Synchronous neural oscillations and cognitive processes

Lawrence M. Ward

Department of Psychology, University of British Columbia, 2136 West Mall, Vancouver, B.C. V6T 1Z4, Canada

The central problem for cognitive neuroscience is to describe how cognitive processes arise from brain processes. This review summarizes the recent evidence that synchronous neural oscillations reveal much about the origin and nature of cognitive processes such as memory, attention and consciousness. Memory processes are most closely related to theta and gamma rhythms, whereas attention seems closely associated with alpha and gamma rhythms. Conscious awareness may arise from synchronous neural oscillations occurring globally throughout the brain rather than from the locally synchronous oscillations that occur when a sensory area encodes a stimulus. These associations between the dynamics of the brain and cognitive processes indicate progress towards a unified theory of brain and cognition.

A popular stance in modern cognitive science is that cognitive processes arise from functionally organized brain processes [1], hence the discipline of cognitive neuroscience, which seeks to understand how this comes about. How can we identify the brain processes closely associated with cognitive processes and understand how the former give rise to the latter? Clearly, a first stage is to describe the functional anatomy of the brain: which areas show increased activity when a particular cognitive task is being performed. Informed by modern functional imaging techniques such as PET and fMRI, we have made an impressive beginning on this task. But cognitive processes are not static; they are dynamic. Even the simplest percept, memory or decision is a process that unfolds in time [2]. A popular way to think about the relationship between brain dynamics and cognitive dynamics is to describe the *sequence* of brain areas that 'light up' during the various stages in the performance of a cognitive task, like the sequence of bumpers hit by a pinball shot from its spring [3–5]. This approach is limited, however, because it cannot describe in any detail what is going on in those lit-up areas. Moreover, it doesn't seem to be able to cope fully with the emerging view of brain processes as reverberations of reentrant activity in a complex neural network [6,7]. A complementary approach that begins with the latter view is to try to describe how the oscillatory activity of the brain, as revealed by the electroencephalogram (EEG) and the magnetoencephalogram (MEG) as well as more invasive recordings, is related to the dynamics of cognitive performance (Box 1). There is increasing evidence that this relationship is revealing, and an increasing theoretical understanding of how it might come about based on computational neural models [8–10]. Here I review recent data and two provocative models from the large literature linking EEG (and MEG) recordings of the large-scale oscillatory activity of the brain with the dynamics of the fundamental cognitive processes of memory, attention, and consciousness. The goal is to make a case for serious consideration of such data and models in the effort to understand the origins and nature of cognition.

There are, of course, limitations to what this approach can tell us about cognition. These include the relatively poor spatial resolution of EEG and MEG (although MEG spatial resolution can approach that of fMRI), the fact that the dendritic field potentials of the cortical pyramidal neurons recorded by EEG and MEG constitutes only part of the brain's relevant dynamics, the correlative nature of the associations reported which beg questions of causality, and various more specialized technical problems such as volume conduction (EEG) and noise filtering (MEG). In addition, it is early days in this endeavor, so that models are not complete; they are simply illustrative of what can be accomplished within the dynamical approach.

EEG oscillations and cognitive processes

The EEG varies with activity, both in humans and other animals, and particularly with the sleep-wakefulness cycle. Moreover, spectral power at various frequencies (Box 2) changes with age; alpha power increases as children mature whereas theta and delta power decrease. These changes are linked to the more general increase in cognitive competence with maturation, whereas the reverse changes signal declining mental abilities in old age [11]. Alpha waves have been apparent in EEG recordings ever since electroencephalography was invented by Hans Berger in the 1930s. Classically, because alpha power was larger with eyes closed than with eyes open, it was thought that alpha reflected a relaxed, unoccupied brain. An overall decrease in alpha power has been linked to increasing demands of attention, alertness, and task load in general [11]. Theta power, by contrast, tends to increase in memory tasks, especially during encoding [8,11,12]. These complementary effects have been thought to reflect different cognitive operations occurring in cortico-thalamic circuits: theta for encoding and alpha for search and retrieval [11]. In what follows I will discuss more recent data and models that are

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Corresponding author: Lawrence M. Ward (lward@psych.ubc.ca).

