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Chosen Review Article
'Synchronous neural oscillations and cognitive processes' by Lawrence M. Ward, 2003 [1].

Review Article Summary
The discipline of cognitive neuroscience seeks to understand how processes observed in the brain give rise to known cognitive processes. In the last decade, there has been a major progress in relating the dynamics of cognitive processes such as memory, attention and even consciousness, to the large-scale oscillatory activity of the brain, as revealed by electro-encephalogram (EEG) and magneto-encephalogram (MEG) recordings.

Neurons can be described as oscillators in which the cell membrane potential is modulated by two processes – a fast action potential and a slow-varying post-synaptic potential. Lowering the post-synaptic potential causes the membrane potential to cross the activation threshold potential later, thus delaying the phase of the neural oscillation. This mechanism enables phase synchronization between individual interacting neurons, as well as between entire assemblages of neurons. A local pulse-coupling to an excitation can lead to global synchronization, which in turn can be rapidly desynchronized by a global inhibitory mechanism.

Moreover, groups of synchronously firing neural oscillators can be modelled as second-order oscillators whose frequencies are eigenvalues of the neural network parameters, while their amplitude reflects the number of neurons in the group.

In simulations of networks of relaxation oscillator neurons, oscillations rose spontaneously at frequencies measured in EEG/MEG recordings – such as delta (0.5-4 Hz), theta (4-8 Hz), alpha (8-12 Hz), beta (12-25 Hz) and gamma (25-70 Hz). One study analyzed a simulated network of 4500 coupled model neurons, consisting of equal numbers of pyramidal, feedforward inhibitory and feedback inhibitory neurons. In this network, oscillations were observed at the gamma frequency (~40 Hz) modulated at the slower theta frequency (~6 Hz). Similar oscillations were observed in EEG/MEG recordings, and were thus attributed to assemblages of synchronously oscillating neurons, particularly cortical pyramidal neurons. It has been argued that these assemblages perform the computations that give rise to cognitive processes.

Intracranial EEG (iEEG) recordings from epileptic patients memorizing words, revealed a correlation between successful memory formation and coupling of the rhinal cortex to the hippocampus via 40 Hz gamma oscillations. Moreover, during successful recollection, greater gamma-band functional connectivity between frontal and parietal cortex was observed, along with increased spectral power in both theta and gamma bands. Specifically, a modulation of the gamma band activity at the theta frequency was observed. Thus interactions of gamma and theta activity, similar to those found in model neural networks simulations, might be involved in memory function.

Back in 1995, Lisman and Idiart presented an oscillatory working memory buffer model with interesting predictions. In this model, memories are stored in groups of pyramidal neurons firing in synchrony. This synchronous firing has to be refreshed periodically due to dissipation. The core assumption of this model is that individual memories are refreshed at the gamma frequency whereas the overall refresh cycle is repeated at the theta frequency. Under this assumption, the number of items that can be held in working memory is roughly the individual memories refreshment frequency divided by the overall refreshment frequency, i.e. ~40/6 ~ 7
memories without loss. This fits nicely with the known "magic number 7±2" for the average capacity of working memory. Though both theta and gamma vary over a range broad enough to accommodate variations in working memory capacity, it remains to be shown that changes in the quotient gamma/theta match respective changes in working memory capacity.

This model was shown to account for the recurrent performances in the Sternberg memory scanning task. In this experiment [8], subjects are given a set of 1-6 unique letters or digits ('2', '7', '4', '9') to remember. Then after a short delay, the subject has to determine whether or not a probe item ('3') is among the items presented. The average reaction time (RT) in the Sternberg task famously increases linearly with the number of items in the list (S), with similar increments for both positive and negative probes. This observation led to the suggestion that the search is exhaustive: Apparently the answer cannot be given until the entire list is scanned. However, when the list-probe delay is short (1.5 seconds or less), reaction time for a positive probe is shorter for items most recently shown. This serial position effect has been used as an argument against the serial scanning suggested by Sternberg.

The oscillatory working memory buffer model accounted for the linear increases with S of the mean, variance and skewness of reaction times [2]. In addition, it accommodated the serial position effect into the serial scanning hypothesis, by assuming that the time for encoding of the positive probe can be primed by previous exposure.

