

Like Ticking Clocks: What Do We Really Know About Oscillating Brains?

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Abstract

Recently, there is a growing interest in cortical oscillations. Though initially suspected to be mere epiphenomena of neural activity, they are now thought to have functional significance in many cognitive processes. This essay will examine possible roles for oscillatory brain activity. In particular, I will focus on perception and memory processes. There is a substantial body of evidence supporting the view that cortical oscillations play a pivotal role in (human) cognition. The synchronous activity of neural networks may thus be the “critical middle-ground (Buszaki & Draguhn, 2004) linking neural activity to behaviour although no straightforward function-to-frequency mappings can (currently) be made. What exactly neural synchrony contributes to cognitive processing, and how it comes about, remains largely unclear to date.

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1 A Curious Clocking Mechanism

In 1929, Hans Berger first recorded alpha waves with human EEG. Subsequent research indicated that waking behaviour is dominated by desynchronised rather than synchronous activity while oscillations were found to be dominant in situations associated with loss of consciousness such as epilepsy or anaesthesia (Steriade, 2001). Today, brain oscillations bear the potential of linking up theories of cognitive processing from neural to behavioural level; they even have been suggested to be the neural correlate of conscious experience (Crick & Koch, 1990; 2007).

Oscillatory brain activity is dynamic, emergent, and self-organising in nature; it can be detected at different scales: depth electrodes invasively record the activity of single units or local field potentials; non-invasive recordings from the scalp surface can be acquired via EEG and MEG. Importantly, analysis of the recorded signal in terms of oscillatory activity does not assume – unlike evoked responses – activity to be time-locked to stimulus onset but focuses on *induced responses* in the frequency domain (Tallon-Baudry & Bertrand, 1999). Additionally, *phase resetting responses*, i.e. reset of the ongoing oscillations to synchronise phase, can be observed (Penny *et al.*, 2002).

Oscillations found, e.g., in EEG during visual search (Tallon-Baudry *et al.*, 1997) and memory tasks (Gruber *et al.*, 2004) have sometimes been dismissed as mere epiphenomena, noise, or even artefacts with no functional significance (Buszaki & Draguhn, 2004; Hermann, Munk & Engel, 2004). Evidence from intracranial recordings in humans (Tallon-Baudry, Bertrand & Fischer, 2001; Jacobs *et al.*, 2007) and animals (e.g. O'Keefe & Recce, 1993) refutes the

suggestion of oscillations being EEG artefacts. The presence of oscillatory activity throughout mammalian evolution (Buszaki & Draguhn, 2004) indicates that oscillations are likely not an epiphenomenon but a functional characteristic of mammalian brains.

Jones and Wilson (2005) suggest rhythmic brain activity functions as a “clocking mechanisms” against which the timing of neural firing is referenced and coordinated. Oscillations thus are a “fundamental property of neural elements” (Thut & Miniussi, 2009) enabling complex interactions within a given brain structure as well as between distributed neural populations across different structures (Singer, 1999; Varela *et al.*, 2001).

The neurobiological origin of oscillatory activity is not very well understood. It is believed that single neurons have the intrinsic ability to resonate at multiple frequencies (Hutcheon & Yarom, 2000) and work as voltage-dependant high-pass and time-dependent low-pass filters. These properties allow for a precise timing of activity within a neural network that can be used to represent information. The summation of selective oscillatory activity can serve for signal detection and amplification (Buszaki & Draguhn, 2004).

Gerstein and Perkel (1969) argue that oscillations are mediated by synaptic connections; these have to be stronger if the initial frequencies of the units to be synchronised are more deviant (Mirollo & Strogatz, 1999). The idea that differential synaptic links underlie the ability to form and/or retrieve coherent representations squares well with Hebb’s (1949) idea of learning being based on synaptic plasticity. Indeed, it has been found that oscillatory brain activity modulates spike-timing dependent plasticity (STDP) (Markram *et al.*, 1997). Axmacher (2010) suggests that oscillations define the time windows within which

STDP takes place.