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Box 1. Synchronous neural oscillations and the EEG

Oscillators display repeated variations in the level of some output. The prototype is the regular movements of a pendulum, resulting in a sine wave of position versus time. Neurons can be described as oscillators in which the voltage across the cell membrane changes according to two processes, the fast action potential (or spike) and the slower-varying post-synaptic potential. FitzHugh [59] recognized this and devised a mathematical model of the neuron, based on van der Pol's relaxation oscillator [60], that describes the global dynamics of all spiking neurons. This model is commonly used in the theoretical study of networks of spiking neurons, particularly in the study of the conditions under which they oscillate and synchronize their activity. Synchronization is arguably how the brain achieves the large-scale integration of its many parallel, distributed information-processing activities, allowing coherent cognition and behaviour [7].

Relaxation oscillators in general, and model neurons based on them in particular, have remarkable properties, demonstrated by computational neuroscientists and mathematicians over the past decade, relevant to how neural networks might achieve cognition. First, because of the dependence of the triggering of the neural spike on the level of the post-synaptic potential, a sufficient injection of current into a model neuron causes the potential to cross the spike threshold (around −50 mV), triggering the spike and resetting the phase of the oscillator (the phase describes where the neuron is in its oscillatory cycle). Fast zero-lag phase locking, or synchronization, between two or more spike-coupled model neurons can be achieved within one or two cycles through this mechanism [61,62]. This is the process by which pacemaker cells in the heart remain synchronized. It is one mechanism by which groups of neurons could attain and maintain synchronization. Moreover, local excitatory pulse-coupling of model neurons can lead to global synchronization, and a global inhibitory mechanism can lead to rapid desynchronization. These properties lead to automatic segregation of synchronously-firing groups of neurons representing stimuli on the receptors and have been used to model visual pattern processing [63]. Finally, the great susceptibility to driving by other oscillators, characteristic of relaxation oscillators and of model neurons based on them, allows changes in the phase and frequency of oscillations (spikes) but not in their amplitude, just as observed in real neurons.

Perhaps more important to cognitive neuroscience is the fact that groups of synchronously firing model neural oscillators can themselves be modeled as second order oscillators, with the amplitude of the oscillations depending on the number of individual oscillators in the group, and frequencies similar to those observed in real brains arising from the properties of the network [64,65]. It has been argued that cognitive processes such as memory, attention, decision-making, and even conscious awareness arise from the computations performed by such assemblages of synchronously active neurons [66]. Moreover, it has been shown how the oscillations of electrical activity recorded by the EEG and the MEG at the scalp could reflect the activities of these assemblages of synchronously oscillating neurons, in particular cortical pyramidal neurons [66]. Oscillations at standard EEG/MEG frequencies such as delta (0.5–3.5 Hz), theta (3.5–7 Hz), alpha (8–13 Hz), beta (15–25 Hz), and gamma (30–70 Hz), arise spontaneously in simulations of networks of relaxation oscillator neurons (Figure I)) [65]. Thus, it makes sense to attempt to relate the electrical oscillations recorded at the scalp by the EEG and the MEG to the dynamics of cognitive processes as a step towards uncovering the way in which mind arises from brain.

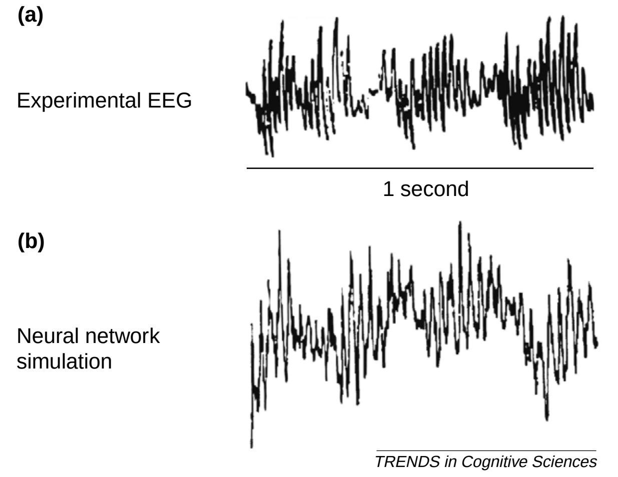

Figure I. Experimentally-recorded EEG oscillations **(a)** compared with oscillations from a network of 4500 coupled model neurons: 1500 each of pyramidal, feedforward inhibitory, and feedback inhibitory **(b)**. In both, the faster oscillations are at the gamma frequency and the modulation of the gamma oscillations is at the theta frequency (adapted with permission from [65].

beginning to flesh out but also to challenge some of these classical conclusions.

