Activation of long-term memory by alpha oscillations in a working-memory task?

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Abstract: We focus on the functional specificity of theta and alpha oscillations and show that theta is related to working memory, whereas alpha is related to semantic long-term memory. Recent studies, however, indicate that alpha oscillations also play an important role during short-term memory retention and retrieval. This latter finding provides support for the basic hypothesis suggested by Ruchkin et al.

We consider four typical findings. (1) Theta oscillations (with a frequency of about 6 Hz) reflect working memory, and (2) upper alpha (with a frequency of about 12 Hz) reflect semantic long-term memory. (3) Increased working-memory load during retention is reflected by increased theta activity over frontal areas and by (4) increased upper alpha activity over parietal regions that are associated with short-term memory storage. Our argument is that the load-dependent increase in upper alpha activity during retention may reflect the activation of long-term memory structures.

Although it has been questioned for a long time, there is still convincing evidence that theta oscillations can also be observed in humans, and that an increase in theta reflects working-memory demands (for an extensive review, see Klimesch 1999). There is also evidence that the topography of theta activity is associated with those cortical regions that are known to play an important role in working memory. As an example, Sarnthein et al. (1998) have found a significant increase in long-range theta coherence between prefrontal and posterior electrodes during a short-term retention task (as compared to a control task). In the verbal task, the pattern of coherent theta oscillations showed a network connecting left occipito-temporal with bilateral prefrontal regions. In the visual task, a more bilateral pattern was observed. The general interpretation of these and similar findings (Anokhin et al. 1999) is that theta oscillations reflect (at least some of those) neural processes that are relevant for working memory, comprising central executive processes located in frontal areas and coordination with short-term storage processes located in parietal areas (Baddeley 2000).

Alpha oscillations show a strikingly different pattern of physiological and functional reactivity. In contrast to theta, alpha oscillations decrease (desynchronize) with (sensory-semantic) task demands. Studies from our laboratory and other investigators indicate that the upper alpha frequency range (of about 10–12 Hz) responds selectively to sensory-semantic memory processes of a complex long-term memory system (cf. Klimesch 1999 for an extensive review). As a more recent example, let us briefly review findings from a sentence-processing task (Röhm et al. 2001). Sentences (such as "A rabbit is in the box, hiding") were presented in four chunks under two task conditions, a reading task and a semantic task. Whereas in the first task, subjects simply had to read the sentences, in the second (semantic) task an additional, semantic process had to be carried out. Subjects were instructed to find the superordinate concept to the noun of the third chunk (which is "container" in response to "box" in the present example). The findings indicate that, for the theta band, the event-related increase in band power is largest during processing of the first chunk and smallest for the fourth chunk. This seems to indicate that processing demands for working memory are largest during the processing of the first chunk (when subjects are prepared to encode the next following chunks) and lowest for the fourth chunk, when all parts can be successfully integrated into a sentence. The opposite pattern of results was obtained for the upper alpha band. Here, the extent of decrease in band power (desynchronization) was largest in the semantic task during the retrieval of the superordinate concept. Thus, the findings suggest that retrieving a superordinate concept from semantic memory is a process that does not draw on the capacity of the working-memory system.

For the retention period of memory-scanning tasks (such as the Sternberg and n-back task), an interesting similarity between the reactivity of theta and upper alpha oscillations, with respect to memory load, was found. Whereas it is well established that theta power increases with load (e.g., Gevins & Smith 2000; Jensen & Tesche 2002), several recent studies have found similar effects in the alpha frequency range, although with a different topography (Jensen et al. 2002; Klimesch et al. 1999; Schack & Klimesch 2002). These latter findings are surprising because it is so well documented that alpha power decreases with task demands.

In a recent study (Schack & Klimesch 2002), we have analyzed this phenomenon of paradoxical alpha synchronization in a Sternberg task with number words. We found that upper alpha power (at 12 Hz) increased significantly with set size at posterior recording sites (particularly at Pz and P4) during retention. Most interestingly, during retrieval, exactly within that frequency range, a significant increase in evoked power at 12 Hz could be observed, even in the event-related potential (ERP). In addition, we found that the extent of phase locking in upper alpha increased with set size. These findings indicate that oscillatory EEG activity in peak alpha frequency (functionally associated with the maintenance of information in working memory during retention) is related to evoked activity and increased phase locking during retrieval and memory scanning. Furthermore, the P3b (at Pz and P4) coincides with the last of three evoked alpha peaks. Thus, these findings strongly suggest that alpha oscillations play an active role in working memory, not only during retention but during scanning and retrieval as well. The latter finding implies that alpha oscillations coordinate the encoding of the probe, the scanning process, and the evaluation of the read-out process, which most likely is manifested by the P3b. When considering the functional specificity of alpha for semantic long-term memory and the topography of alpha phase locking and evoked activity over parietal areas, we may conclude that phase-locked alpha during scanning and retrieval reflects the "coactivation" of storage networks in long-term memory (LTM) where numbers are presented.

Retention systems of the brain: Evidence from neuropsychological patients

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Abstract: Studies of neuropsychological patients are relevant to models of how long-term memories are stored. If amnesia is considered a binding deficit and not a difficulty in transferring information from short-term to long-term memory, it is unclear why context-free semantic learning is impaired. Also the model should account for the reverse temporal gradient seen in patients with semantic dementia.

The dissociation of short-term and long-term memory abilities in amnesic patients is considered one of the most important findings supporting the idea that there are separate stores. However, Ruchkin et al. note that this dissociation could be accounted for if one assumes that the deficit in amnesia is one of binding rather than the formation of long-term memory representations. By this view, there are no differences between the long-term memory representations in amnesic patients and neurologically intact individuals. Although amnesic patients are able to dynamically bind representations in working memory, they are impaired at the formation of bindings between the elements of a memory that support its long-term retrieval. According to this view, the brain structures damaged in amnesia (e.g., medial temporal lobe structures) play a role in forging these new bindings between preexisting elements in long-term memory.