Additional support for this model was provided by an experiment in which subjects performed the Sternberg task while listening to a train of auditory clicks [7]. The frequency of the gamma oscillations was found in a previous study to be determined by the presentation rate of such clicks. Reaction time at the Sternberg task was modulated by the click rate, as predicted by the oscillatory buffer model. Furthermore, both iEEG [4] and MEG studies have indicated that theta power increases with memory load at the Sternberg task. The iEEG study found an increase in theta power only during encoding and retention, and a decrease during scanning, whereas the MEG study found an increase in theta power in the frontal cortex throughout the entire task session. This discrepancy suggests that theta oscillations play different roles in different cortical areas.

The oscillatory working memory buffer model provides a theoretical linkage between brain oscillatory processes and dynamic memory processes. However there remain further challenges to this model, both in terms of accounting for additional empirical facts regarding working memory, and in terms of the functional anatomy of the brain regions associated with working memory, such as the frontal and temporal areas.

Additional studies provided evidence for increased synchronized oscillatory activity in the human brain associated with attention and consciousness. One study for instance found an increase of alpha power with memory load in the Sternberg task [5], suggestingly reflecting the need to suppress distraction. In another study, widespread coherence was found between the MEG recordings at various non-sensory brain sites, and the MEG recordings at sensory neurons responding to a stimulus that is currently in consciousness. No such coherence was found for stimuli present on the retina but currently not in consciousness. Based on this finding, it was suggested that the neural basis for consciousness is a so-called 'dynamic core' of synchronous firing occurring globally across various brain areas. Locally synchronous firings evoked by external stimuli remain unconscious unless integrated into the dynamic core. This hypothesis is not testable yet, as at present, it is unknown exactly how does an assemblage of synchronously oscillating neurons accomplish the computations involved in any cognitive process, let alone consciousness. Another question for future research is whether the observed synchronous neural oscillations are deeply related somehow to the dynamics of cognitive processes with which they are associated, or are they merely symptoms reflecting the occurrence of these processes.
First Research Article Analysis

Chosen article: 'An Oscillatory Short-Term Memory Buffer Model Can Account for Data on the Sternberg Task' by Ole Jensen and John E. Lisman, 1998 [2].

In this article, the authors set out to show their previously suggested concept of oscillatory working memory buffer can quantitively account for data from Sternberg task experiments. Furthermore, the authors analyze the serial position effect found for short list-probe delays, trying to accommodate this effect into the serial scanning hypothesis, upon which their memory buffer concept relies.

The authors first demonstrate how two simplistic forms of their memory buffer concept fail to account for the measured dependence of the average reaction time (RT) on the number of items (S) presented in the Sternberg task. They then propose two possible models for an oscillatory working memory buffer. The first model assumes the frequency decreases as the number of items held in working memory is increased. The other model assumes the phase of ongoing oscillations is reset by the probe. These models are mutually exclusive – in the first model there is no reset of the oscillations when the probe arrives, whereas in the second model there is no theta adaptation.

Both models are shown to quantitively account for the previously reported reaction time distributions (mean, variance and skewness). The serial position effect is then explained in the following manner. In both models, the average reaction time is decomposed into the following terms:

\[ RT = t_{\text{identify}} + t_{\text{wait}} + t_{\text{scan}} + t_{\text{skip}} + t_{\text{motor}} \]  
(Eqs. 2, 21 in [2])

The identification time \( t_{\text{identify}} \) of a positive probe is then assumed to be primed by the recent introduction of the equivalent item during presentation of the list:

\[ t_{\text{identify},i} = c_{\text{prime}} + t_{\text{prime}} \]

Where \( c_{\text{prime}} \) is a constant and \( t_{\text{prime}} \) is an exponentially saturating function:

\[ t_{\text{prime}} = \alpha \cdot [1-\exp(-t/\tau_{\text{prime}})] \]  
(Eq. 33 in [2])

Where \( t \) denotes the time since previous presentation and \( \alpha, \tau_{\text{prime}} \) are constants.

The authors demonstrate how this simple assumption, of an exponentially decaying priming of the probe identification time, accounts for the serial position effects found for various retention times. To my untrained eye, their best fit doesn't seem to match the experimental graph too well (see fig. 10 at [2]), and no error bars are provided as an aid. What's more, the equations accounting for this theoretical graph (Eqs. 34-36) are formulated in a rather ambiguous way. Nevertheless, there's no fundamental reason to preclude the existence of a proper distribution of \( t_{\text{prime}} \) that fits well the experimental serial position effect measurements. Thus, even if the authors fail to demonstrate an entire explanation for the serial position effect, they do pave the way for such a decoupling between a primed probe identification and an unprimed serial scan.