Theta and gamma and memory

Theta in memory encoding

Although theta oscillations are apparent in lower animals such as rats, they are seldom seen directly in EEG recordings from humans and it has been difficult to understand what the classically-observed increases in theta power meant [13]. Recently, however, intracranial EEG (iEEG) recordings made from epileptic patients have revealed strong theta oscillations from many areas of the human brain [14–15]. In these experiments, periods in which theta oscillations were apparent were more frequent when patients were navigating through a virtual maze by memory alone, relative to when they were guided through the maze by arrow cues. The theta periods were longer the longer the maze. Theta did not covary, however, with the time taken to make decisions at choice points; instead gamma oscillations were more prevalent the longer the decision time. Thus, theta oscillations are more closely linked to encoding and retrieval in memory than they are to other cognitive processes.

Gamma and transient coupling of brain areas

Gamma oscillations too play a role in memory. iEEG recordings from epileptic patients memorizing words reveal that during successful memory formation the rhinal cortex is first coupled to the hippocampus via 40 Hz gamma oscillations and then decoupled from it [16]. Gamma oscillations have been suggested to be a general mechanism for accomplishing such transient coupling of functional brain areas based on evidence of gamma band coherence across the brain during associative learning [17]. Moreover, during successful recollection, as opposed to merely experiencing a feeling of familiarity, there is greater gamma-band functional connectivity between frontal and parietal cortex along with more spectral power in both theta and gamma bands [18]. In this study, gamma-band activity was observed to be modulated at the theta rate. This suggests that interactions of gamma and theta activity might be involved in memory function.

Box 2. Spectral power and the EEG

The EEG (MEG) records a time series of electrical voltages (magnetic field strengths) at several sites on the scalp. Sampled at a rate of up to 1000 Hz at up to 256 different scalp sites for up to two hours, the EEG, for example, could generate a data matrix 7.2 million samples long by 256 sites high, for a total of 1.8432 billion pieces of data. There are many analysis techniques to try to wrest some understanding from this mass of data. One of the most useful is spectral power analysis, which allows us to measure the extent to which the neurons generating the EEG are oscillating synchronously at various frequencies.

Fourier's Theorem states that any repeating series of oscillations can be analysed into a set of the simplest possible oscillations, sine and cosine waves, of various frequencies and amplitudes. In obtaining the power spectrum of a time series of EEG samples, the voltage fluctuations recorded by an EEG electrode from moment to moment are analysed into various sine wave frequencies. The square of the so-called Fourier coefficient (the amplitude of the sine or cosine wave at a particular frequency) at each frequency is called the spectral power of that frequency, and it represents the amount of energy in the fluctuations at that frequency. The fluctuations in spectral power at an EEG frequency with changes in experimental tasks or over time can reveal relationships between the processing activity of groups of neurons and cognitive processes, or between separate groups of neurons at disparate sites in the brain.

Figure I shows some typical EEG power spectra for various electrode sites (the black dots on the schematic head) over a short time period of a few seconds; notice the different sites at which the various frequencies can be recorded. Other techniques, such as digital filtering of the original time series, can be used to obtain a record of the oscillations from moment to moment at a particular frequency. The instantaneous phase and amplitude of such records can be separated and records from various scalp sites can be juxtaposed over space and time to study the short- and long-range interactions of groups of neurons.

