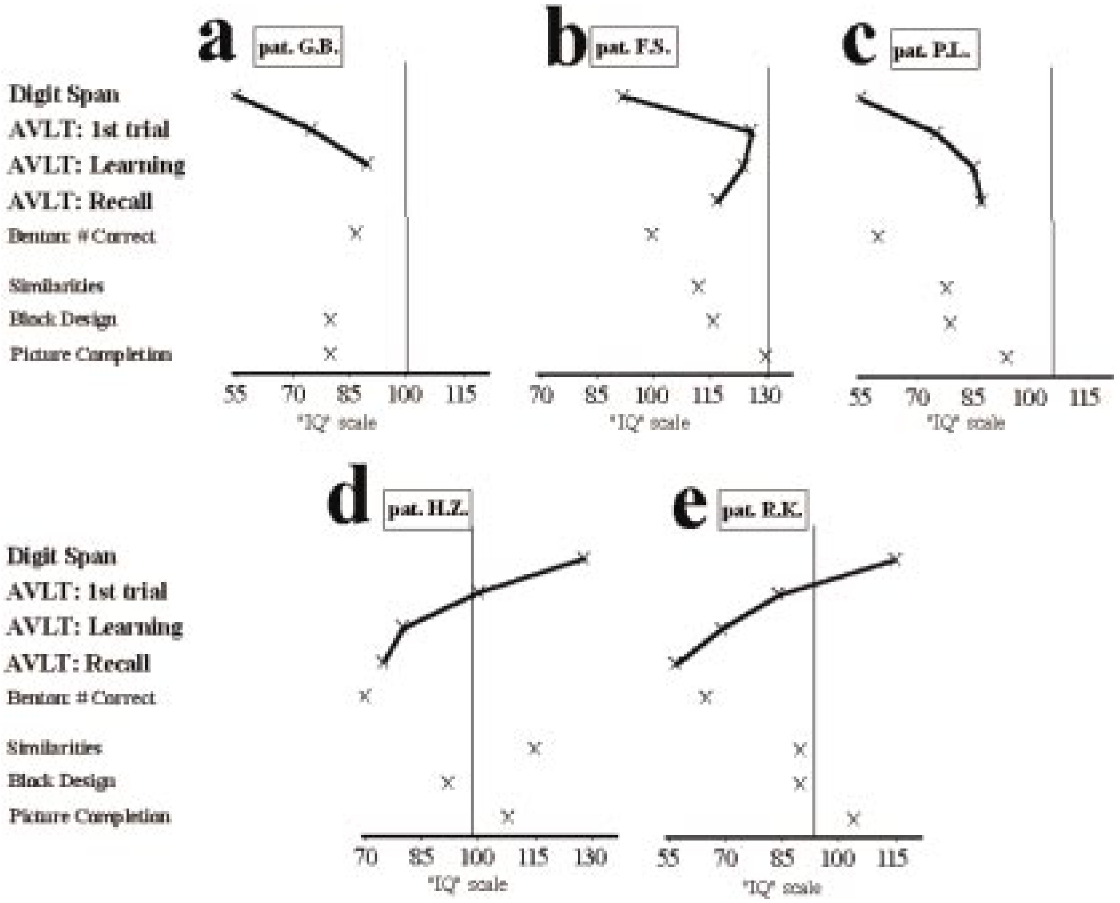

Figure 1 (Verleger). Double dissociation between memory functions measured by Digit Span and by AVLT. To have a common scale, all tests scores were converted to the IQ scale, transforming their means to 100 and their standard deviations to 15. Premorbid cognitive level, indicated by the vertical line, was estimated with a vocabulary test (Lehrl 1977), and basic aspects of cognitive functions were evaluated with the Wechsler Adult Intelligence Scale subtests: Picture Completion, Communalities, and Block Design (Tewes 1991). Benton's test of visual retention was included as an additional test of memory, but it did not clearly contribute to the double dissociation (being affected in all patients, except in Wernicke aphasia, panel a).