The authors formulate three distinct experimental predictions that can be used to test the two proposed buffer models:

1. If the adapting theta model is correct, the slow-wave oscillation during the retention period should systematically decrease in frequency with higher memory loads.

2. According to both models, the fraction of the theta period occupied by active memory representations should increase with memory load (S). Thus both models predict an increase in theta amplitude with S. According to the reset model, the number of activated neurons per theta cycle will increase linearly with S, whereas according to the adapting theta model it will increase sub-linearly with S.
3. Only the theta reset model predicts a reset of the phase of theta oscillations following the identification of the probe. Moreover, within the context of this prediction, the reset of the theta cycle should occur earlier for probes matching items late in the list, compared with negative probes and probes matching items early in the list. Evidence for such priming of the theta reset timing would support the proposal that priming of the encoding of the probe accounts for serial position effects.

All three predictions were tested in several studies rather shortly after this paper was published. The first was shown to be null (most decisively by [4]), while the other two were corroborated (for instance by [3,4,6]) in accordance with the theta reset model. I haven’t found a study directly testing whether the encoding of the probe is primed for probes matching items late in the list, as suggested in the third prediction. However my search was far from exhaustive.

It goes to show the importance of this article, which is still relevant in an 8 year perspective. It is endowed with clarity and vision, relating a 40 year old psychophysical test [8] to present-day neuroscientific research tools. Despite its relative weakness in explaining the serial position effect, it outlines an important theoretical framework in a field lacking just that.

One major argument against the suggested memory buffer models is disturbingly not mentioned at all in this article. Previous studies [13,14] have reported an extended working memory span for digits among native Chinese speakers, versus native English speakers. The Chinese subjects, at all K-2 grade levels, remembered at least 2 more digits, on average, than did American or Japanese subjects. This was attributed to the significantly shorter pronunciation duration for Chinese number words compared with English number words. As the total pronunciation duration for a subject's maximum span did not differ between Chinese and American children, these findings were used as evidence for a temporally limited store.

The memory buffer models suggested by Lisman & Jensen fail to address these lingual differences. Though both theta and gamma vary over a range broad enough to accommodate variations in working memory capacity, these are not linked with the memorized item pronunciation duration.

One possible way to accommodate the lingual difference within the framework of the buffer model, is to relate a higher gamma frequency to shorter words. Another way is to assume shorter words yield a higher probability \( P_a \) that the an answer is available after scanning through the first possible theta cycle. Either possibility have profound implications upon RT distributions, that should have been discussed in this article. Ignoring altogether the effect of word length on working memory span makes this important study somewhat deficient.
Second Research Article Analysis

Chosen article: 'Reset of human neocortical oscillations during a working memory task' by Rizzuto et al., 2003 [3].

In this article, the authors set out to examine the role of oscillatory phase in human cognition. Their motivation arises from studies in rodents that correlated both the amplitude and phase of rhythmic slow-wave EEG activity with learning and memory, and studies in humans that revealed high-amplitude of slow-wave activity during working memory tasks. Task events requiring encoding or retrieval processes were hypothesized to reset the phase of ongoing oscillations. This hypothesis was tested by recording iEEG signals from nine epileptic subjects while they performed a modified Sternberg task.

In this modified Sternberg task, the number of list items was fixed to four, and a temporal jitter of 150 milliseconds was introduced between each item. That is, each list item was displayed for 700 ms followed by a uniformly distributed delay of 275±75 ms. This jitter ensured that each stimulus arrived at a random phase with respect to ongoing oscillations, so that prestimulus phase was uniformly distributed for all frequencies above 6.6 Hz.

As expected, significant phase locking was demonstrated after the appearance of both the orienting stimulus, list items and probe. This phase locking was observed in a broad spectrum of frequencies between 4-40 Hz, with a majority of sites exhibiting phase locking in the 7-16 Hz range. Many more electrodes exhibited phase locking to probes than to list items or the orienting stimulus. Furthermore, at each frequency, a similar number of electrodes exhibited significant phase locking to both positive (in-set) and negative (out-of-set) probes. This finding suggests that the widespread phase locking to probes is not a consequence of item repetition, as only positive probes are repeats of list items.

