starts with short-term (recent) memory impairment; at this stage, sensorimotor functions are spared (Goedert and Spillantini, 2006; Kumar and Singh, 2015). Theta oscillatory activity is present in the primary and secondary sensory areas and the motor areas, but the amplitudes are much higher than those in healthy participants (Ferreri, Pauri, Pasqualetti, Fini, Dal Forno and Rossini, 2003). The theta response over the occipito-parietal area is also higher (Yener and Başar, 2013; Yener, Güntekin, Öviz and Başar, 2007; Yener, Güntekin, Tülay and Başar, 2009). The higher-than-normal theta amplitudes in the ventral, occipitotemporal "what" pathway (object perception), and in the dorsal, occipitoparietal "where" pathway (visuospatial perception) (Ungerleider and Posternak, 2004; Ungerleider and Mishkin, 1982) suggest that AD patients compensate for their memory problems by a hyperactive sensory-motor system (Yener and Başar, 2013).

## **2.2. Theta in Attentional Processing**

According to the fields of cognitive psychology and cognitive neuropsychology (Banich and Compton, 2011; Goldstein, 2011; Richard, Frackowiak, Friston, Raymond, Price, Zeki, Ashburner and Penny, 2004), attention is a complex modulatory process that consists of interrelated subprocesses (Hoffman, 1990). Attention has a central place, and is the fastest growing research area in these scientific fields (Posner and Rothbart, 2007).

There are two general types of attention: passive and active. Passive attention is preattentive and preconscious (Näätänen, Paavilainen, Rinne and Alho, 2008). Active attention can be selective, focused, or sustained (vigilance). In selective attention, a relevant stimulus is selected among a multitude of stimuli. Focused attention is responsible for turning the focus of attention to the selected stimulus. Sustained attention or vigilance is responsible for focusing attention on a selected stimulus or stimulus pattern over an extended period of time (for reviews, see Driver, 2001; Oken, Salinsky and Elsas, 2006).

Two processes closely related to attention are the orientation reaction (OR) and arousal. The first one, OR, is an inbuilt reflex in humans and animals for producing an immediate response to even the slightest change in the environment (Sokolov, 1963). Passive attention, which is experimentally triggered by usually the passive oddball tasks (OB-p), is an involuntary OR response. One of the indices of involuntary OR is the mismatch negativity (MMN) event-related potential (ERP) component (Näätänen, Paavilainen, Rinne and Alho, 2008). Active attention, which is experimentally triggered by usually the active oddball tasks (OB-a), is a voluntary OR. Putative indices of active OR have been identified as the P3a or the novelty P3 component of P300 (Polich, 2007; Sokolov, 1990).

The second attention-related process, arousal, is represented by physiological activation and cortical responsiveness. Arousal is responsible for variations of attention (or consciousness) over the wakefulness-sleep spectrum. As the following section shows, theta oscillation plays a role in both the active and passive types of attention and the two attention-related processes, OR and arousal (for a review, see Karakaş and Başar, 2006a).

### **2.2.1. Theta in Wakeful Attention**

The relationship between the hippocampal theta and attention-related processes, arousal and OR, has been outlined in earlier studies. One early study by Vanderwolf (1969) demonstrated the co-occurrence of the theta rhythm with an autonomic

arousal response, piloerection. The review article by Green and Arduini (1954) showed that arousal is represented by an inverse relationship between the hippocampal theta and cortical representations of the arousal response (e.g., desynchronization). Inactivation, on the other hand, is represented by large, irregular theta waves (LIR) in the hippocampus, and slow waves in the cortex.

Kemp and Kaada (1975) found maximal hippocampal theta during tonic OR (as in fixed staring or visual searching). During phasic OR (as in reflexive head turning, stereotyped movement, or unidirectional locomotor activity), on the other hand, hippocampal theta is attenuated. These findings led to a modified explanation of the relationship between arousal and theta oscillation (Kemp and Kaada, 1975). According to this modification, hippocampal theta increase is positively correlated with the degree of arousal when it accompanies the fight-or-flight response. Habituation-induced arousal, such as in stereotyped movement or unidirectional locomotor activity, is negatively correlated with the hippocampal theta.

Later studies demonstrated OR-induced desynchronization in theta and the other oscillatory components (Barry, Steiner and De Blasio, 2012). A person's own name is a powerful source of OR. In participants with varying degrees of consciousness (vegetative state, minimal consciousness, and normal consciousness), strong theta and theta synchronization were displayed upon hearing one's own name (Fellinger, Klimesch, Schnakers, Perrin, Freunberger, Gruber, Laureys and Schabus, 2011).

Demonstration of the relationship between theta oscillation and attention was pioneered by Adey, Dunlop and Hendrix (1960). Attention was represented by theta oscillation at the dendritic layer of the hippocampal pyramidal cells (Radulovacki and Adey, 1965). A large body of the literature explains the relevance of the theta response to attentional processing through a complex set of cognitive processes whereby attention becomes focused on the task-relevant template in short-term memory (Başar-Eroğlu, Başar, Demiralp and Schürmann, 1992; Demiralp and Başar, 1992; Karakaş, 1997; Yordanova and Kolev, 1998; Klimesch, 1999). An example of

the relevance of the theta oscillation to focused attention is displayed during performance in the stimulus omission task. In this task, blocks of auditory stimuli are presented with fixed interstimulus intervals. In each block, there are four actual stimuli, and one omitted stimulus. Human participants are asked to focus attention on the successively presented auditory stimuli and, after the fourth stimulus, indicate the time point at which a fifth stimulus should have occurred.

In the stimulus omission task, expectancy (anticipation) of the fifth (omitted) stimulus triggers OR (Sokolov, 1963); OR, in turn, supports focused attention. This task has been employed in two companion studies, one on humans (with scalp electrodes) and another on cats (with embedded electrodes in the hippocampus) (Başar-Eroğlu and Başar, 1991; Demiralp and Başar, 1992; Demiralp, Başar-Eroğlu, Rahn and Başar, 1994). In both humans and cats, the fourth (last in the series) auditory stimulus and the ensuing omitted stimulus produced theta EOs. These findings demonstrate the role of the theta oscillation in focused attention and OR. The findings also support the critical role of the hippocampus in theta rhythmicity.

Posner and Rothbart (2007) asserted that variations in the theta response represent different types and degrees of attention. In a study on the event-related oscillations (EROs), Karakaş, Erzençin and Başar (2000) manipulated attention through a series of tasks that consisted of 1000-Hz deviant and 2000-Hz standard stimuli. In the active oddball task (OB-a) participants selected the deviant stimuli and counted them; this task basically requires selective attention. In the single-stimulus (SS) task, participants counted the targets; this simple task requires only focused attention. Stimuli of the passive oddball task (OB-p) were identical to those of the OB-a task. However, in OB-p, participants focused attention on an irrelevant task, being led to believe that this is the experimental task; the OB-p task triggers preattentive processing of the deviant stimulus.

The study by Karakaş, Erzençin and Başar (2000) showed that all three tasks trigger an early theta response that terminates before the P300 (P3b) ERP component.

Focused attention (SS task) and preattentive change detection (OB-p task) were represented by short-duration theta responses. Selective attention (OB-a task) was represented by a high-amplitude theta response that also had a long duration. These findings show that the theta response can represent different forms of attention through variations in amplitude and duration (Posner and Rothbart, 2007).

Attention-producing tasks produce two ERP components at the 200 ms poststimulus period. The OB-p task triggers preattentive processing, and this processing is represented by the N2a ERP component. The OB-a task triggers attentive processing, and this processing is represented by the N2b ERP component. The later N2b is elicited by input to an attended channel, and this ERP component represents selective attention (for a review, Patel and Azzam, 2005; Campbell and Colrain, 2002; Näätänen and Picton, 1986; Paavilainen, Cammann, Alho, Reinikainen, Sams and Näätänen, 1987; Perrin, Garcia-Larrea, Mauguere and Bastuji, 1999). The study by Karakaş, Erzen and Başar (2000) found that phases of the theta rhythm coincide with N2a, which represents preattentive processing (OB-p task); and N2b, which represents selective attention (OB-a task). These findings represent the multifunctional role of the theta response in attentive processing.

Focused and selective attention facilitates task-relevant perception, cognition, and response production (Anderson, Reder and Lebiere, 1996). However, attentive processing does not only involve facilitatory action. A simultaneously occurring action inhibits non-relevant or incompatible sensory/perceptual systems or incompatible responses (Hasher and Zacks, 1988; Frazier, Demaree and Youngstrom, 2004; Kamarajan, Porjesz, Jones, Choi, Chorlian, Padmanabhapillai, Rangaswamy, Stimus and Begleiter, 2004; Schweizer, Moosbrugger and Goldhammer, 2005; Neumann, 1996; Sainsbury, 1998; Vinogradova and Dudaeva, 1972). The inhibitory action thus contributes to a selectively heightened sensory/perceptual and/or motor processing.

The facilitatory and inhibitory aspects of attentional processing are displayed at both the cellular and the systems level. Hippocampal cells fire when the input is novel (facilitatory, incrementing effect), and they become habituated when stimulation is repetitive (inhibitory, decrementing effect) (Vinogradova, 1970, 1976; Vinogradova and Dudaeva, 1972). Extracellular recordings of neuronal activity show that theta oscillation is the mechanism that sustain the response to a selected stimulus, and simultaneously protect it against interference (Vinogradova, 2001). At the systems level, hippocampus and the structures in mainly the posterior brain usually have a facilitatory effect on information processing. Areas of the prefrontal cortex such as the anterior cingulate cortex, however, generally exercise an inhibitory effect (Herd, Banich and O'Reilly, 2006). This dual function is explained in the biased-competition model (Desimone and Duncan, 1995) as the suppression of neural activity to task-irrelevant stimuli (inhibition) and the biasing of neural activity to task-relevant stimuli (facilitation).