The idea that amnesia is a deficit in long-term binding is appealing. Patients with amnesia exhibit severe deficits in episodic memory, or memory for experienced events. Fundamental to the definition of episodic memories is the idea that they are comprised of disparate temporal and contextual (external and internal) elements that uniquely determine each episode. If amnesic patients were unable to bind these elements in the long term, they would exhibit impaired retention of episodes once they are no longer held in working memory. However, amnesic patients, particularly those in whom medial temporal lobe damage extends outside of the hippocampus, are also impaired at learning new semantic information, such as facts and new vocabulary words (Squire & Zola 1998). They also exhibit impaired memory based on familiarity (Yonelinas et al. 1998). For these types of memory it is not clear how formation of semantic memories depends on long-term binding. Learning a new vocabulary word could be viewed as forming new connections between the phonological elements of the word and semantic elements. However, it is not obvious why amnesic patients would be impaired at this type of binding, but not the type of binding that supports non-declarative forms of learning that are intact in amnesia, such as priming for novel information, text-specific facilitation of reading speed with practice, and sequence-specific learning in the serial reaction time task (Squire et al. 1993). It may be that amnesic patients are specifically impaired in binding that leads to consciously accessible (or declarative) information. However, it seems somewhat more parsimonious to hypothesize that they are impaired at the formation of declarative memory representations, rather than in a particular set of binding processes.

In addition to studies of amnesia, equally important insights into memory function have been gained by research on how depth-of-processing manipulations facilitate later memory retrieval (Craik & Lockhart 1972). If one hypothesizes that the encoding of new memories results in the creation of new representations, one would suppose that deep, semantic encoding of information would create a richer, more interconnected, and more robust memory representation than when only surface features are processed. However, if one views the creation of new memories as the formation of new bindings between pre-existing elements, one would interpret deeper encoding as leading to more extensive binding. However, one might predict that if amnesic patients have deficient long-term binding processes, they would not benefit as much as neurologically intact individuals would from deeper processing at study. In fact, depth-of-processing effects are generally proportional for amnesic patients (Hamann & Squire 1996), suggesting that amnesia and depth of processing affect memory independently.

Another neuropsychological syndrome that is relevant to the study of memory representations is semantic dementia. Semantic dementia (SD) is a clinical term given to the temporal variant of frontotemporal dementia in which the affected patient shows progressive focal atrophy of the inferolateral aspect of the left and/or right temporal lobes with (in the early stages) relative sparing of the hippocampal complex (Graham & Hodges 1997). Although SD patients show a severe loss of semantic information (i.e., picture naming, verbal definitions of words, category fluency) and produce errors that reflect a loss of subordinate information while having superordinate information relatively preserved, they are able to recall recent life events with relative clarity and often perform relatively well on tests of nonverbal working memory (Hodges & Miller 2001). Patients with SD have also been found to show a temporal gradient in recognition of famous people that is the reverse of that shown by amnesic patients. Hodges and Graham (1998) reported that four patients with semantic dementia were better able to recognize currently famous individuals than previously famous individuals from a set of names of famous and nonfamous people. They were also better at identifying information about currently famous people. These results provide compelling evidence that individuals with lateral temporal damage are able to store memories, initially, in a part of the brain (presumably the medial temporal lobes) that remains intact. Older knowledge, perhaps because it has been relocated to regions that are damaged by the disease process, does not fare as well. If long-term memories are simply bound representations of pre-existing knowledge, it is unclear why recent memories are spared if they depend on the same set of stored representations as more remote memories. It would seem that new memories and older memories should be equally affected by a loss of semantic knowledge. Rather, these data seem more consistent with the idea that recent memories depend on different neural representations than older memories. If memory representations depend on different neural substrates as they age, and if working memory is simply activation of long-term memory, this raises the question of how "activated" recent and remote memories may differ.

Ruchkin et al. have made a compelling case for their view based on electrophysiological and behavioral evidence from neurologically intact individuals. It is important to account for the data from neuropsychological patients, as well. It may be that their model can be made consistent with neuropsychological findings, if certain assumptions are made as to the processes impaired in these patients. Hopefully, these assumptions will be testable as a means to further assess their model.

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Long-term memories, features, and novelty

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Abstract: Ruchkin et al. make a strong claim about the neural substrates of active information. Some qualifications on that conclusion are: (1) Long-term memories and neural substrates activated for perception of information are not the same thing; (2) humans are capable of retaining novel information in working memory, which is not long-term memory; (3) the content of working memory, a dynamically bound representation, is a quantity above and beyond the long-term memories activated, or the activity in perceptual substrates.

Ruchkin et al. present compelling evidence that information in working memory, rather than existing in a special purpose buffer distinct from the neural substrates specialized for perceiving that kind of information, is a state of activation in those same substrates under the control of frontal cortex. As the authors note, this is a more parsimonious scheme than duplicate representation architectures for the perception and storage of the myriad kinds of information we deal with. The view that attention activates representations, even in low-level visual areas, has also been demonstrated for nonverbal information by Kastner et al. (1999) and others, and the control of posterior representations by frontal cortex was embodied in our computational model of working memory (Kroger et al. 1998).

It might be possible to make a more explicit distinction between "long-term memory" in the sense of semantic information that is activated (e.g., in inferior temporal cortex) during retention of verbal information in working memory, and the neural substrates that are engaged as information is perceived. In terms of verbal information, there may be a great deal of overlap, as perceived words typically activate areas specific to semantic information storage. However, as a general principle of information storage, some caution is called for. It is well established that cells in primary visual