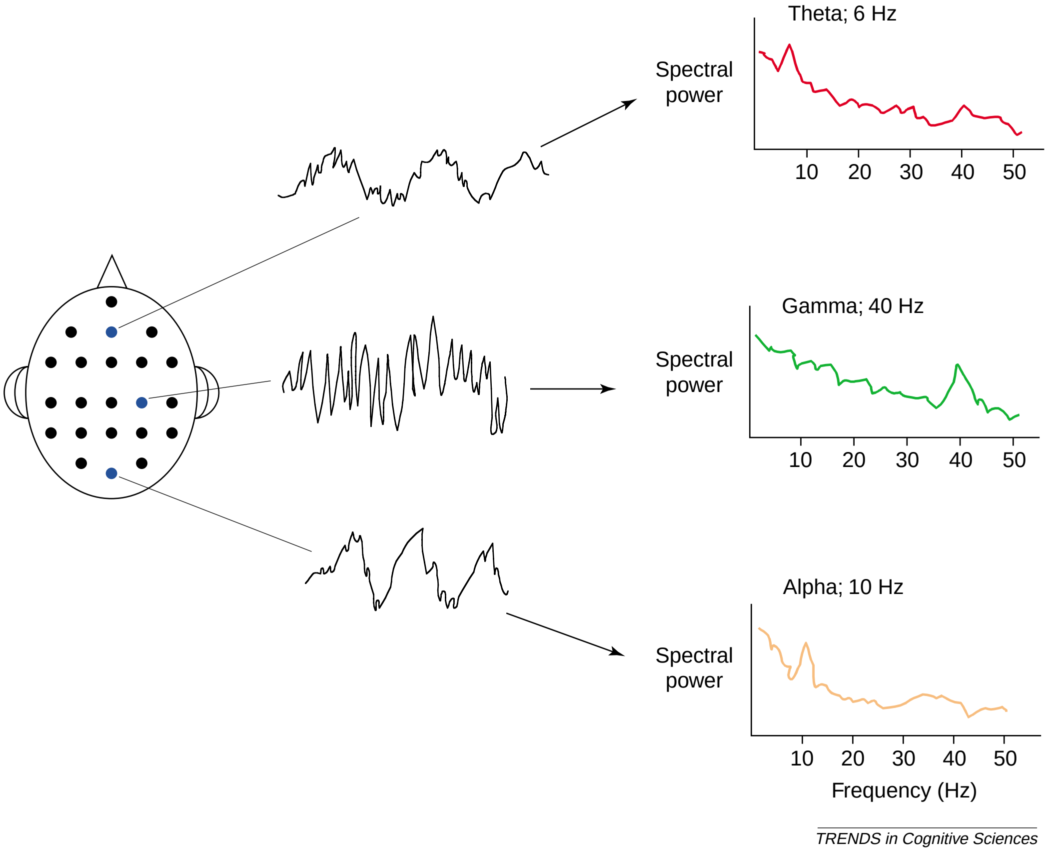

Figure I. Some idealized power spectra showing peaks at canonical EEG frequencies. Although any of the frequencies can occur at any electrode site, alpha power modulations are often recorded at posterior sites, theta at frontal sites, and gamma over sensory cortices.

An oscillatory model of short-term memory

Among the models of memory processes that have been proposed linking neural oscillations to memory processes (e.g. [19–22]), one in particular describes a close relationship between theta and gamma oscillations arising from the neural basis of short-term, or working, memory. Figure 1a illustrates some aspects of this model, which was constructed by Lisman and Idiart [23]. In the model, memories are stored in groups of pyramidal neurons firing in synchrony. The synchronous firing tends to dissipate with time, however, and needs to be refreshed periodically, much as a computer monitor screen does. The individual memories are refreshed at the gamma frequency and the overall refresh cycle is repeated at the theta frequency. The model requires that gamma oscillations modulated at the theta frequency be present in the human brain. Such oscillations have been recorded from human cortex (see Box 1, Figure I, [18,23]).

If memories are refreshed at the gamma rate once per theta cycle, then the number of items that can be held in short-term memory is approximately the gamma frequency divided by the theta frequency, or about 40/6,