The winner of the 1988 award of the Society of Psychophysiological Research, Evgeny N. Sokolov (Graham, 1989), explains facilitatory and inhibitory attention within the context of the OR (Sokolov, 1990; Pribram, 1980; Başar, 2004). In this model, the hippocampus forms a neuronal model (a memory trace that the preceding stimulus repetitions have left in the nervous system), and matches this standard with each incoming stimulus. OR is triggered by a mismatch between the elaborated neuronal model and the incoming stimulus (novelty response; facilitatory effect). If the incoming stimulus matches the neural trace (showing that the stimulus is being repeated), the novelty detectors in the hippocampus become habituated (inhibitory effect), electrophysiological activation decreases, and the stimulus is behaviorally ignored (Sokolov, 1990; Kirvelis and Vanagas, 2014).

According to the previous studies, theta oscillation represents different forms of facilitatory attention, such as selective attention (OB-a task), focused attention (SS task, stimulus omission task), and preattention (OB-p task). Besides these facilitatory forms, theta oscillation also represents inhibitory attention. As the

following sections will show, the theta response is multifunctional not only with respect to different types of attention (Posner and Rothbart, 2007) but also with respect to disparate behavioral functions such as navigation, episodic memory, and stages of memory processing.

*A Clinical Model.* One of the symptoms of attention deficit hyperactivity disorder (ADHD) is inattention (American Psychiatric Association, 2013). By its symptomatology, ADHD serves as an efficient model for studying attentional processing.

The quantitative EEG (q-EEG) obtained in early childhood is characterized by slow waves in the delta and theta frequency ranges. In normally developing children that are around 7.5 years of age, slow oscillations are replaced by high-frequency oscillations (Barry, Clarke and Johnstone, 2003). In ADHD, however, these changes occur at around 10 years of age. Consistent with the maturational lag model (Kinsbourne, 1973), delta and theta dominated q-EEG patterns of 10 year-old ADHD children cease to exist, high-frequency oscillations emerge, and there is a spontaneous improvement in attentional processing (Erdoğan Bakar and Karakaş, submitted).

Even then ADHD cases can demonstrate aberrance of EEG oscillatory patterns that potentially serve as a lifespan biomarker of ADHD. According to the maturational deviance model (Klinkerfuss, Lange, Weinberg and O'Leary, 1965), adult ADHD is caused by abnormalities in central nervous system functioning. The abnormalities, characterized by an increased q-EEG theta at frontal and decreased beta and alpha at the temporal and parietal recording sites, are not considered normal in any age, and these are not likely to mature normally (Bresnahan and Barry, 2002; Clarke, Barry, McCarthy and Selikowitz, 2001; Hermens, Kohn, Clarke, Gordon and Williams, 2005). In adult ADHD participants, such a pattern is accompanied by inattention and disorders of executive functions that the prefrontal areas are responsible for (Makris, Buka, Biederman, Papadimitriou, Hodge, Valera, Brown, Bush, Monuteaux,

Caviness, Kennedy, Seidman and Kennedy, 2007; Barkley, 1997; Pennington and Ozonoff, 1996).

Taking into account the significance of theta oscillation to attentional processing, Lubar and colleagues (1991) combined the slow theta and fast beta that characterize ADHD in a theta-beta ratio (TBR). Presently, this ratio is used in routine clinical practice both as a prognostic criterion (Monastra, Lubar, Linden, VanDeusen, Green, Wing and Fenger, 1999) and as a reliable diagnostic criterion of ADHD (for a meta-analysis, see Arns, Conners and Kraemer, 2012).

### **2.2.2. Attentional Theta in Sleep**

One of the first sleep studies on the amplitude frequency characteristics of auditory EPs was conducted on cats with chronically implanted electrodes (Başar, Gönder, Özesmi and Urgan, 1975b). Slow wave sleep (SWS) was characterized by theta activity that was distributed to a network consisting of the hippocampus, reticular formation, neocortical and subcortical centers in the auditory pathway.

Hoedlmoser and colleagues (Hoedlmoser, Griessenberger, Fellingner, Freunberger, Klimesch, Gruber and Schabus, 2011) manipulated vigilance by depriving human participants of sleep. As the duration of sleep deprivation increased, the reaction time to the psychomotor vigilance task and the ratings of subjective sleepiness also increased. The amplitudes of ERP components, specifically the P1 component of the visual evoked potential showed a progressive decrease. Increasing sleepiness, and decreasing vigilance was accompanied by a progressively increasing tonic EEG activity in specifically the theta and delta bands, and decreasing values in the delta/theta phase locking. This study concluded that the delta/theta phase-locking represents overnight changes in vigilance, and hence of attention.

According to Näätänen and Gaillard (1983) and De Lugt, Loewy, and Campbell (1996), sleep N2 is comparable to the awake N2b, which is an index of selective attention (Campbell and Colrain, 2002; Näätänen and Picton, 1986; Paavilainen,

Cammann, Alho, Reinikainen, Sams and Näätänen, 1987; Perrin, Garcia-Larrea, Mauguere and Bastuji, 1999). Among the sleep stages, stage 2 is characterized by the highest reactivity to environmental stimulation (Kryger, Roth and Dement, 2011). The theta response to the OB-p task is higher in stage 2 in comparison to the theta responses in the REM and non-REM stages of sleep. In stage 2, a specific phase of the theta rhythm coincided with sleep-N2 (Karakaş, Bekçi, Çakmak, Erzenin and Aydın, 2007; Karakaş, Çakmak, Bekçi and Aydın, 2007). These findings suggest that there is some form of attentional processing in stage 2.

In REM, reactivity to the environmental stimuli is at its lowest value, however, the EEG is dominated by beta waves that characterize alert wakefulness (Kryger, Roth and Dement, 2011; Rechtschaffen and Kales, 1968). According to these findings, REM EEG is as in alert wakefulness, but this activity is not coupled with a low threshold to environmental stimulation. Theta oscillation provides a key to the paradox of the dreaming brain. In REM, OB-p task triggers an early short-duration theta oscillation (Karakaş, Bekçi, Çakmak, Erzenin and Aydın, 2007; Karakaş, Çakmak, Bekçi and Aydın, 2007). Such a theta is also a characteristic of the OB-p response in wakefulness. The OB-p task produces sensory memory, where cognitive processing is preconscious and preattentional (Karakaş, 1997; Karakaş and Başar, 2004; Muller-Gass and Campbell, 2002; Näätänen, 1992). According to a large group of studies (for reviews, see Muller-Gass and Campbell, 2002; Näätänen, 1992), sensory memory that is produced by the OB-p task is well-formed for the frequently presented, standard stimulus since it is to be used as a comparator for noting the mismatch between the sensory memory representation of the standard stimulus, and the physical and temporal attributes of the deviant stimulus (Sokolov, 1990; Atienza and Cantero, 2001; Näätänen, Schröger, Karakaş, Tervaniemi and Paavilainen, 1993). In REM, the duration of the theta response to the standard stimulus is relatively longer than that of the response to the deviant stimuli (Karakaş, Bekçi, Çakmak, Erzenin and Aydın, 2007; Karakaş, Çakmak, Bekçi and Aydın, 2007). These findings, specifically the similarity between the wakefulness and REM OB-p responses (i.e., a relatively longer theta duration to the standard

stimulus) suggests that, as in wakefulness, there is some form attention, in this case preattentive processing, in REM.

### **2.3. Theta in Navigation and Episodic Memory**

Both voluntary movement, with which Type 1 theta is involved, and intention to move, with which Type 2 theta is involved, require active involvement with the environment. Stimuli in the external environment (especially the visual stimuli) must be processed in order to execute actual or intended movements. The stimuli in the internal environment (specifically the kinesthetic stimuli) must be processed for forming motor plans, performing motion correction, and using these cues to generate successive responses. The constellations of these processes require a higher level of visuospatial behavior (Banich and Compton, 2011) than is obtained upon the relatively simpler sensory-motor integration (Section 2.1). Not surprisingly, early research on the sensory-motor correlates of theta oscillation has gradually evolved into navigation, a cognition that involves a higher level of visuospatial processing than the sensory-motor integration.

Based on their systematic investigation of hippocampal functioning, O'Keefe and colleagues provided an explanation of the neurocognitive nature of navigation. The roadmap of these studies started with an extensive investigation of the firing properties of hippocampal neurons in response to environmental manipulations (O'Keefe, 1976; O'Keefe and Dostrovsky, 1971). This work culminated in a book (O'Keefe and Nadel, 1978) on place cells. The book presents the functional role of the hippocampus in building up a cognitive map that spatial memory uses. This was displayed by Kahana and colleagues (Kahana, Sekuler, Caplan, Kirschen and Madsen, 1999) in epilepsy patients with intracranial electrodes. In these patients, virtual maze navigation was represented with episodes of theta activity which were more prominent for the complex mazes than for simpler ones.

Early studies (for a review, see Green and Arduini, 1954; Kramis, Vanderfold and Bland, 1975; Sainsbury, Heynen and Montoya, 1987) had already shown the

relevance of the hippocampal theta and voluntary response to Type 1 RSA, and the relevance of motionless alertness (freezing) and intention to move to Type 2 RSA. They had also described the relationship between the locomotor dynamics and theta rhythmicity (Vanderwolf, 1969). O'Keefe and Recce (1993) discovered that when a rat enters the firing field of a place cell, spiking occurs at the late phase of the theta rhythm. As the rat moves through the firing field, spiking shifts to the earlier phase of the theta rhythm. When rats pause at a decision point, place cells fire with strong gamma rhythms, representing upcoming sequences of locations (Johnson and Redish, 2007). O'Keefe and colleagues (O'Keefe and Burgess, 1996) also discovered the boundary vector cells, which respond to specific distances from barriers in the environment. These studies paved the way for an investigation of navigatory activity via the theta rhythm of the hippocampal cells.