1.1 Patterns

Which pattern of oscillatory activity arises in a network is dependent upon (i) its precise neural architecture and (ii) the initial conditions (baseline activity, noise, thresholds) of the network and its constituent units (Buszaki & Draguhn, 2010; Kirov, 2009). Generally, oscillations occur at different temporal and spatial scales. Alpha (α) activity (8-13Hz) is typically associated with resting states during wakefulness while beta (β) activity (13-25Hz) is normally found when the subject is either concentrated and alert or in REM sleep. Gamma (γ) activity (>25Hz) can be further subdivided into low (25-50Hz) and high (50-140Hz) γ , though the exact nomenclature is not consistent across studies. Both gamma and theta (θ) (4-8Hz) are believed to play a “mechanistic role” (Düzel, Penny & Burgess, in press) in memory processes such as formation of representations, off-line maintenance, and retrieval. Theta activity is also found in infants and sleeping adults. In very deep sleep, slow delta (δ) waves (0.5-4Hz) are observed. Oscillatory activity at these different frequency bands is thought to mark different processing modes and brain states (Thut & Minussi, 2009) where neighbouring frequencies may reflect competing brain states (Buszaki & Draguhn, 2004).

Generally, slow rhythms are associated with synchronous activity in large spatial domains whereas higher frequencies accompany faster more local events in the brain. Different types of oscillations can co-exist in the same and/or different brain structures and even reinforce or inhibit one another (Buszaki & Draguhn, 2004). How exactly neural oscillations work together to facilitate cognition is

still unclear, however.

2 Oscillatory Activity in Perception & Memory

Rhythms at different frequencies have been related to different cognitive functions. Axmacher *et al.* (2006) argue that different frequency bands play a role in subsequent steps of memory formation. Thut and Miniussi (2009) suggest that oscillations may be topographically specific – e.g., α -activity may be intrinsic to posterior and rolandic sites – thus reflecting functional specificity of cortical areas. A meta-analysis across ten studies supports this view (Thut & Miniussi, 2009): while α and β oscillations are more affected by stimulation of sensory and motor areas than dorso-lateral prefrontal cortex (DLPFC) stimulation, δ and θ are more affected by the latter than the former. But are there really such straightforward mappings from frequency bands to function and/or brain area?

2.1 Binding & Gestalt Perception

Since representations in neural networks are essentially *distributed*, multiple units jointly represent features of a single item. In order to form coherent precepts, these need to be *bound* together. In order to achieve this, the representing units may be active in synchrony (Engel *et al.*, 1997; Yamaguchi & Shimizu, 1994) where different objects are coded in different frequencies and/or phases. Comparing Gestalt and non-Gestalt figures, Tallon-Baudry and colleagues (1996) found that only Gestalt stimuli – giving the illusion of a continuous figure – are accompanied by two types of γ -response: an early evoked signal associated with bottom-up processing of low-level perceptual features and a late (after 250-

350ms) induced signal over occipital areas which is associated with formation of a task-relevant object representations.

Extending this binding-by- γ view, it has been found that induced (late) γ -activity increases during visual search; an effect likely due to top-down effects of previously acquired object representations on perception (Tallon-Baudry & Bertrand, 1999).

2.2 Attentional Selection

Attention is well known to affect what we perceive. Thut and Miniussi (2009) report attentional influences on perception to be mirrored by fluctuations in posterior α -activity from visual, occipital, and parietal areas: oscillatory activity decreases in regions corresponding to unattended space. α -activity may thus modulate the incoming flow of information along dorsal areas.

This role may not be *unique* to α -band activity, however. For γ and δ -oscillations have also been linked to attentive processes (Fell *et al.*, 2003; Lakatos *et al.*, 2008).

2.3 Temporal, Spatial, & Configural Coding

Spatial representation is prominently connected with hippocampal *place cells* (e.g. O'Keefe, 1979); assemblies of these jointly encode the animal's current location. *Grid cells* in the entorhinal cortex show a regular firing pattern at θ -frequency. They provide input to hippocampus the convergence of which is believed to form place cells (Gorchetchnikova & Grossberg, 2007). Spatial memory in rats has been associated with coherent θ -activity in hippocampus and pre-

frontal cortex (e.g. Jones & Wilson, 2005). In humans, θ -activity has been found to increase during spatial navigation (see Ekstrom *et al.* (2003) for intracranial recordings and Cornwell *et al.* (2008) for an MEG study). Taken together, these findings attribute a functional role to θ -oscillations in spatial coding.

Axmacher and colleagues (2006) report that spatial as well as temporal coding of objects is indexed by stimulus-locked phase reset of ongoing γ -oscillations in addition to θ . Both rhythms may interact to maintain subsequent items in working memory (WM); a computational model (Jensen & Lisman, 2005) suggests that on each θ -cycle the neurons representing one item may fire while they do so only in specific γ -subcycles; firing at different γ -subcycles would correspond to different items. Siegel, Warden and Miller (2009) report an analogous interaction of δ and γ -activity in monkeys. As Düzel and colleagues (in press) suggest, this could, e.g., explain the limited capacity of STM.