Neuronal synchronization accompanying memory processing

Sabine Weiss[a] and Horst M. Mueller[b]

[a]*Brain Research Institute, Cognitive Neuroscience Group, University of Vienna, A-1090 Vienna, Austria, and SFB 360, University of Bielefeld, Germany;* [b]*Experimental Neurolinguistics Group – SFB 360, Faculty of Linguistics, University of Bielefeld, 33501 Bielefeld, Germany.*
sabine.weiss@univie.ac.at **horst.mueller@uni-bielefeld.de**
http://www.univie.ac.at/cognitiveneuroscience/
http://www.lili.uni-bielefeld.de/~enl/

Abstract: In their target article, Ruchkin et al. propose sustained neuronal interaction of prefrontal and posterior cortex involved in memory-storage mechanisms with respect to electrophysiological findings on the relationship of short-term and long-term memory processes. We will evaluate this claim in light of recent evidence from our laboratory on EEG coherence analysis of memory processes accompanying language comprehension.

Referring to several event-related potential (ERP) studies and one electroencephalographic (EEG) coherence study, Ruchkin et al. support the view that the same multiple memory systems serve short-term as well as long-term memory, and that only the degree of coactivation between the relevant memory systems differs. In contrast to models proposing specialized neural systems as short-term buffers, Ruchkin et al. postulate that short-term storage mechanisms involve an increase in neural synchronization during both the encoding/comprehension and the retention phases. In particular, they propose an increased synchronization between the prefrontal cortex, serving as a top-down controlling system, and the posterior cortex, which participates in perception and encoding.

One of the few methods suitable for measuring frequency band-related neuronal synchronization accompanying cognitive processes in healthy humans is the calculation of coherence between EEG or magnetoencephalographic (MEG) signals. During the last 20 years, several cognitive processes, such as memory, language, music processing, and thinking, have been studied with EEG coherence (for reviews, see Petsche & Etlinger 1998; Rappelsberger & Petsche 1988). Consistent with Ruchkin et al.'s results on EEG coherence accompanying memory processes, increased neuronal synchronization, in particular between signals at distant electrodes (large-scale coherence), was described for various different, complex cognitive tasks (for reviews, see Bressler & Kelso 2001; Petsche & Etlinger 1998). Other measures, such as phase synchronization (Varela et al. 2001) or phase relations (Schack et al. 2003), which indicate direction and propagation speed of information transfer, are even more promising for investigating large-scale synchronization. In general, high coherence correlates with long-lasting negativities in the ERP and is often found during increased task complexity and efficient information processing, whereas low coherence is often found in pathological conditions (for reviews, see Petsche & Etlinger 1998; Weiss & Mueller 2003).

In an EEG coherence study, Ruchkin et al. found increased theta coherence (4–6 Hz) during sentence comprehension, but not during retention. The reverse was true for the 10–14 Hz band. These frequency-specific results partly correspond to our findings on EEG coherence changes in an experiment where subjects process English relative clauses (Weiss & Mueller 2003; Weiss et al. 2001). Within the theta band (5–7 Hz), more complex relative clauses showed significantly higher coherence in the post-relative clause, whereas within the beta-1 band (13–18 Hz), they already showed higher coherence at the beginning of the relative clause and in the post-relative clause. One of the possible interpretations of these findings is that theta activity is related to working memory and that beta-1 correlates to the activation of a separate parsing buffer, similar to that proposed by Caplan and Waters (1999). This means that, at the beginning of the relative clause, the load of the parsing buffer significantly differs between the two sentence types, whereas the load of working memory does not significantly differ at this stage. Another possibility is that the beta-1 band reflects syntactic working memory and theta is correlated with efficient processing during verbal memory encoding. This may partly explain Ruchkin et al.'s present results. Although these questions have to remain open at present, coherence within different frequency bands possibly reflects different aspects of sentence processing (Weiss & Mueller 2003; Weiss et al. 2001).

The finding of Ruchkin et al. on increased neuronal large-scale synchronization during memory processes corresponds well with our findings on EEG coherence during memory encoding of words (Weiss & Rappelsberger 2000; Weiss et al. 2000). In these studies, nouns – later successfully recalled – exhibited overall enhanced synchronization but showed typical patterns, especially between left frontal and posterior sites. This increased neuronal synchronization occurred regardless of modality (auditory or visual material) and word category (concrete or abstract). In addition, the degree of interhemispheric synchronization was higher during encoding of later-recalled nouns, suggesting an increased hemispheric interaction. In order to avoid detecting strictly linear dependencies, and because coherence concerns correlation across trials of both amplitude and phase, phase synchronization was also calculated (Schack & Weiss 2003). Differences in evoked- and induced-phase synchronization for recalled versus non-recalled nouns appeared for theta, alpha, and gamma oscillations. Gamma oscillations at *Fz* and *Cz* were nested in theta oscillations for recalled nouns. Recently, Schack et al. (2002) found increased phase coupling of theta-gamma EEG rhythms during short-term memory processing by means of bispectral analysis, suggesting an amplitude modulation of gamma frequencies by slow oscillations. The pattern of anterior–posterior EEG coherence and phase synchronization accompanying verbal memory encoding allowed us to assess the probability of whether nouns would be recalled or not.