The discoveries reported by O'Keefe and colleagues (O'Keefe, 1976; O'Keefe and Dostrovsky, 1971; O'Keefe and Nadel, 1978; O'Keefe and Recce, 1993), who were awarded the Nobel Prize in 2014, revealed the role of the hippocampus in different types of navigatory activity. Navigation by dead reckoning, where continuous detection is made of the course and the distance from some reference point, occurs through the activation of the unidirectional place cells in the hippocampal CA1 layer. Landmark/map-based navigation occurs, on the other hand, via the activation of the omnidirectional place cells in the entorhinal cortex. Both types of navigation are represented by theta oscillation, with theta thus forming a link between the two forms of navigation (Buzsaki, 2006).

The functional neuroanatomy of the hippocampus and its connections, the temporal coding of sensory information via the theta oscillation of the place cells, and the existence of dynamically functioning boundary cells paved the way for an analogy between navigation and episodic memory (Andersen, Morris, Bliss and O'Keefe, 2007). The analogy is based on the critical importance of the temporal and spatial aspects: navigation occurs at a specific time and place (Section 2.3), and episodic memory is about personally experienced events that happened at a

specific time and place. Both are context-dependent controlled processes (Tulving, 1972; Richard, Frackowiak, Friston, Raymond, Price, Zeki, Ashburner and Penny, 2004).

Buzsaki (2006) gives an account of this analogy in the following manner: the algorithms that are used in first-order (neighborhood) and second-order (short-cut, detour) navigation in the visuospatial space are also used when navigating in the cognitive space. In navigation, self-referenced (or egocentric) relationships in the visuospatial space produce a map of the physical space. In episodic memory, self-referenced relationships between perceived, conceived, or imagined items produce a map of the cognitive space. The common element in both of these processes is sequencing. Navigatory behavior is based on spatial sequencing of physical distances between places or objects. Episodic memory, on the other hand, is based on temporal sequencing of positional and chronological distances between events.

As the previously reported findings indicate (for a review, Green and Arduini, 1954; also O'Keefe and Recce, 1993; Vanderwolf, 1969), both navigatory behavior and episodic memory are represented by the hippocampal theta. Neuroanatomically, the oscillation is specifically demonstrated in the CA3 pyramidal cells and the recursive connections of the CA3-CA3 and the CA3-CA1 layers (Buzsaki, 2006). The early work by Klimesch and colleagues had provided neuropsychological evidence on the relevance of the theta rhythm to episodic memory. Episodic memory is represented by event-related synchronization (ERS) in the theta band (Klimesch, Schimke and Schwaiger, 1994) over the anterior limbic system (Klimesch, 1996). Theta ERS differentiates good performers of episodic memory from bad performers (Dopelmayr, Klimesch, Schwaiger, Auinger and Winkler, 1998; Klimesch, Schimke and Schwaiger, 1994).

Yamaguchi (2003) explained the creation of novel sequences through theta phase precession. According to this process, when the subject enters a cell's place field, spikes first occur at the late phases of the theta cycle. Subsequently, spikes occur at

progressively earlier phases of the theta cycles (O'Keefe and Recce, 1993; Skaggs, McNaughton, Wilson and Barnes, 1996). Accordingly, phase-locking between the local field theta oscillation, and the neural oscillators that also have graded activity in the theta frequency range creates stable phase relations between neural activities in successively changing neural populations. The feedforward and feedbackward projections in the hippocampal network create selective associations between components of episodic memory or components of the visuospatial field (navigation), enabling storage of temporal sequences.

The previous subsections showed that hippocampal theta is responsible for multiple cognitive-affective processes. The multiplicity of function is possible because frequency is one of the variables that characterize an oscillation (Başar, 1988, 1998, 1999). The functional significance of an oscillation changes according to a large set of variables, some of which are related to the oscillatory activity while others are not. The oscillation-related variables are enhancement, attenuation, blocking, duration (prolongation), latency, time-locking, phase-locking, frequency-locking and superposition of oscillations in different frequency ranges. The oscillation-unrelated variables are recording site, the experimental task, developmental level and species of the research participant, and coherence between brain areas (for a review, see Karakaş and Barry, 2017). The oscillation-related and unrelated variables and combinations of these variables change the functional meaning of the theta oscillation, and cause it to represent different cognitive-affective processes.

### **3. From the Hippocampus to the Whole Brain: From Binding to a Selectively Distributed Theta System**

Theta represents the cognitive-affective processes that hippocampus is responsible for. However, theta is not unique to the hippocampus. This oscillation is the major operating rhythm in a network that is selectively distributed to the brain. Furthermore, hippocampus does play a critical role in selected cognitive-affective processes, but even this role is achieved via interaction with the other brain areas which are generally a part of the distributed theta network.

### 3.1. Binding: Hippocampal Contribution

The hippocampus receives its input, via the perforant pathway, from disparate neocortical and subcortical areas such as the amygdala, cingulate cortex, frontal lobe, temporal lobe, orbital cortex, olfactory cortex, and sensory areas (Andersen, Morris, Bliss and O'Keefe, 2007; Lopes da Silva, Witter, Boeijinga and Lohman, 1990; Lopes da Silva and Arnolds, 1978; Lopes da Silva, Arnolds and Nijst, 1984). These areas are selectively responsible for cognitive-affective processes such as sensation, perception, attention, and executive functions (for a review, see Banich and Compton, 2011; Andersen, Morris, Bliss and O'Keefe, 2007; Stuss and Benson, 1986).

Accordingly, the information that arrives at the hippocampus has already been preprocessed in multiple cortical areas (Vinogradova, 2001). All of these cortical areas project and are represented in the hippocampus in a compressed manner (Green and Arduini, 1954; Amaral and Lavenex, 2006; Buzsaki, 2002; O'Keefe, 2007; Stark, 2007). Units of cortically preprocessed information that arrive at the hippocampus are disseminated to multiple layers of densely packed neurons that make up the complex neuroanatomy of the hippocampus (Andersen, Morris, Bliss and O'Keefe, 2007). The parallel organized circuits (CA1 and layer 3 of the entorhinal cortex) and recurrent circuits (CA3 and layers 2 and 5 of the entorhinal cortex) work in alternation. Information becomes integrated when recurrent circuits are activated; it becomes segregated when parallel circuits are activated (Buzsaki, 2002).

Due to the multiple layers of densely packed neurons and the strongly curved layers, theta oscillations that arrive from multiple pathways impinge on the hippocampal layers with varying phase relationships (Buzsaki, 2002). As a function of their position within the hippocampus, the phase and amplitude of theta oscillations change in very complex ways (Buzsaki, 2006). This neural architecture leads to "relational" processing, and to hippocampal binding (Banich and Compton,

2011). What brings the environmentally triggered multimodal elements of an episode (as in episodic memory) or a scene (as in navigation) together is binding.

Binding is represented by the theta rhythm. It is hypothesized that related items of information are packaged in theta cycles; in other words, each theta cycle represents a chunk of related information. This entity can consist of a discrete sample of sensory/perceptual information or a specific relationship among sensory/perceptual, cognitive, and motivational (emotional) factors (Kepecs, Uchida and Mainen, 2006); elements of an episode (coherent episodic memory) (Goldstein, 2011; Jezek, Henriksen, Treves, Moser and Moser, 2011); or over-represented segment sequences in a maze (coherent spatial concept) (Gupta, van der Meer, Touretzky and Redish, 2012). During navigation and phase precession, spikes on early theta phases represent current location and those in later phases represent upcoming locations (Lisman and Redish, 2009).

### **3.2. Association**

#### **3.2.1. Theta Oscillation Reflects Supramodal Associative Processing**

Hippocampal binding, which is represented by the theta oscillation, is a mechanism by which inputs arriving at the hippocampus become connected. Another mechanism is the formation of associations between disparate sources of information. Theta is again a major player in this associative process. Accordingly, the associative theta is mainly recorded from multimodal tertiary association cortices, such as the prefrontal, parieto-temporo-occipital and limbic cortices (Lang, M., Lang, W., Diekmann and Kornhuber, 1987; Mizuki, Tanaka, Isozaki, Nishijima and Inanaga, 1980; Mundy-Castle, 1951; Remond and Leservre, 1957; Walter, Etevenon, Pidoux, Tortrat and Guillou, 1984; Westphal, Grözinger, Diekmann, Scherb, Reess, Leibing and Kornhuber, 1990).

The relationship of the theta oscillation to associative processing can functionally be demonstrated in studies on bisensory stimulation. Sakowitz, Schürmann and Başar (2000) conducted such a study, and found that the bimodal evoked response is

mainly recorded over the multimodal prefrontal association areas. Stimulation led to a marked theta response that could not be accounted by a linear addition of the responses to two unimodal stimuli. These findings show that bimodal stimulation associates auditory and visual in very complex ways.

Another instance of association is demonstrated in cross-modality studies. The effect was studied by Başar and colleagues in two companion papers. One of the papers was on scalp recordings of humans (Başar and Schürmann, 1994), and the other was on deep recordings of freely moving cats (Başar, Başar-Eroğlu, Rahn and Schürmann, 1991). These cross-modality experiments studied visual and auditory EOs at the primary visual cortex. At both the scalp recordings (humans) and deep recordings (cats), adequate stimuli (visual stimuli with EO recordings from the primary visual cortex) produced an early (0-250 ms time window) alpha response. Inadequate stimuli (auditory stimuli with EO recordings from the primary visual cortex) produced a long-duration theta response. According to Başar and colleagues, alpha response represents primary sensory processing. However, theta response represents a supramodal associative-cognitive processing.

### **3.2.2. Association Between Theta and the Other Oscillatory Components**

Section 2 showed that some of the cognitive-affective states that are currently discussed in cognitive neuroscience can be represented by hippocampal theta. This is possible because the functional meaning of singly occurring theta changes according to oscillation-related and oscillation-unrelated modulatory effects (for a review, see Banich and Compton, 2011; Karakaş and Barry, 2017). Oscillations of different frequency bands can also co-occur; simultaneity of occurrence and the resulting superposition, is in fact another oscillation-related variable. According to the principle of superposition, a given neuroelectric electrical response (EO or ERO) is the consequence of the temporal superposition of oscillatory components in different frequency ranges (for a review, see Karakaş and Barry, 2017). As the following sections will show, when theta is associated with oscillations in the other frequency bands, diverse cognitive-affective processes become possible.