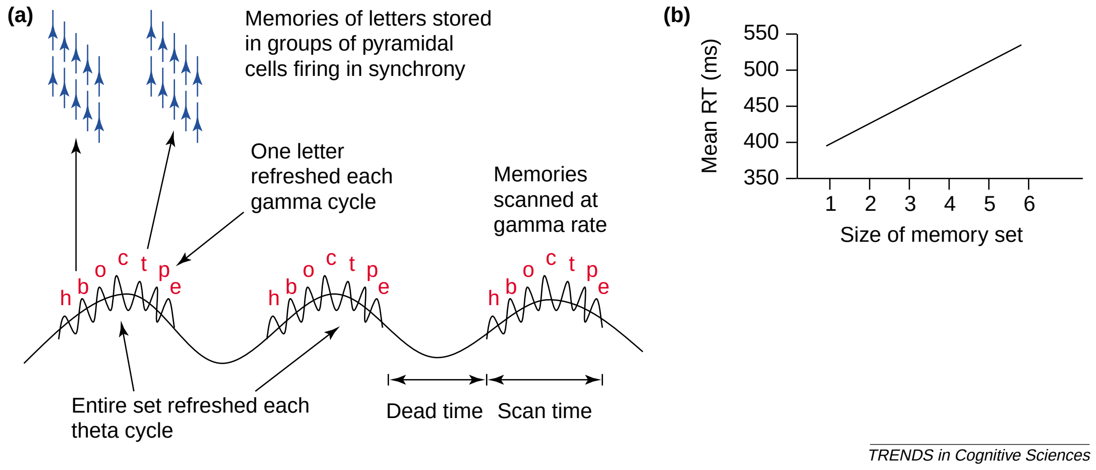

Figure 1. **(a)** Cartoon of some aspects of Lisman and Idiart's [23] model of short-term memory, including a representation of how the model could function during the Sternberg memory scanning task. Notice the blending of the gamma and theta oscillations. **(b** Representation of a typical result in the Sternberg memory scanning task: the reaction time (RT) for whether a probe letter is in the memory set increases linearly as the number of letters in the set increases, similarly for both 'no' and 'yes' responses, although the line for 'no' responses is typically above that for 'yes' responses.

or ~ 7 memories without loss. This is just the number, 7 ± 2, suggested by Miller as the average short-term memory capacity [24]. One recent estimate of short-term memory capacity, however, is somewhat lower, around 3–5 items [25]. If accepted, this number could present a problem for the gamma/theta model. This estimate is not universally accepted, however; in particular it does not refer to items held in memory but rather to processing capacity [25]. Nonetheless, the model needs to be able to accommodate variations in short-term memory capacity with task factors and individual differences. As theta can vary at least over the range 3.5 Hz to 7 Hz and gamma over the range 30 Hz to 70 Hz, a fairly broad range of capacities can be accommodated by the model, from around 3 or 4 items to nearly 20 items. It remains to be shown, however, that either theta or gamma frequencies (or both) vary appropriately with the same factors, so that the quotient gamma/theta equals the particular capacity found empirically in a particular situation.

The model can also account for how short-term memory could function in the Sternberg memory scanning task [26]. In this task, experimental subjects are given a set of items to remember, say the letters 'd', 'g', and 'z', and then, after a short delay, are asked to say whether or not a probe item, say 'a', is among the items in the memory set. Time to respond in this task typically increases linearly with the number of items in the memory set (Figure 1b). The model not only accounted for the linear increases with memory set size of the mean, variance and skewness of response times, but also for the faster responding for items most recently entered into the memory set when the list-probe delay is short. An experiment in which subjects performed the memory-scanning task while listening to a train of auditory clicks provides additional support [27]. A previous study had demonstrated that the presentation rate of such clicks tends to determine the frequency of the gamma oscillation [28], thus theoretically influencing the rate at which short-term memories could be scanned. Memory scanning times showed the predicted modulations as a function of the click rate, confirming the importance of a 'gamma-clocked' scanning process. Moreover, both iEEG and MEG have revealed evidence that theta power increases during the performance of the Sternberg task, more so the greater the memory load. Interestingly, the MEG study found that theta power in the frontal cortex increased during all phases, encoding, retention and scanning [29], whereas the iEEG study found an increase in theta power only during encoding and retention, and a decrease during scanning [30]. Because different neurons were monitored in the two studies, in particular the iEEG electrodes were distributed in grids over various regions of cortical surface, these results indicate that theta oscillations might play different roles in different cortical areas. One possibility is that several different memory processes interact by phase locking their theta (and other) rhythms to communicate results and commands. This is supported by another iEEG study that found increased phase locking (but decreased theta power) in the theta and alpha frequency bands between various, even distant, sites in the brain during a difficult working memory task, suggestive of the interactions of a central executive process with an occipital visual scratch pad, an articulatory loop, and a limbic monitor [31].

There remain challenges to the gamma/theta model of short-term memory both in terms of developing the model to account for additional empirical facts about short-term memory (alternative models can account for the basic Sternberg data and may do better with other memory facts [32]), and also in terms of the functional anatomy of the brain regions associated with short-term memory, such as frontal and temporal areas. The gamma/theta model, however, does show that it is theoretically possible to bring brain oscillatory processes into close correspondence with dynamic memory processes.