2.4 Maintenance in Working Memory

In the brain, transient events can be maintained to persist as active representations. For instance, Jensen *et al.* (2007) report continued synchronous γ -activity proceeding visual stimulus presentation that is not necessarily restricted to early sensory areas. Analogously, persistent θ -activity has been found in medio-temporal, parietal and prefrontal areas during maintenance (Mehta, 2005).

Axmacher and colleagues (2008) report slow potentials in medial temporal lobe (MTL) and a load-dependant increase of γ -activity in the rhinal cortex during WM maintenance; MTL recruitment and high- γ (51-75Hz) top-down influences on inferior temporal areas (IT) increases with the number of items being

maintained. These effects could possibly be explained by subject's recourse to concepts or specific memory strategies under high WM load.

If the above is correct, one may expect θ and/or γ -synchrony in subjects performing a delayed matching-to-sample task. Intracranial recordings from epileptic patients reveal β -synchrony between extrastriate areas, however (Tallon-Baudry *et al.*, 2001).

To maintain and coordinate configural information (along the ventral visual stream) θ -synchrony between temporal and occipital regions may be specially relevant (Cashdollar *et al.*, 2009). While this θ -network may be dependant upon the hippocampus, non-configural maintenance is associated with a hippocampus-independent fronto-parietal network (Cashdollar *et al.*, 2009).

2.5 Novelty & Encoding

Novelty acts as a learning signal (Düzel *et al.*, 2010); its assessment takes place early during LTM encoding and the likelihood of an item to be stored varies with its novelty (Tulving *et al.*, 1996). At the neural level, novelty detection has been linked to part of hippocampus (CA1). Lever and colleagues (2010) report that the preferred θ -phase of firing in CA1 shifted when rats were placed in a novel environment. This phase shift correlated with remapping of place cells and is thus indicative of hippocampal plasticity. In humans, memory enhancement has been reported when participants were exposed to novel environments prior to learning (Fenker *et al.*, 2008).

2.6 Consolidation & Plasticity

LTM is thought to be based on long-term plasticity – possibly due to increased γ -synchrony (Jensen *et al.*, 2007) – within dedicated cortical networks; prominently anterior temporal areas including hippocampus but also distributed neocortical areas (e.g. Patterson, Nestor, & Rogers, 2007; Squire & Knowlton, 1995). The resulting functional changes may reflect the redistribution of representing information – a view supported by computational models (e.g. Murre, 1996).

In the brain, there appears to be a two-way information transfer between neocortex and hippocampus where each direction is associated with a specific kind of memory and phases of sleep. During sleep, information learned during wakefulness is continuously replayed (Buszaki & Draguhn, 2004) causing functional long-term changes. Human *early sleep* is dominated by slow wave sleep (SWS; <1Hz) and specifically benefits hippocampus-dependant declarative LTM whereas *late sleep*, dominated by rapid-eye-movement (REM) sleep benefits procedural more than declarative memory (Plihal and Born, 2008).

Consolidation from hippocampus to neocortex may be triggered by sharp-wave rhinal ripples (~200Hz) during SWS (Stickgold *et al.*, 2005) indicating the reactivation of new memories (Marshall & Born, 2007). In rats, replay of place cell activity experienced during waking has been observed in fast ripples (Lee & Wilson, 2002; Wilson & McNaughton 1994). Born and Marshall (2010) report that in humans, ripple amplitudes during SWS increase with the amount of information presented during waking.

Consolidation from neocortex to hippocampus has been associated with θ -activity in REM sleep (Stickgold *et al.*, 2005). θ oscillations may enhance LTP

in CA3 of hippocampus which is induced by γ -synchrony between hippocampus and parahippocampus (Axmacher *et al.*, 2006). In rodents, hippocampal θ has been found to coordinate activity in neocortex (e.g. Hyman *et al.*, 2005). It has thus been suggested that hippocampal θ -phase biasing could control information transfer from neocortex to hippocampus (Düzel *et al.*, in press).

Thus far, likely due to experimental limitations, there has been a focus on declarative memory. However, to fully understand memory encoding in the brain – during sleep or otherwise – investigations into episodic memory will also be required.

2.7 Retrieval: Recollection & Familiarity

Retrieval from LTM can be examined within a dual-process framework that defines two component processes for recognition memory: recollection and familiarity (e.g. Jacoby & Dallas, 1981). *Recollection* is memory with recourse to contextual/episodic information and typically requires integration of different kinds of information (sensory, temporal, spatial, etc.). *Familiarity* is memory *per se*, viz. based on conceptual knowledge and/or associations but without recourse to contextual cues.