*Theta/delta association.* In an early work, Stampfer and Başar (1985) showed that P300 is characterized by enhancement and prolongation of the theta oscillation superimposed on the delta oscillation. Studies on OB-a tasks supported this finding. Cognitively, OB-a tasks require active attention. Active attention is represented at the P300 (P3b) latency by a high amplitude and long duration theta response that is superimposed on the delta response (Karakaş, Erzengin and Başar, 2000; Polich and Criado, 2006). In the OB-p task, attention is directed elsewhere; attention to the experimental task (the deviant stimulus) is passive. This type of attention is represented by only a short-duration theta response (Karakaş, Erzengin and Başar 2000).

The latency and the amplitude of the P300 component increases with increasing cognitive load (Kahana, Sekuler, Caplan, Kirschen and Madsen, 1999; Pinal, Zurrón and Díaz, 2014). Cognitive load is represented by a specific superposition and a phase relationship between the theta and delta oscillations at the 300 ms latency. In high cognitive load, the positive-going arm of the delta oscillation is in phase with the second positive-going arm of the theta oscillation. This pattern ceases to exist as the load decreases (Güntekin and Başar, 2014; Karakaş, Erzengin and Başar, 2000).

*Theta/alpha association.* Memory task performance is represented by phase-locking between the theta and alpha oscillations at the P1-N1 time window (Klimesch, Schack, Schabus, Doppelmayr, Gruber and Sauseng, 2004; Gruber, Klimesch, Sauseng and Doppelmayr, 2005; Schack, Klimesch and Sauseng, 2005). Findings on cross-coupling between the theta and alpha oscillations led the authors to conclude that the theta oscillation represents WM and the alpha oscillation represents semantic memory.

*Theta/gamma association.* While early gamma response is basically related to sensory/perceptual processing (Karakaş and Başar, 1998), late gamma response is related to higher cognitive processing (Başar-Eroğlu and Başar, 1991; Karakaş,

Başar-Eroğlu, Özesmi, Kafadar and Erzenin, 2001). P300-specific delta and theta oscillations are superimposed by a late appearing gamma oscillation (Başar-Eroğlu and Başar, 1991; Karakaş, Başar-Eroğlu, Özesmi, Kafadar, Erzenin, 2001). Superimposed late gamma oscillations occur in multistable visual perception (Başar-Eroğlu, Strüber, Kruse, Başar and Stadler, 1996), attention (Sheer, 1984), memory (Lisman and Jensen, 2013), memory match and utilization (Hermann, Munk and Engel, 2004). These findings show that a pattern consisting of superimposed delta, theta, and gamma oscillations represents diverse cognitive-affective processes.

Scalp-recordings of the late 300-ms gamma response may appear with a weak time- and phase-locking (Fell, Hinrichs and Röschke, 1997; Herrmann, Munk and Engel, 2004). Deep recordings from the H13 layer of the cat brain, however, display a strong P300-40 Hz complex (Başar-Eroğlu and Başar, 1991; Başar-Eroğlu, Başar and Schmielau, 1991; Başar-Eroğlu, Schmielau, Schramm and Schult, 1991). Findings show that focused attention and the related OR are represented not only by the theta oscillation (Demiralp and Başar, 1992), but by a theta-gamma cross-coupling. This coupling reflects bottom-up processing for allocation of attention and a simultaneously occurring top-down processing for activation of memory stores (Sauseng, Klimesch, Gruber and Birbaumer, 2008).

Accordingly, gamma oscillation is modulated by the slower rhythms. Theta provides the absolute phase reference that is necessary for encoding order, and gamma cycles play a role in the high precision timing of the order of events (Lisman, 2005). Places are encoded by a spatial pattern of gamma firing neurons, and spatial sequences are encoded by gamma subcycles that are superimposed on the theta cycle (Buzsaki and Wang, 2012; Buzsaki, Leung and Vanderwolf, 1983). These findings show that theta/gamma cross-coupling represents sequencing, where of units of information are encoded in a serial order.

Gamma rhythmicity plays a role in also theta phase precession (Dragoi and Buzsaki, 2006), according to which spikes in the early theta phases represent current

location, and those in later phases represent upcoming locations (Lisman and Radish, 2009). During theta phase precession, the spikes that are generated by the CA1 place cells are modulated by gamma oscillations (Senior, Huxter, Allen, O'Neill and Csicsvari, 2008). Evidence indicates that the theta-modulated gamma oscillations that arrive at the dendrites increase the membrane potential and, thus, enhance signal propagation.

Maintenance of visual information in short-term memory is based on the cross-frequency phase synchronization between theta and gamma oscillations in the parietal recording sites (Sauseng, Klimesch, Heise, Gruber, Holz, Karim, Glennon, Gerloff, Birbaumer and Hummel, 2009). WM is represented by frontal midline theta and cross-frequency phase-coupling between frontal theta and distributed gamma (Griesmayer, Gruber, Klimesch and Sauseng, 2010). In both, the powers are higher during the manipulation of the retained stimuli than during their retention. The manipulation/retention difference pertaining to the theta/gamma coupling is most pronounced in the first half of the delay period, while the manipulation/retention difference pertaining to the frontal midline theta is most pronounced in the second half of the delay period. The authors conclude that theta/gamma coupling reflects monitorization of the temporal sequence of items, and the frontal midline theta reflects rehearsal processes.

*WM as associations between co-occurring oscillations.* The previously described findings show that the creation and maintenance of some integrative cognitive-affective processing are based on the associations between the theta oscillation and the various other oscillations that vary according to oscillation-related and oscillation unrelated variables (Başar, Öniz, Özgoren, Schmiedt and Başar-Eroğlu, 2004). Such a *modus operandi* is the indispensable neuroelectric basis of particularly the complex cognitive-affective processes, such as WM.

WM is characterized by simultaneous storage and processing of information. Cognitively, this is achieved by two slave systems, the phonological store and the

visuospatial sketchpad, that operate under the monitorization and control of the central executive (Baddeley, 1997). The prior slave system is responsible for maintenance of temporal sequences, and the latter is responsible for maintenance of spatial sequences (Baddeley, 1997). Sequencing, the item-level control mechanism of WM, is represented by coupling between the theta and gamma oscillations and phase resetting of the theta oscillation (Sauseng, Griesmayer, Freunberger and Klimesch, 2010). The process-level mechanism, which is responsible for integrating the cognitive processes under the WM umbrella, is represented by theta synchronization between relevant areas of the brain. When theta and upper alpha are phase synchronized, theta represents executive functions, and alpha represents reactivation of long-term memory codes (Klimesch, Schack and Sauseng, 2005). In WM, theta oscillation underlies organization of sequentially ordered items; gamma oscillation underlies maintenance of information; and alpha oscillation underlies the inhibition of irrelevant stimuli (Roux and Uhlhaas, 2014). Prefrontal theta represents retention; high WM performers demonstrate enhanced theta response (Hsieh, Ekstrom and Ranganath, 2011). Power of the theta response represents the cognitive load of the WM task (Klimesch, Schack and Sauseng, 2005).

### **3.3. Connectivity and Synchrony**

*Structural connectivity and synchrony.* Another way by which the distributed theta system produces its unique constellation of cognitive-affective processes is “connectivity” between brain areas (for a review, see Başar, Güntekin, Yener and Başar-Eroğlu, 2016). That theta is not unique to the hippocampus, that there is a synchronized theta network was first shown by Adey and colleagues (Adey, Dunlop and Hendrix, 1960). This pioneering work was an investigation of the theta synchronization in cats undergoing conditioning. The authors studied the extent and the patterns of theta synchronization in cats by means of spectral and coherence functions and demonstrated the increase in theta event-related coherence during behavioral conditioning.

Subsequent research discovered other theta displaying brain areas, attesting that theta is the fingerprint of not only the hippocampus but also the other limbic structures (Lopes da Silva, 1992) and, at large, the other brain areas. Theta oscillation is displayed in cats with chronically implanted electrodes at the hippocampus (CA1, CA3), auditory cortex, visual cortex, reticular formation, and motor cortex (Demiralp, Başar-Eroğlu, Rahn and Başar, 1994; Başar, Gönder, Özesmi and Ungan, 1975a and b). Theta oscillation is displayed at the entorhinal cortex, perirhinal cortex, retrosplenial cortex, medial mammillary body, supramammillary nuclei of the hypothalamus, anterior nuclei of the thalamus, amygdala, inferior colliculi, and several brain stem nuclei (Buzsaki, 2002). Findings such as these indicated that there is a selectively distributed theta network in the brain. The medial septal area, which is a part of this network, has reciprocal connections with the hippocampus and is connected to brain areas that also display the theta rhythm (Andersen, Morris, Bliss and O'Keefe, 2007). Destruction of the area eliminates the theta rhythm (Buzsaki, 2002; Stewart and Fox, 1990), suggesting that the medial septal area is the generator of the theta oscillation (for reviews, see Colgin, 2013; Vertes and Kocsis, 1997).

The studies by Lopes da Silva and colleagues were focused on the transmission of information over the distributed theta system. These studies showed that information is transmitted between the limbic cortex, the target structures (e.g., ventral striatum) and the associated subiculum-nucleus accumbens pathway via the theta oscillation (Lopes da Silva and Arnolds, 1978; Lopes Da Silva, Arnolds and Nijst, 1984). RSA is the gating mechanism that directs the flow of information in the distributed theta system (Lopes da Silva, Witter, Boeijinga and Lohman, 1990). Theta then matches the resonances between hippocampal outputs and circuits of the target structures, thereby facilitating long-term potentiation in the circuitry (Lopes da Silva, 1992).

*Cognitive-affective correlates of connectivity and synchrony.* The various cognitive-affective processes are based on distinctive connectivity patterns in the selectively

distributed theta network. Multimodal sensory-motor integration is produced via connectivity between the hippocampus and the sensory-motor areas. Movement and navigation are produced via connectivity between the hippocampus and areas responsible for egocentric and allocentric reference frames of space. Episodic memory is produced via connectivity between the hippocampus and areas responsible for multimodal sensory-perceptual processing, and high level cognitive-affective processing. Scripts, scenarios, and episodic memories are outcomes of also this complex network (for a review, see Banich and Compton, 2011; Goldstein, 2011).