Alpha and gamma and attention

Attention is a dynamic process. The attention 'spotlight' typically moves from one location in space to another over a period of less than a second to a few seconds, like the spotlight at a variety show. Very general dynamical models of this process have been proposed [33], and much is known about the attention orienting process on the scale of hundreds of milliseconds [34]. The cyclic organization of infants' attention at around 0.5 Hz to 2 Hz is closely related to how efficiently they process information and possibly to intelligence [35]. Now links are beginning to emerge between the dynamical mechanisms postulated by attention researchers and the large-scale oscillations of the brain. Just as theta and gamma appear to be important rhythms for memory processes, so alpha and gamma appear to be prominent in attention.

Alpha and attentional suppression

First, and in contrast to the earlier notion that alpha synchronization indexes 'cortical idling', it is becoming apparent that alpha oscillations indicate that attention is actively suppressing cortical activity related to distractors as a part of the process of focusing attention on important targets. For example, alpha power increases with memory load in the Sternberg memory-scanning task, reflecting the increases in the need to suppress distraction [36]. Moreover, when attention is directed internally towards mental imagery, alpha power at attention-relevant scalp sites is greater than during externally-directed, information-intake tasks, reflecting suppression of external input during the imagery task [37]. Also in this study, when external task load increased, alpha power increased, reflecting the need to suppress competing information sources.

Changes in alpha power can also anticipate attentional demands, as when a cue indicating an upcoming auditory stimulus induced increased alpha power over parieto-occipital (visual) cortex compared with when the cue indicated an upcoming visual stimulus [38,39]. In purely visual tasks, such changes occur precisely over visual cortical areas where neural activity representing distractors in the visual field is likely to occur [40]. Interestingly, induced alpha power decreased over the entire scalp ~300–700 ms after attended visual stimuli appeared in comparison with when unattended stimuli appeared, whereas beta power (~16 Hz) increased around 600 ms after the stimulus occurred [41]. The alpha decrease was around the time that gamma power increased, possibly representing temporal binding of visual features [42], suggesting that gamma synchronization for feature binding might require alpha desynchronization.

Gamma and attentional processing

Gamma oscillations in general are associated with processing of attended stimuli, with increased induced gamma power occurring ~250–300 ms after an attended-stimulus presentation in a variety of paradigms, particularly in the visual modality [43]. It has been proposed [44] that suppression of gamma synchronization associated with the second of two targets in a rapid serial visual presentation task is responsible for its significantly lower frequency of detection when presented within ~500 ms of the first target, called the 'attentional blink'. [45] The idea is that the even earlier evoked-gamma synchronization (~100 ms post-target) that should be triggered by the second target is suppressed by the ongoing processing of the first target, resulting in a failure to induce the later gamma oscillations that allow the second target to be perceived and remembered.

A model of attentional entrainment

Several models of the dynamics of attention consistent with the modulations of alpha and gamma oscillations just described have been proposed [46–48]. All of these models describe hypothetical neural dynamics that accomplish attentional tasks such as preparation, orienting, feature binding, filtering, and so forth, postulating various synchronous neural oscillatory processes as necessary to the intercommunication of the neuron groups. Because of its dynamical nature, however, I wish to focus here on a model that describes how attentional oscillations can be entrained by external stimuli. Large and Jones's oscillatory model [49] is illustrated in Figure 2. Attentional effort, or resource, is assumed to occur in oscillatory pulses, distributed in time by a simple phase oscillator whose period and phase can be entrained by rhythmical external stimuli such as music. When not entrained the phase and period drift around, possibly at an average frequency of ~0.5 to 2 Hz, and the focus widens. In the presence of external rhythmical stimuli, however, period and phase become entrained to the rhythm, and focus narrows to the emphasized points in time. The consequence of this focus on specific time points is that stimuli that occur when expected are processed more effectively, whereas those that occur at unexpected times suffer processing deficits [49–51]. Importantly, under such conditions alpha oscillations are phase-locked to the occurrences of the entraining stimuli, even when they are omitted, indicating that attentional resources are being mustered for those specific processing moments [52].