Importantly, a significant negative correlation was found between postprobe power change and phase locking in the 9-16 Hz frequency range. This finding indicates phase locking in these frequencies reflects a reset of ongoing oscillations. However, as phase locking outside the 7-16 Hz range correlated positively with postprobe power changes, it is possible that phase locking in these frequencies arises from stimulus evoked activity. This discrimination between phase reset and poststimulus increases in band power is achieved for the first time in this study, referable to the prestimulus phase randomization described above. This is clearly the experimental highlight of this study.

In the 7-12 Hz frequency range, where phase-locking was most widespread, electrodes exhibiting preferential reset to probes were bilaterally found in the inferior temporal lobe and occipital lobes, as well as on the right parietal lobe. Interestingly, none of the electrodes implanted in frontal, prefrontal and suborbital frontal sites exhibited preferential reset to any stimulus class.

The preferential reset to probes, observed at the largest number of recording sites, could reflect either the memory comparison process or motor-preparatory mechanisms. The experimental procedure employed in this study can't tell the two mechanisms apart. However, one can easily come up with at least two modifications to the experimental procedure that would help doing just that. First, a 'RESPOND' signal (such as '?') can be presented 1-2 seconds after the probe is shown. Rather than instructing the participants to press a key as soon as they decide whether the probe item was in the preceding list, they can be instructed to press that key only once they see the '?' signal. Moreover, a 'CLICK' signal (such as '!'') can be presented several seconds after each trial. The participants could then be instructed to press a key once they see the '!' sign. Both modifications were meaningless when Sternberg first formulated this working memory task, but can tell a lot when newer-days EEG\MEG tools are available. Ideally, one should observe how, following probe presentation, the participant comes up with the answer. This answer is then chewed over by the participant until the '?' signal is recognized. Motor
mechanisms should then be observable. These could be compared to the identification of the '!' signal, followed by its relation to the instruction to press a key (an instruction which is in itself retrieved to working memory from long term memory), finally followed by the motor response. It is likely that motor-preparatory mechanisms would be present already after the participant comes up with an answer. The '!' signal could help distinguishing these motor-preparatory mechanisms from the memory comparison activity, which should be less significant following the '!' signal. The following table summarizes which mechanisms should be present following each stimulus:

<table>
<thead>
<tr>
<th></th>
<th>Orienting stimulus ('*')</th>
<th>List Item</th>
<th>Probe</th>
<th>Post-probe Retention</th>
<th>RESPOND Stimulus ('?')</th>
<th>CLICK Stimulus ('!')</th>
</tr>
</thead>
<tbody>
<tr>
<td>Attention</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Item Identification</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Relation to Instruction</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Encoding to Working Memory</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Working with Working Memory</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>?</td>
<td>-</td>
</tr>
<tr>
<td>Motor-preparatory Mechanisms</td>
<td>-</td>
<td>-</td>
<td>?</td>
<td>?</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Motor Mechanisms</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

The underlying assumption in this table is that all incoming verbal stimuli have to undergo identification and encoding to working memory in order to be related to the relevant instruction in the experimental context. However, only the presentation of the list items, the probe and possibly the RESPOND stimulus are assumed to trigger more complex computations with the items stored in working memory. This assumption is conceptually convenient but experimentally unproven.

The findings of this study corroborate the phase reset model suggested by Jensen & Lisman [2]. As discussed above (page 4), the reset of the theta cycle should occur earlier for probes matching items late in the list, compared with negative probes and probes matching items early in the list. Evidence for such priming of the theta reset timing would support the proposal that priming of the encoding of the probe accounts for serial position effects. The retention period in this study [3] was 500±75 ms, short enough for the theta reset priming prediction to be testable. However, no such analysis was reported. It should be stressed that by further data analysis alone, one should be able to extract confirmation or refutation for this theoretical prediction. Then again, my literature survey wasn't comprehensive enough to rule out later publication of such a test.

The temporal jitter introduced in this study yielded an important discrimination between phase reset and stimulus evoked activity. As a significant positive correlation was found between phase locking and postprobe power increase for frequencies below 7 Hz, it makes sense to strive for fully randomized prestimulus phase in these frequencies as well. It is unclear why the temporal jitter was not increased to 250 milliseconds or more, so that prestimulus phase would be uniformly distributed for all frequencies probed in this experiment (4 Hz and up).
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