Execution of novel finger-movement sequences requires interregional connectivity between the frontal and parietal cortices. In this way, sensory/perceptual information is integrated with executive control of the motor response (Sauseng, Hoppe, Klimesch, Gerloff and Hummel, 2007). Long-range theta oscillation that travels over connectivity pathways between the frontal and posterior areas vary according to whether the trial is a stay or switch one (Sauseng, Klimesch, Freunberger, Petchstorfer, Hanslmayr and Doppelmayr, 2006). Long-range theta coherence represents top-down control of behavior (Sauseng, Klimesch, Freunberger, Petchstorfer, Hanslmayr and Doppelmayr, 2006), and memory processes pertaining to accessing and manipulating information in the memory stores (Klimesch, Freunberger, Sauseng and Gruber, 2008). A later study suggested that long-range theta coherence is related to episodic memory, and long-range alpha coherence is related to semantic memory (Klimesch, Freunberger and Sauseng, 2010). The division of labor between the hippocampal and neocortical systems is represented by an integrative pattern of theta-based ERS in the hippocampus and theta-based event-related desynchronization (ERD) in the neocortex (Hanslmayr, Staresina and Bowman, 2016).

*Hippocampus and the selectively distributed theta network.* The previously described findings have highlighted the critical role of the hippocampus in theta generation. Theta oscillation is mainly generated in the cells of the hippocampal formation (Colgin, 2013; Buzsaki, 2006; O'Keefe and Burgess, 1996; O'Keefe and

Recce, 1993). However, theta oscillation is not confined to the hippocampus; theta oscillations that are entrained by theta oscillators are distributed throughout the brain. The traveling theta waves in this network reflect the interaction of weakly coupled oscillators (for a review, see Colgin, 2013; Lubenov and Siapas, 2009).

Intra-structurally, the hippocampus provides for highly associated information (process: binding). This information is disseminated (via the fornix) to a resonant communication network that operates over large populations of parallel networks that are selectively distributed in the brain (Başar, Schürmann and Sakowitz, 2001; Buzsaki 2002, 2005, 2006; O'Keefe, 2007; Green and Adey, 1956). Interstructurally, the information is further encoded in this network and/or used in behavioral performance (process: connectivity), or, as in the cinematographic model, small patterns from multiple modalities integrate to form large patterns (Freeman, 2006). In brief, the intrastructural associations in the hippocampus (namely, binding), and the interstructural connectivity between the hippocampus and cortical areas provide a densely associated pool of information that travels over a densely interconnected, and highly synchronized hippocampo-cortical system (Amaral and Lavenex, 2006; O'Keefe, 2007). The hippocampo-cortical interplay in the theta oscillation (Buzsaki, 1989; Fogel, Smith and Beninger, 2009; Miller, 1991a, 1991b) produces the theta-enhanced, selectively distributed parallel processing that is responsible for cognitive-affective processing.

### **3.3.1. Theoretical Approaches to Connectivity and Synchrony**

Connectivity and synchrony via the theta oscillation is not exempt from counterarguments, which are mainly based on the comparability of scalp and hippocampal recordings or the relationship of theta to single-neuron firing (Lopes da Silva, 1992). Green and Arduini (1954) reported only brief bursts of hippocampal theta in scalp recordings of primates. In their large, systematic study on epilepsy patients, Cantero and colleagues (Cantero, Atienza, Stickgold, Kahana, Madsen and Kocsis, 2003) could obtain intracortical recordings of hippocampal theta in REM and in the transitions between sleep and wakefulness. However, no correspondence

was observed between the hippocampal and cortical theta. They concluded that the two events are independent and served by independent mechanisms. These findings, coupled with the size of the hippocampus, the distance between the hippocampus and cortex, and the weaker theta in humans in comparison to the theta in nonhuman species provide evidence against a direct hippocampal-cortical correspondence, and suggest a passive volume conduction of the theta rhythm to the cortex (for a review, see Anderson, Morris, Bliss and O'Keefe, 2007).

According to a larger part of the literature, however, widespread theta is not the outcome of volume conduction or any other passive mechanism. Widespread theta is the outcome of an active process, and theta is the major operating rhythm in the selectively distributed theta network. Based on extensive research on the oscillatory dynamics of the brain, Başar proposed the concept of "whole-brain work" (Başar, 2006). Within the context of the whole-brain, the selectively distributed oscillations allow for selective cooperation between brain structures; this anatomophysiological organization results in the supersynchrony that evolved brains possess. The selectively supersynchronized whole-brain makes the higher cognitive processes involving integrative functions, such as memory, possible (Başar, 1998, 1999, 2011; Başar, Başar-Eroğlu, Karakaş and Schürmann, 1999a, b; Başar, Başar-Eroğlu, Karakaş and Schürmann, 2001). Based on their studies, Klimesch and colleagues also conclude that information about memory is stored within a distributed theta network (Sauseng, Klimesch, Gruber and Birbaumer, 2008).

Early theories and formulations about the brain emphasized localization of function. According to the neuron theory (Cajal, Ubeda Purkiss and Fox, 1954) and the still influential Brodmann areas (Brodmann, 1909), discrete structures (neurons and BA, respectively) are responsible for discrete functions. Contemporary neuroanatomical brain theories are consistent, however, with Başar's concept of whole-brain work. According to Fuster (2006), cognitive information is stored in cognits, which are webs of distributed, intermeshed, and overlapping networks. According to John (1988), the brain is organized into giant modules or hyperneurons; its functions are

performed by these hyperneurons. The holographic hypothesis of memory structure (Pribram, Nuwer and Baron, 1974) assumes that levels of presentations (e.g., the stimulating environment) are transferred to computed re-presentations (neuronal models) by Fourier-like transformation. This unconstrained Fourier coordinate system is spread “everywhere and everywhen to entangle the parts with one another” (Pribram, 2007, p. 2735). The contemporary thinking about the brain and its functions is aptly summarized by the term, “dynamic localization” (Luria, 1966), which suggests that “The task of neuroscience is not to localize the centers, but, rather, identify the components of the various complex systems that interact to generate the mental functions” (Solms and Turnbull, 2003, p.64).

*Interim summary.* Theta oscillation, the topic of the present paper, is one of the major operating rhythms of the mammalian brain. The hippocampus is critical, but theta oscillation is not confined to the hippocampus. Theta is served by a complex network that is selectively distributed to the neocortical and subcortical areas of the brain. Functionally, theta oscillation represents diverse cognitive-affective functions such as attentional processing, sensory-motor integration, navigation, and memory. As the subsections of Section 3 show, these functions are produced within a highly interconnected network, and an intense transfer of the theta band activity (and any other co-existing bands) between the neocortical and subcortical structures. Such a system makes any counterargument to the cortical correspondence of hippocampal activity pointless.

#### **3.4. The Formation of Memory within the Selectively Distributed Theta System: Theoretical Approaches**

In the rat, the hippocampal theta may be phase-locked to the frontal midline theta; however, the two thetas can also be independent (Mitchell, McNaughton, Flanagan and Kirk, 2008). According to these authors, studies on connectivity and coherences are necessary but, as is, the cognitive functions of the midline theta and its relationships to hippocampal theta are not clear, at least in rats.

However, there is a long list of empirical findings and theoretical formulations addressing the interplay between the prefrontal cortex and hippocampal structures. During the latter part of the 20<sup>th</sup> century, Miller (1991a, 1991b) performed a functional and electrophysiological analysis of the associations between the hippocampus and the cortex, and developed the cortico-hippocampal interplay model. According to this model, there are specific patterns of loops between the hippocampal neurons and those that are widely dispersed to the frontal and parietal cortices. These loops are strengthened through a process of Hebbian synaptic strengthening (Hebb, 1949), and this strengthening produces a tonic state of activation in the cortex. Functionally, the loops represent contexts, be it in the form of associations between pieces of information (as in perception) or events (as in schemas and scripts). These contexts, in turn, represent the background information that is used in identifying or manipulating specific items of information or specific events.

According to the cortico-hippocampal interplay model, connectivity between these structures occurs through resonance in the theta frequency range (Miller, 1991c). There are consistent phase relationships between nodes at the prefrontal cortex and hippocampus, and the total conduction delay time in each of these patterns of loops corresponds to the theta period. This model is a preliminary attempt to explain the distributed theta network and its role in associative-cognitive performance.

The cortico-hippocampal interplay model (Figure 1) is used by Buzsaki (1989) to explain memory (Table 1). In the stage 1 of the two-stage model, neocortical information is transmitted to the hippocampus. This is the acquisition stage, and processing is represented by the theta oscillation. In Stage 2, the hippocampal information is transmitted to the neocortex. This stage is characterized by repeated reactivation of acquired information, and is represented by sharp waves (SPWs). This stage occurs during the SWS stage of sleep, consummatory behavior, and immobility.

Buzsaki's (1989) two-stage model was applied by Fogel, Smith and Beninger (2009) to memory processing in sleep. This model is based on findings from epidural electrodes in rats. In the model, stage 1 involves the organization and consolidation of newly acquired information. These processes occur via the hippocampal-neocortical dialogue and occur in the REM stage. This stage is represented by high theta activity. Stage 2 involves the neocortical refinement of information. This stage occurs in the SWS stage, and is represented by spindles. It should be noted that stages 1 and 2 in the Fogel, Smith and Beninger (2009) sleep model correspond to stage 2 in Buzsaki's model, where stage 1 is the hippocampal activation stage, and stage 2 is the transfer of information to the neocortical areas.