Gruber and colleagues (2008) dissociate these processes at the neural level: while induced θ in distributed areas reflects recollection processes, induced γ in predominantly occipital areas is indicative of associative/conceptual processing. Similarly, Guderian and Düzel (2005) associate recollection with induced θ -synchrony in a distributed (prefrontal, visual, and mediotemporal) areas. This may indicate a role for θ -activity as a binding mechanism in episodic retrieval.

cognitive function	frequency band	location
pre-stimulus signature of successful encoding	θ	medio-temporal
bottom-up low-level feature binding	early γ	occipital
top-down activation of object representation	late (250-350ms) γ	occipital
attention	α, γ, δ	posterior
modulation of incoming information along dorsal visual stream	α	posterior
location coding, spatial navigation	θ	hippocampal place cells, entorhinal grid cells; prefrontal cortex
STM: spatial & temporal sequences	rat: γ, θ monkey: γ, δ	temporal & occipital
STM: configural	θ	hippocampus-dependant: temporal & occipital
WM maintenance	γ θ δ β	early & higher sensory areas; rhinal cortex (load-dependant) medio-temporal, parietal, prefrontal medio-temporal (load-dependant) extrastriate areas
novelty induced plasticity	θ	CA1, hippocampus
LTM encoding: redistribution of stored representations	γ	anterior temporal & distributed areas; hippocampus & parahippocampus
declarative LTM (early sleep/SWS) replay of learned information	δ (<1Hz); ripples (200Hz)	hippocampus \rightarrow neocortex; ripples in rhinal and hippocampal areas
procedural LTM (late sleep/REM)	θ	neocortex \rightarrow hippocampus (LTP in CA3); coordination by hippocampus (?)
retrieval: recollection	θ	prefrontal, visual, medio-temporal
familiarity	γ	posterior/occipital

Figure 1: Oscillatory brain activity associated with neuroanatomical locations and cognitive functions.

2.8 What Does All This Mean?

In summary, a coherent picture as to what frequency bands may support exactly which cognitive processes and how oscillations are topographically organised across cortex does not emerge. It does not seem to be the case that specific frequencies can be mapped, in a one-to-one fashion, to different steps of memory formation. For instance, different phases of the θ -frequency band seem to correspond to encoding and retrieval in CA1, respectively (Manns *et al.*, 2007). Topographic organisation of brain oscillations seems an equally problematic suggestion; especially since some frequencies (γ , θ) tend to affect distributed networks. Thus, the current evidence does not support rigid mappings from frequencies to functions and/or locations. See Figure 1 for a schematic overview.

2.9 Match and Utilisation

Hermann and colleagues (2004) make an attempt to integrate γ -activity observed during perception and recollection into a coherent model. According to their match-and-utilisation model (MUM), bottom-up sensory feature encoding is followed by feature integration (binding) that is subsequently *matched* with information from LTM that has been loaded into STM. The result of this comparison (match or mismatch) can be *utilised*, e.g., to update memory information or select a behavioural response such as reallocating attention. While match accounts for early γ -activity observed in combination with binding (see section 2.1), utilisation accounts for late γ -activity associated with top-down activation of internal representations (Tallon-Baudry & Bertrand, 1999).

MUM is a valuable attempt to account for oscillatory brain activity with

a model of cognitive function. However, it is restricted to γ -activity only. It leaves open how short-term maintenance, encoding, and consolidation processes are achieved and does not provide neuroanatomical information. An extension of MUM could, e.g., take our knowledge of place cells and oscillatory activity during sleep into consideration where different frequency bands need to be integrated.

3 The Picture Remains Incomplete

Thus far, only oscillatory activity directly correlated with cognitive processing has been considered. However, as ongoing oscillatory activity may index the brain's internal state, it may be predictive of cognitive processing not yet initiated (Thut & Miniussi, 2009).

3.1 Pre-Stimulus Activity

Research using *subsequent-memory paradigms* supports this view: for instance, Otten and colleagues (2006) report that activity elicited prior to onset of a stimulus can predict whether or not it will later be recalled. In a 2010 study, they showed that pre-stimulus activity predictive of successful encoding is consistent for visual and auditory stimulus presentation. Whether a certain type of study task or specific memorising strategies are responsible for/modulate this effect, remains to be investigated.