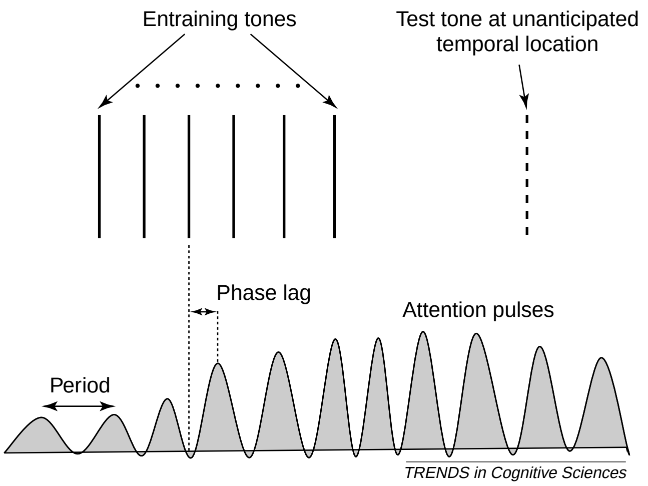

Figure 2. Cartoon of Large and Jones's [49] theory of oscillatory attention (based on [50]). The 'hills' at the bottom represent pulses of attentional resource concentration, which are distributed in time according to a phase oscillator, whose period and phase can become entrained to rhythmical external stimuli (represented by vertical black bars). When the attentional oscillator is not entrained, attentional pulses are broad (large period), representing a relatively temporally unfocused state. They become narrower (more focused in time) when the oscillator is entrained, and drift again when the external stimuli cease. Performance is best when target stimuli occur at expected times (peaks of the attentional pulses).

Gamma and consciousness

Crick and Koch suggested over a decade ago that synchronous neural firing at the gamma frequency might be the neural correlate of visual awareness [53]. Since then several important studies have reported correlations between conscious awareness and synchronous neural activity at various frequencies. In one of these, the EEG was recorded while subjects viewed an ambiguous visual stimulus that could be perceived as either a face or as a meaningless shape [54]. When subjects reported seeing a face, phase synchronization at the gamma frequency occurred across widely-separated brain areas; this synchronization did not appear when a meaningless pattern was reported. In a different context, awareness of the signaling properties of a stimulus in an associative learning experiment was correlated with long-range synchrony at the gamma frequency [55]. Finally, changes in conscious awareness of one or the other of two binocularly-rivaling visual stimuli are accompanied by a change in the synchrony of the firing of the neurons representing the stimuli. There is widespread coherence between the MEG at various non-sensory brain sites and the MEG of sensory neurons responding to a stimulus that is currently in consciousness, whereas there is no such coherence for stimuli present on the retina but currently not in consciousness ('suppressed' in terms of binocular rivalry) [56]. Coherence is related to the square of the correlation coefficient between two time series, in this case of MEG measurements. This finding led Edelman and Tononi [57,58] to suggest that the neural basis for consciousness is what they called a 'dynamic core' of synchronous firing occurring globally across many brain areas, whereas the locally synchronous firings evoked by external stimuli are unconscious unless integrated into the dynamic core.

Box 3. Questions for future research

- Approximate frequency doublings generate the centers of the EEG frequency bands: 2.5, 5, 10, 20, 40. Ratios of canonical frequencies are thus approximately powers of two. Why? What properties of neurons or neuron assemblies could generate this series? Why are particular frequencies associated with particular cognitive processes?
- Why would cognitive processing be accomplished at the peak of the theta cycle, or be gated by it? And why the gamma frequency for detailed operations? Why do gamma frequency oscillations emerge spontaneously from neural network dynamics? What is(are) the role(s) of the gamma frequency oscillations in cognitive dynamics?
- Exactly how does a neuronal assembly accomplish the computations involved in memory? Attention? Other processing?
- Are the oscillations we observe at the scalp only generally reflective of cognitive processing, or are nuances of their dynamics (perhaps unobservable at present) deeply related to the dynamics of the cognitive processes with which they are associated?
- Can dynamical models account for the details of empirical data generated in the paradigms of cognitive psychology, or must more conventional, static models, instead, be appealed to in the end?

Synchronous neural oscillations and cognitive science

The research I have discussed supports the idea that the neural oscillations revealed by the EEG and the MEG are closely related to dynamic processes of cognition. They are consistent with the idea that fundamental cognitive processes arise from the synchronous activity of neurons in the brain. Moreover, specific oscillations can be identified with particular cognitive processes: theta and gamma rhythms with memory encoding and retrieval, alpha and gamma rhythms with attentional suppression and focusing, and global synchronization at the gamma frequency with consciousness (see Box 3 for future research questions). These associations, in turn, promote the effort to develop dynamical models that unify the details of the time evolution of cognitive processes with those of the underlying neural processes. Such models both provide a complementary perspective on cognition to the more traditional statical models, and represent progress beyond those models in our understanding of cognition.

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