In the Diekelmann and Born (2010) model, the order and the functional characteristics of stages are slightly different. According to this model, stage 1 involves "systems consolidation". In this stage, hippocampally formed memories are reactivated, and they are redistributed to the relevant neocortical sites. These processes occur during SWS, and is represented by slow waves, spindles and ripples. Stage 2 involves "synaptic consolidation." In this stage, memories are consolidated at cortical sites. This process occurs during REM, and is represented by high theta activity (for a review, see Poe, Walsh and Bjorness, 2010). It should be noted that stages 1 and 2 in the Diekelmann and Born (2010) model again correspond to stage 2 in Buzsaki's model. However, unlike the Fogel, Smith and Beninger (2009) model, stage 1 involves the transfer of information to the neocortical sites, and stage 2 involves cortical consolidation.

Memory is a multistage process (Atkinson and Shiffrin, 1968), and is comprised of the stages of encoding (acquisition), consolidation, and retrieval (Goldstein, 2011; Richard, Frackowiak, Friston, Raymond, Price, Zeki, Ashburner and Penny, 2004). The standard model of memory consolidation (Squire and Alvarez, 1995; McGaugh, 2000) accounts for all three stages of memory processing using the cortico-

hippocampal interplay model. Table 1 is a simplified representation of this interplay in the sequential stages of memory.

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Please insert Table 1 about here.

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In the standard model, stage 1 is the encoding stage (Frankland and Bontempi, 2005). In this stage, there is activation in many parts of the cortex, and each area encodes its relevant input. Prefrontal cortex (specifically ventrolateral and dorsolateral prefrontal cortices), focuses on and organizes the encoding process; these areas are responsible for strategically mediated aspects of memory (Fernandez, Effern, Grunwald, Pezer, Lehnertz and Dumpelman, 1999). The way memories are encoded at the prefrontal cortex predicts subsequent performance (Brewer, Zhao, Desmond, Glover and Gabrieli, 1998; Wagner, Desmond, Glover and Gabrieli, 1998). This encoded information is then transferred to the hippocampus, where attributes of a scene or an episode (event) are bound into coherent memory traces. The hippocampus is responsible for relational processing (Section 3.1); it thus shows greater activation when it is encoding relations (for a review, see Cohen, Ryan, Hunt, Romine, Wszalek and Nash, 1999). In conclusion, encoding is a joint function of the hippocampus and the prefrontal cortex.

A higher theta power is obtained during the acquisition of the words that can later be remembered (Klimesch, Doppelmayr, Russegger and Pachinger, 1996), indicating that the theta oscillation is specifically associated with the encoding phase of episodic memory. During encoding, there is also a strong theta synchronization (Klimesch, 1999), which is stronger in good memory performers (Doppelmayr, Klimesch, Schwaiger, Auinger and Winkler, 1998). The latency of this encoding-related parietal theta is approximately 300 ms (Doppelmayr, Klimesch, Schwaiger, Auinger and Winkler, 1998; Klimesch, Hanslmeyer, Sauseng, Gruber, Brozinsky, Kroll, Yonelinas and Doppelmayr, 2006).

Stage II is the consolidation stage (Squire and Alvarez, 1995; McGaugh, 2000; Frankland and Bontempi, 2005). Consolidation transforms the encoded information from a fragile state, in which it can be easily disrupted, to a more permanent state, in which it is resistant to disruption. These processes thus pave the way for long-term retention of information in particularly episodic memory (Tulving, 1972).

In the consolidation stage, the hippocampus replays and reactivates the specific networks of the recently formed memory for a few hours. The firing of neurons is enhanced and there is a patterned activation of neural pathways, concomitant with greater neurotransmitter release and lasting neural changes. This is the synaptic consolidation stage (Andersen, Morris, Bliss and O'Keefe, 2007) and is indexed in rodents by long-term potentiation (LTP). This stable increase in synaptic consolidation can last from hours to weeks (for a review, see Raymond, 2007).

The consolidation process can be triggered by conscious rehearsal of the material, but it can also occur spontaneously during relaxed wakefulness and sleep. As memories become consolidated, activation in the hippocampus decreases. Synaptically consolidated memories progressively become disengaged from the hippocampus and are transferred to the neocortex. Transfer of cognitive information is basically performed during SWS and is mediated by sharp-wave ripples (SWRs) (Rattenborg, Martinez-Gonzales, Roth and Pravosudov, 2011).

Memory processing of emotional information is slightly different. Consolidation, disengagement of consolidated traces, and transfer to the neocortex are performed in stage II (and the following Stage III) and in REM sleep (Rattenborg, Martinez-Gonzales, Roth and Pravosudov, 2011; Hutchison and Rathore, 2015). However, as with cognitive information, theta oscillation is the mediator in this process (Karakas, Bekçi, Çakmak, Erzenin and Aydın, 2007; Karakas, Çakmak, Bekçi and Aydın, 2007).

Systems consolidation is based on synchronous firing of the neurons in the theta network. Consolidation makes the neurons more likely to fire together in the future; as a result, components in the network become permanently sensitized to each other. In this systems consolidation stage, memories become independent of the hippocampus; they can be retrieved and activated independent of the hippocampus (Frankland and Bontempi, 2005; Nadel and Moscovitch, 1997). This process is dynamic: first, system consolidation continues over a period of weeks to years and allows for a gradual reorganization of the brain regions that constitute the distributed theta system. Second, the system is modified by new experiences; connections are rerouted and organizations are rearranged. Reconsolidation, a mark of brain plasticity, provides an opportunity to update existing memories (Andersen, Morris, Bliss and O'Keefe, 2007).

Stage III is the retrieval stage. There are different views with respect to the structural basis of retrieval. According to the standard model of memory, retrieval is a function of the neocortex. By this third stage, the intracortical connections have become strong enough to link different parts of the cortex (Frankland and Bontempi, 2005). The neocortex stores the consolidated memory traces and integrates them with preexisting ones. Attempts at retrieval are reflected in a travelling wave that spreads antero-posteriorly, actual retrieval is represented by a reverse action from the posterior to the frontal sites (Sauseng, Klimesch, Gruber, Doppelmayr, Stadler and Schabus, 2002; Klimesch, Schack and Sauseng, 2005). These studies show that retrieval is performed in the neocortex.

A second view on retrieval asserts that, retrieval is a function of the hippocampus. According to Tulving (1972), episodes are stored with mental tags, showing where, when, and how episodes had been picked up. The reactivation model (Sutherland and McNaughton, 2000), assumes that the hippocampus has a storage of indices. Analogous to the mental tags of Tulving (1972), these indices show where, in the neocortical processors, different aspects of an event are stored. Knowing their places, the hippocampus retrieves components of a specific memory, and combines

them into a pattern of the memory trace. In retrieval, memory traces are repeated, and according to the multiple trace model (Nadel and Moscovitch, 1997), each repetition forms the trace anew, and traces becomes stronger with each repetition.

According to a third view, retrieval is a function of neither the hippocampus nor the neocortex. Different areas of the brain are selectively responsible for retrieval of different cognitive-affective processes (for a review, see Banich and Compton, 2011). Hippocampus and medial lobe structures are responsible for retrieving an item within its temporal and spatial context. The anterior prefrontal cortex guides the search in long-term memory, while the posterior prefrontal cortex selects the most appropriate items. Retrieval by the left parietal cortex is modality-nonspecific and task-nonspecific; the brain area is responsible for the retrieval of older memories by way of recognition. Retrieval in the prefrontal cortex shows lateralization for verbal (left) and spatial (right) material. Generation of items to be retrieved occurs in the left hemisphere, and monitorization of the memory store occurs in the right hemisphere. The left prefrontal cortex is responsible for retrieval pertaining to familiarity, and the right parietal region is responsible for retrieval pertaining to recognition memory.

Regardless of how retrieval is explained, the neurophysiological correlate of this last stage of memory is theta. Magnetoencephalography of retrieval in healthy human participants displays theta oscillation (Osipova, Takashima, Oostenveld, Fernández, Maris and Jensen, 2006). The only significant oscillation in the retrieval-related event-related desynchronization/ synchronization is theta. During fear conditioning in mice, the amygdala-hippocampal network displays retrieval-related theta (Seidenbecher, Laxmi, Stork and Pape, 2003).

Klimesch and colleagues (for a review, see Klimesch 1999) had already shown the association between theta and episodic memory as well as theta and encoding. However, they found an even higher theta as participants retrieved information (Klimesch, Doppelmayr, Schimke and Ripper, 1997). What distinguished encoding

theta from the retrieval theta is the anatomical site that the theta oscillation is recorded from (Sauseng, Klimesch, Doppelmayr, Hanslmayr, Schabus and Gruber, 2004). Encoding-related theta is observed in the right hemisphere; theta coupling occurs between the right dorsolateral prefrontal cortex and the right posterotemporal cortex. Retrieval-related theta is observed bilaterally, and theta coupling occurs between the prefrontal cortex and bilateral temporoparietal brain areas.

Klimesch and colleagues demonstrated the relevance of the theta oscillation to many aspects of the retrieval process. Retrieval-related theta occurs at around 400 ms. The strength of the theta time-locking is a predictor of memory performance (Doppelmayr, Klimesch, Schwaiger, Stadler and Röhm, 2000). Early theta synchronization represents retrieval by recognition (knowing without conscious recollection), late theta synchronization represents retrieval by free recall (remembering) (Klimesch, Doppelmayr, Yonelinas, Knoll, Lazzara, Röhm, and Gruber, 2001). The researchers then noted that the power does not discriminate new pictures from successfully retrieved old ones. This finding led the authors to conclude that the theta during retrieval does not represent retrieval *per se* but represents a general processing that occurs during formation of episodic memory (Klimesch, Doppelmayr, Stadler, Pöllhuber, Sauseng and Röhm, 2001).

*A Clinical Model.* AD, which starts with problems in recent memory (Goedert and Spilantini, 2006; Banich and Compton, 2011), is an efficient model for understanding the neural correlates of memory degradation. AD patients have difficulty in retaining what they have learned; they thus display anterograde amnesia (Kolb and Whishaw, 2015). In the terminology of memory trace formation, they display disorders of encoding and consolidation. Hippocampus is closely related to encoding and consolidation (Section 3.4, Table 1). In AD, the earliest and most severe degenerative changes are at the paralimbic cortex, specifically the entorhinal cortex. The latter is the major relay station between the hippocampus and the neocortex (Andersen, Morris, Bliss, O'Keefe, 2007). These

neurodegenerative changes are accompanied with decreased theta response (Yener and Başar, 2013; Yener, Güntekin and Başar, 2007; Yener, Güntekin, Tülay and Başar, 2009).