In an MEG study, Guderian *et al.* (2008) found increased pre-stimulus θ -oscillations for remembered than forgotten items. Source localisation indicated this activity may originate from MTL which is prominently implicated in memory (see section 2.6).

3.2 Beyond Correlation

All the correlational observations reported here cannot rule out oscillatory brain activity is an epiphenomenon. In order to approach this issue, interaction techniques may be applied to carry out targeted interventions on brain oscillations.

Though such induced effects are not often frequency specific – thus possibly secondary to physiological changes (Thut, 2010) – rhythmic transcranial magnetic stimulation (rTMS) shortly before or during perceptual/cognitive tasks was found to modulate performance in a frequency dependant manner (Kilmesch *et al.*, 2003). Similarly, Kanai *et al.* (2008) used transcranial current stimulation (tACS)¹ on occipital areas to induce frequency dependant phosphenes (β -stimulation in illuminated, α -stimulation in dark environment). Induction of slow oscillations during non-REM sleep and learning (but not during other wakefulness and REM sleep) was found to enhance synchrony and improve declarative memory (Kirov *et al.*, 2009). Capotosto and colleagues (2009) demonstrated top-down influences as TMS application to frontal eye-field and intraparietal sulcus disturbed the attentional α -pattern (cf. section 2.2).

Together these studies indicate a causal link between oscillatory brain activity and perceptual as well as memory processes.

Possibly interaction with brain oscillations can even be carried out at neurotransmitter level: for instance, dopaminergic pathways appear to interact with mechanisms of θ -generation (Mesulam, 2004; Yamawaki *et al.*, 2008).

¹TMS rapidly induces an electromagnetic current primarily affecting superficial cortical areas. tACS is based on the application of constantly alternating low intensity currents through electrodes on the scalp over seconds; sinusoidal stimulation at different frequencies can thereby be achieved.

4 Summary & Outlook

Overall, current evidence indicates functional significance of cortical oscillations; different frequency bands seem to support a variety of cognitive functions. The impression emerges that γ -activity is particularly relevant for perceptual grouping, visual memory maintenance, and conceptual top-down processing whereas θ and α are more involved in interregional long-distance connections and the unification of cognitive operations as well as attention. However, straightforward frequency-to-function mappings are not supported at this stage. Indeed given the brain is a highly complex distributed system, it seems rather unlikely.

In a distributed system, mechanisms for temporal coordination and information integration are required; and oscillations are the most energy efficient way to put them in place (Buszaki & Draguhn, 2004). Whether or not the oscillatory system requires a master – or possibly different masters specialised for different functions – remains to be investigated. It has been suggested that hippocampus plays such a role (Düzel *et al.*, in press). Other loci, such as (for declarative memory) the pulvinar nucleus of the thalamus, have been suggested to mediate and coordinate distributed information (Hart & Kraut, 2007).

As brain oscillations underlie many (perhaps all) cognitive functions, they provide the explanatory glue potentially linking different theories of cognitive functioning from neural to behavioural level. Indeed, oscillations are an illustration of how *what fires together dynamically wires together* (Hebb, 1949) and thus of how the principal organisation of a behaving/cognitive system could be understood.

The conjunction of invasive and non-invasive recordings with intervention

techniques will further illuminate the causal/functional role of brain oscillations. They undoubtedly aid cognition but it remains unclear *how* exactly they do so. Recordings may be combined with computational approaches such as dynamic causal modelling and extensions of it, e.g. a weakly coupled oscillator approach (Penny *et al.*, 2009). Pattern classification algorithms may be used to decode large-scale neural activity and investigate the reactivation of memories (Düzel *et al.*, in press).

Since oscillatory brain activity is dynamic, emergent, and self-organising in nature, models of cognition should, possibly, be formulated in terms of dynamical systems theory, i.e. as sets of differential equations, rather than connectionist networks. Sophisticated models of dynamic oscillatory brain activity may help us understand better how the brain works and how neural oscillations support cognition.

A better understanding of brain oscillations is of therapeutic relevance: interaction with oscillatory activity may be used in brain disorder treatment and rehabilitation, e.g. to induce a new oscillatory balance into a (due to injury) disturbed neural network (Thut & Miniussi, 2009). Neurofeedback could potentially be applied to train memory (Düzel *et al.*, in press), and to reduce disturbing auditory sensations in patients with tinnitus (Dohrmann *et al.*, 2007). Possibly, a better understanding of the functional significance of sleep may help to treat sleeping disorders ever more prominent in a 24-hour society. In the far future, oscillatory interventions could perhaps even be carried out to trigger targeted forgetting of traumatic experiences.

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