Ruchkin et al.'s findings and our results argue that EEG-coherence analysis is an important tool for studying high-level cognitive processes, such as language or memory. This method supports a somewhat different view on brain function, insofar as the actual information processing is not correlated with location, but with interaction. With the calculation of coherence, it is also possible to get information on the temporal dynamics during cognition with the same temporal resolution as with ERPs (Schack et al. 2003). In addition, coherence is a frequency-dependent measure, and patterns of coherence networks tend to differ between frequencies. The meaning of coherence networks may be interpreted differently depending on the frequency band investigated, because different components of a cognitive task are presumably processed via different frequencies (Basar 1998). During linguistic information processing, our own studies point at different roles of high- and low-frequency synchronization. Activities within the theta frequency range (around 3–7 Hz) seem correlated with language-related mnemonic processes, and theta coherence increases if task demands increase and more efficient information processing is required. The alpha frequency (8–12 Hz) is probably important for sensory and, in the higher range, for semantic processing, whereas the beta (13–30 Hz) and gamma (>30 Hz) frequencies seem to be correlated with more complex linguistic sub-processes, such as syntax or semantics (for a review, see Weiss & Mueller 2003). Large-scale information transfer via frequency coding is possibly one of the mechanisms that facilitate parallel processing within the brain, since a single signal may contain different aspects of information within various frequency ranges.

ACKNOWLEDGMENTS
Supported by the Austrian Science Foundation ("Herta Firnberg" project T127) and the German Science Foundation (SFB 360).

Authors' Response

Working memory: Unemployed but still doing day labor

Daniel S. Ruchkin,[a] Jordan Grafman,[b] Katherine Cameron[c], and Rita S. Berndt[d]
[a]*Department of Physiology, Program in Neurosciences, University of Maryland School of Medicine, Baltimore, MD 21201;* [b]*National Institutes of Health, Cognitive Neuroscience Section, NINDS, Bethesda, MD 20892;* [c]*Department of Psychology, Washington College, Chestertown, MD 21620;* [d]*Department of Neurology, Program in Neurosciences, University of Maryland School of Medicine, Baltimore, MD 21201.*
druchkin@mindspring.com grafmanj@ninds.hih.gov
katherine.cameron@washcoll.edu rberndt@umaryland.edu
http://intra.ninds.hih.gov/Lab.asp?Org_ID=83
http://faculty.washcoll.edu/bios/cameron_katherine.html
http://neuroscience.umaryland.edu/faculty.asp?FacultyID=4

Abstract: The goal of our target article is to establish that electrophysiological data constrain models of short-term memory retention operations to schemes in which activated long-term memory is its representational basis. The temporary stores correspond to neural circuits involved in the perception and subsequent processing of the relevant information, and do not involve specialized neural circuits dedicated to the temporary holding of information outside of those embedded in long-term memory. The commentaries ranged from general agreement with the view that short-term memory stores correspond to activated long-term memory (e.g., **Abry**, **Sato**, **Schwartz**, **Loevenbruck & Cathiard** [**Abry etal.**], **Cowan**, **Fuster**, **Grote**, **Hickok & Buchsbaum**, **Keenan**, **Hyönä & Kaakinen** [**Keenan et al.**], **Martin**, **Morra**), to taking a definite exception to this view (e.g., **Baddeley**, **Düzel**, **Logie & Della Sala**, **Kroger**, **Majerus**, **Van der Linden**, **Colette & Salmon** [**Majerus et al.**], **Vallar**).

We first discuss comments on the scope of the target article and respond to questions raised about the utility and validity of event-related potential (ERP) data in the study of short-term memory. We then address neurophysiological data that appear to contradict the contention that activated long-term memory is the representational basis for short-term memory, followed by a discussion of neurophysiological data presented in the commentaries that support the contention. We then address misinterpretations of our position, the issue of activation of long-term memory in the processing of novel information, and briefly comment on sleep and memory consolidation.