The previous models concede that theta is the critical oscillation in the interplay between the hippocampus and neocortex. The progressively increasing memory problem from mild cognitive impairment (MCI) to AD is represented with progressively decreasing theta coherence between the frontal and parietal areas (Yener, Güntekin and Başar, 2006). A review paper on the topic concludes that the decrease in theta event-related coherence is a biomarker of the progression from MCI to AD (Başar and Güntekin, 2013).

#### **4. Limitations**

The goal of this article was to present a state-of-the-art review outlining the critical developments that have contributed to our present understanding of theta oscillation and its cognitive-affective correlates. Within the limits of a journal article, the present paper could only present a selective and concise summary of the empirical findings and theoretical issues pertaining to the cognitive-affective correlates of the theta oscillation. Had this work been a book on theta oscillation, many other empirical and theoretical aspects of theta could have been discussed. Some of these aspects are mentioned below as limitations of this review article.

The first hippocampal recordings of theta band activity were made by Jung and Kornmüller (1938) in rabbits. A majority of the findings on theta oscillation are for the limbic cortex, specifically the hippocampus, of the rodents (for reviews, see Green and Arduini, 1954; Stumpf, 1965; Colgin, 2013). Theta rhythm is continuous in rodents (Buzsaki, Haubenreiser, Grastyan, Czopf and Kellenyi, 1981), but it occurs in bouts in bats, monkeys, and humans (Kahana, Sekuler, Caplan, Kirschen, Madsen, 1999; Killian, Jutras and Buffalo, 2012). The present review does not provide a comparative evaluation of the theta rhythm over the evolutionary spectrum.

The present paper mainly focused on the theta activity of the hippocampal--neocortical system. Future studies should more extensively discuss the other structures in the theta network, such as the thalamus, brainstem-diencephaloseptal system, and the reticular activation system, for a more extensive structural coverage of the theta network (Başar, Özesmi and Ungan 1973; Vertes, Hoover, Viana, and DiPrisco, 2004).

Theta oscillation is closely related to one type of declarative (explicit) memory: episodic memory. The present review article also focused on the theta correlates of episodic memory. Meanwhile, the notion of discrete memories (Tulving, 1972) is not consistent with the ideas of the holistically functioning brain or the selectively distributed theta network hereto discussed. According to Schneider and Shiffrin (1977), episodic memory and semantic memory are two different instances of context-dependence and control; episodic memory involves context-dependent controlled processing, while semantic memory involves context-independent automatic processing (Pribram, 1977). In the network model of cortical representations phyletic, sensory, episodic and semantic memories are hierarchically organized (Fuster, 2006). Higher levels are based on the lower levels, and lower levels are nested in the higher ones. According to Başar (2004), memory and the other forms of cognitive processing (attention, perception, and learning) are all based on brain oscillations. These processes are closely integrated, and none can be considered independent of the others. With its emphasis on mainly the episodic memory, the present review article failed to discuss the theta oscillation within the context of an integrated memory system.

## **5. Summary and Conclusions**

The present review article on the theta oscillation and its functional correlates can be summarized as follows:

- The theta rhythm was discovered in the hippocampus of rodents. This discovery was followed by a large group of research on mainly the

hippocampal theta and its functional correlates (Figure 1). The early studies was on the role of hippocampal theta rhythm on episodic memory and visuospatial processing. Later studies showed that theta is functional in a large spectrum of cognitive-affective processes that range from sensory/perceptual processing, motor processing (e.g., Type 1 RSA, Type 2 RSA, LIR), attention-related processes (arousal, OR), passive attention (preattention), facilitatory active attention (selective attention, focused attention), inhibitory active attention, navigation (e.g., dead-reckoning, landmark/map-based) to different types of memory (episodic memory and working memory). Theta oscillation represents these different processes by variations (Section 2.3.) in oscillation-related variables (e.g., amplitude, frequency, latency, duration, phase-locking, synchronization/desynchronization, superposition of oscillations with different frequency ranges), and oscillation-unrelated variables (e.g., recording site, the experimental task, developmental level and species of the research participant, coherence between brain areas). The neuroanatomical characteristics of the hippocampus (its unique location in the brain, its connections with cortical and subcortical areas, its complex, layered histology) also facilitates this immense task. Due to its neuroanatomy, the phase and amplitude of the hippocampal theta rhythms change in very complex ways, and this makes relational processing possible. Inputs that converge on the hippocampus are bound together. Binding is the mechanism whereby memory traces are formed. Examples: Binding between multimodal elements of a scene, which ultimately results in navigatory behavior. Binding between attributes, which produces an episode and ultimately an episodic memory.

- Theta is a characteristic of hippocampal physiology, and theta-based cognitive-affective processing is a contribution of the hippocampus to information processing. However, hippocampus is not the only brain area where theta is observed. Hippocampus is a part of a theta system that is selectively distributed to cortical (e.g. prefrontal, parieto-temporo-occipital,

and limbic cortices) and subcortical areas. Due to this neural architecture, the hippocampus is connected to the other brain areas in very complex ways, producing what is called the cortico-hippocampal interplay. One mechanism for combination of inputs is binding; there, inputs are combined to form memory traces. A second mechanism is association. Supramodal and multimodal processing is based on associations between two or more sensory systems.

- Another type of association occurs between theta and oscillations in the other frequency bands. Theta oscillation can occur by itself, as in the foregoing part of the summary, or it may occur with oscillations in other frequency band. In the latter case, different oscillations co-occur on the time axis, forming specific patterns of superposition. Integrative cognitive-affective processing is represented by these coupled oscillations. For example, degrees of cognitive load are represented by specific superpositions and a phase relationship between the theta and delta oscillations. Focused attention and OR are represented by theta-gamma cross-coupling. Short-term maintenance of visual information is based on the cross-frequency phase synchronization between theta and gamma oscillations in the parietal recording sites.
- Another mechanism for combination of inputs, connectivity, determines the coherence patterns between selected brain areas. For example, sensory-motor integration is the result of the functional connectivity between the hippocampus and sensory-motor areas. Navigation is the result of the functional connectivity between the hippocampus and areas responsible for egocentric and allocentric reference frames of space. Scripts, scenarios, and episodic memories are a results of functional connectivities between the hippocampus, on the one hand, and areas responsible for multimodal sensory-perceptual processing and high-level cognitive-affective processes, on the other.
- Theta-based cortico-hippocampal interplay is used, by the standard model of memory consolidation and supporting findings, to explain the sequential

stages of memory (Table 1). Encoding (stage 1) is performed in all the task-relevant cortical areas; this activity is organized by the prefrontal cortex. Information on encoded material is transferred to the hippocampus, where different attributes are bound into coherent memory traces. Encoding stage is represented variations of the theta oscillation in latency, power, synchronization/ desynchronization and coupling. Consolidation (stage 2) involves a repeated transfer of information between the cortex and hippocampus. (2a) The hippocampus replays and reactivates the specific networks of the recently formed memory to produce synaptic consolidation. This process is represented by high theta activity. (2b) As memories become consolidated, activation in the hippocampus decreases. Synaptically consolidated memories become progressively disengaged from the hippocampus and are transferred to the cortex. Information is replayed and redistributed to cortical sites for further refinement. This stage is represented by sharp-wave ripples of the theta oscillation. (2c) In the systems consolidation stage, memory traces in relevant areas of the cortex are integrated with preexisting ones; they are thus reorganized and reconsolidated. These activities are represented by firing of the distributed theta network, theta coherence, synchronization and desynchronization. Retrieval stage 3) is the last stage. According to the standard model of memory, the cortex retrieves the memory traces from their relevant cortical sites. Attempts at retrieval is reflected in a travelling wave that spreads antero-posteriorly and actual retrieval is represented by a reverse action from the posterior to the frontal sites. This stage is represented by bilateral coupling of the theta oscillation. In other models, retrieval is ascribed to the hippocampus, or to selected brain areas in the brain. However, irrespective of the nature of the responsible brain area or system, processing is again based on the theta oscillation, which varies in power, time-locking, latency of synchronization and coherence.

To conclude, mechanisms of interstructural binding (in the hippocampus), mechanisms of interstructural association formation and coherence (connectivity of the cortico-hippocampal network) result in a densely connected pool of information. This information travels over an interconnected, and highly synchronized system (cortico-hippocampal system) in the form of theta waves; theta is the major operating rhythm of the system. Theta oscillation represents many of the cognitive-affective processes that cognitive psychology and cognitive neuroscience encompass.

## 6. Future Directions

- The concept of the wholistically operating brain and the connectivity patterns in selectively distributed networks are presently at the focus of attention of the cognitive neuroscientists. Advancement in this area is heavily dependent on the development of a technology by which a reliable and practical quantification of inter-areal coherence matrices will be possible. The recently introduced CLAIR model (Başar, Düzgün and Güntekin, 2014) allows quantified mapping of discrete cognitive-affective function via unique patterns of connectivities between selected brain areas. CLAIR or any other similar model will be able to quantitatively describe the highly connected network in which theta (and the other oscillations) operate. Prospective research and development should thus be focused to the quantification of the functional neuroanatomy, and the delineation of inter-areal coherences of each cognitive-affective process.
- Theta responses that appear at specifically the later poststimulus time windows have weak-time and phase locking to the stimulus. These “induced” rhythms are studied by the single-sweep analysis technique (Başar and Bullock, 1992). As this review article shows, literature on theta is largely based on averages and studied as phase-locked evoked and/or event-related activity. Future scientific endeavors should make use of the single-trial methodology and analyze single-sweeps (Başar and Bullock, 1992). Such a scientific activity will greatly contribute to our understanding of the

nonphase-locked, induced theta and thus enrich our knowledge on the theta oscillation. (Demiralp, Yordanova, Kolev, Ademoğlu, Devrim and Samar, 1999; Klimesch, Russegger, Doppelmayr and Pachinger, 1998)

- With a history of over a century, research on the spontaneous activity (EEG) of the brain is definitely more advanced than the event-related activity. The prestimulus oscillations (theta or any other) have strong influence on the power and the morphology of the poststimulus ones (Başar, Başar-Eroğlu, Rosen and Schütt, 1984; Başar, Rahn, Demiralp and Schürmann, 1998; Doppelmayr, Klimesch, Pachinger and Ripper, 1998). This issue has not received the attention it deserves. Future studies should focus on the effect of, for example, the spontaneous theta on the poststimulus theta response.
- In healthy children, cognitive-affective development starts with the first year of life and shows a rapid increase until late childhood. In parallel, slow waves (delta and theta) that compose the spontaneous activity of the brain (EEG) decrease while fast waves (alpha beta and gamma) increase. Such a consensus is not yet achieved for the development of the oscillatory components in the evoked, event-related and induced oscillatory activity. Existing developmental research does not satisfactorily consider the selectively distributed networks of the brain oscillations. Research on the first 10-12 years of life should include systematic studies on the development of theta (and all the other oscillatory components) that compose the evoked and induced activity of the wholistically functioning brain.
- At the present, the theta oscillation, and oscillations in general are evidence-based. Relevant literature has reached a certain level of maturity, and this level justified the study of the brain oscillations in neuropsychiatric disorders (e.g., Alzheimer dementia, Parkinson's dementia, bipolar disorder, attention deficit hyperactivity disorder). Research has shown that these disorders can be characterized by variations in oscillation-related and oscillation-unrelated parameters of the theta oscillations and oscillations in the other frequency ranges. Robust disorder-specific patterns of oscillatory activity

have been discovered. Findings on the variations and the patterns of oscillatory activity thus stands as promising biomarkers for differential diagnosis, subtype classification, and stage estimation. Existing review articles on the oscillatory dynamics of cognitive-affective processes in neuropsychiatric either discuss all of the oscillations or they do not amply cover the theta oscillation (Başar, 2012; Başar and Güntekin, 2008, 2012, 2013; Yener and Başar, 2010). A review article on the role of specifically the theta oscillation in clinical disorders is timely. Such an article will bring together the existing theta findings on clinical disorders, point to auxiliary criteria for diagnosis, indicate biomarkers for treatment evaluation (pharmacotherapy, psychotherapy or surgery) and monitorization of disease progression.

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**FIGURE CAPTION**

**Figure 1.** Brain's theta network in neuro-cognitive functions.

**TABLE LEGEND**

**Table 1.** Cortico-hippocampal theta network in memory: Acquisition, consolidation and retrieval.

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**Table 1. Cortico-hippocampal theta network in memory: Acquisition, consolidation and retrieval.**

Stage	Characteristic levels/ stages of consciousness	Structures	Functions	Theta response parameters
<b>Stage 1 Acquisition</b>	Preconscious	All relevant cortical areas	• Encoding	Coupling
		Prefrontal cortex • Between right prefrontal cortex (specifically ventrolateral regions) and postero-temporal sites	• Focuses on and mediates organizational/strategic aspects of encoding	• Desynchronization • Power increase • Synchronization
	Unconscious	Transfer from the cortex to the hippocampus • Input to the entorhinal cortex and periformant pathway over cortico-entorhinal projections		
		Hippocampus	• Binding disparate aspects of cortical experiences into a coherent episode	• Desynchronization • Power increase • Synchronization
<b>Stage 2 Consolidation</b>	Levels of wakefulness, stages of sleep and REM	Hippocampus	• Replay and reactivation of memory network for a few hours • Synaptic consolidation may last from hours to weeks	• High theta activity
	SWS wakefulness	Transfer from the hippocampus to the cortex • Output over the entorhinal cortex and over the fornix to anterior structures	• Reactivation and redistribution of hippocampal memories to neocortical sites for a cortical refinement of information	• Sharp -wave/ripple complexes (SPW-Rs) • Sharp slow waves (SP) • Spindles
	Unconscious	Neocortex	• Memories become independent of the hippocampus • Components of neocortical network become sensitized to each other • Consolidated memory trace become integrated with preexisting ones • Brain areas are reorganized, memory is reconsolidated, and updated: Neocortical refinement is dynamic • Systems consolidation may last from weeks to years	• Synchronization • Desynchronization • Firing of the distributed theta network • Theta coherence
<b>Stage 3 Different conceptualizations of retrieval</b>	Levels of wakefulness, stages of sleep and REM	1) Hippocampus (along with perirhinal cortex, medial temporal lobe structures)	• Provides indices (mental tags) that point to the domain-specific cortical regions where the pieces had been stored • Pieces are then combined into the episode that is to be retrieved	
		2) Neocortex (bilateral) • Between bilateral prefrontal cortex and temporo-parietal sites • Attempts at retrieval represented by antero-posteriorly spreading waves • Actual retrieval represented by reverse action	• Retrieves the consolidated and integrated traces from the relevant cortical sites (e.g. verbal material left-lateralized, spatial memory right-lateralized)	• Bilateral coupling

		3) A selectively distributed super-synchronized memory network in the brain	• Specific parts of brain responsible from different forms of retrieval	<ul style="list-style-type: none"><li>• Power</li><li>• Time-locking</li><li>• Early theta synchronization (e.g. recognition)</li><li>• Late theta synchronization (e.g. remembering)</li></ul>
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**Highlights**

A review of specifically the cognitive-affective correlates of the theta oscillation is currently unavailable.

Hippocampus is centrally located in a selectively distributed theta network. Theta-based hippocampal binding brings together the environmentally triggered multimodal elements of episodes or scenes, and make multimodal sensory/perceptual and motor processing, facilitatory and inhibitory attention, navigation and episodic memory possible.

The densely associated pool of information that are represented by the theta oscillation travel over a densely interconnected, and highly synchronized hippocampal-cortical system.

In this network, the theta-based cortico-hippocampal interplay produces many cognitive-affective processes, chief one being memory with its encoding, consolidation and retrieval stages.

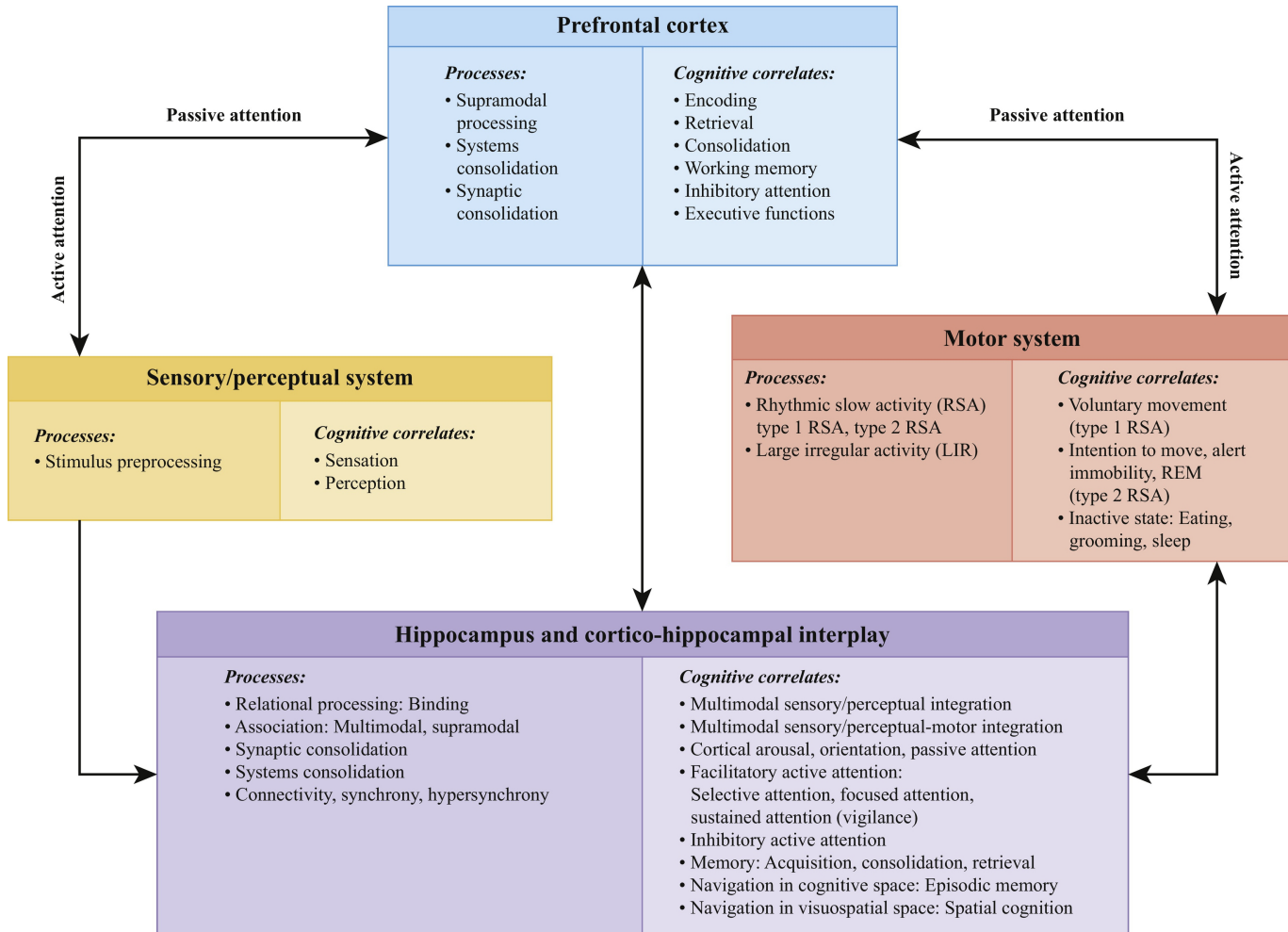


Figure 1