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ORIGINAL ARTICLE

The electrophysiological correlates of the working memory subcomponents: evidence from high-density EEG and coherence analysis

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Abstract Synchronization between prefrontal (executive) and posterior (association) cortices seems a plausible mechanism for temporary maintenance of information. However, while EEG studies reported involvement of (pre)frontal midline structures in synchronization, functional neuroimaging elucidated the importance of lateral prefrontal cortex (PFC) in working memory (WM). Verbal and spatial WM rely on lateralized subsystems (phonological loop and visuospatial sketchpad, respectively), yet only trends for hemispheric dissociation of networks supporting rehearsal of verbal and spatial information were identified by EEG. As oscillatory activity is WM load dependent, we applied an individually tailored submaximal load for verbal (V) and spatial (S) task to enhance synchronization in the relevant functional networks. To map these networks, we used high-density EEG and coherence analysis. Our results imply that the synchronized activity is limited to highly specialized areas that correspond well with the areas identified by functional neuroimaging. In both V and S task, two independent networks of theta synchronization involving dorsolateral PFC of each hemisphere were revealed. In V task, left prefrontal and left parietal areas were functionally coupled in gamma frequencies. Theta synchronization thus provides the necessary interface for storage and manipulation of information, while left-lateralized gamma synchronization could represent the EEG correlate of the phonological loop.

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Introduction

Working memory (WM) supports keeping of information in mind and manipulating or 'working with' information [1]. WM can be fractioned into a control system—the central executive and two lateralized slave systems for rehearsal of modality-specific information (phonological loop for verbal and visuospatial sketchpad for spatial information, respectively) [2].

To capture a number of phenomena unexplained by the original model, Baddeley has later introduced the episodic buffer, a system capable of binding information from the subsidiary systems into unitary representation [3, 4]. As synchronized oscillations are fundamental mechanism for establishment of temporal relationship between neural responses [7], the binding and integration of information are best addressed by electrophysiological studies.

When the information in the environment is no longer available and not yet stored in the long-term memory, the process of holding information online requires synchronously activated neural networks [5]. A measure of continuous synchronization in a given frequency band between the two signals is the electroencephalographic (EEG) coherence [8–11]. High EEG coherence can be interpreted as functional coupling between two anatomically separate regions, as it requires a constant phase relationship between two signals [11]. Functional connectivity can be assessed by comparing regional differences in neural activation and this can be done in several frequency bands by spectral decomposition of the EEG signal [12].

The main challenge of mapping functional networks by scalp EEG lies in its low spatial resolution. Many electrophysiological WM studies have been using scalp EEG with International 10–20 System [5, 13, 14]. Synchronization of large cortical areas from human observations may simply be due to the low spatial resolution of scalp EEG, as animal studies have shown oscillations involving discrete active locations surrounded by areas of inhibition [15].

There are also notable inconsistencies regarding the evidence from functional neuroimaging and EEG studies. Functional neuroimaging data are supporting the role of dorsolateral prefrontal cortex (DLPFC) in executive functions [16–19]. Conversely, many EEG studies reported the involvement of frontal midline structures in synchronization with posterior [14] and/or adjacent cortical areas [20, 21] suggesting their executive role in integrating information between the subsystems.

Synchronization in theta (4–7 Hz) frequencies during WM maintenance was first described by Sarthein et al. [5]. In the same study involving six participants, theta synchronization was lateralized to the left hemisphere in verbal task and to the right hemisphere in spatial task, but these findings did not reach statistical significance [5].

Our aims were to reproduce and clarify some results (spatial patterns, lateralization trends) obtained by previous studies [5, 14, 20, 21] by employing similar methodology, but increasing the number of participants, individually tailoring the submaximal WM load (controlling for individual differences in task difficulty) and notably increasing spatial resolution by the use of high-density EEG. To map the functional networks, we used high-density EEG and coherence analysis.

Materials and methods

Subjects

Ten healthy (five men) right-handed (one ambidextrous), participants (mean age: 34 years, range 25–41 years) were recruited. Handedness was assessed by Edinburgh Handedness Inventory. All subjects gave their informed written consent. The study was approved by the National Medical Ethics Committee of the Republic of Slovenia.

The Sternberg-like tasks

In the Sternberg task [22], the subject is asked to memorize a list of items, for example, digits. After a certain time period, the digit is presented to the subject, who has to judge and indicate whether the stimulus did or did not belong to the memorized list [22].

In our study, the subjects performed two Sternberg-like tasks:

(1) V (verbal): The subjects were asked to keep in mind a string of consonants.
(2) S (spatial): The subjects were asked to keep in mind an order of positions.

In both tasks, the subjects had to maintain the order of stimuli and report whether the probe was present in the indicated position within the set. They responded to the appearance of the probe by pressing left mouse button for YES and right button for NO.

The Sternberg-like tasks also permit the manipulation of WM load, which was tailored to each subject. After getting familiar with the task, the subjects were asked to subjectively determine the number of items they could keep in mind with maximal effort. They were then given a sample task, consisting of 10 trials. If the correct response rate was below 100 %, we repeated the sample task with the same number of items. If the correct response rate was 100 %, the sample task was repeated with an additional item.

If necessary, we further adjusted the number of items (up to two times). The correct response rate of all averaged sample trials (up to three) between 85 and 95 % was accepted as submaximal load. The testing was performed separately for V and S tasks.

Importantly, in Sternberg task the individual WM processes (encoding, maintenance, retrieval and rest) are clearly separated in time. We calculated task-related coherences (TRCoH) by subtracting rest period coherences from active maintenance coherences. In that way, changes in coherence can be attributed to a specific cognitive process—or active maintenance, while other changes unrelated to the task are cancelled out. Increasing WM load would increase the difference between maintenance and rest, enhancing the functional networks involved in active maintenance by exerting its effect on TRCoH.

The tasks were organized in blocks of 20 trials and then semi-randomized. There were four blocks per task and the instructions appeared at the beginning of each block.

The monitoring of the behavioural testing was programmed in E-prime 2.0. Each event (item presentations, appearance of a probe, motor response) was given a specific marker that appeared in real time simultaneously with the EEG signal. The motor responses were marked as either correct or incorrect.

The tasks were programmed in E-prime 2.0 and projected on PC screen. At the end of the task, the subjects were asked to complete a strategy questionnaire.

EEG recordings

128-channel EEG with Ag/AgCl⁻ electrodes in 5-5 International System (actiCAP) was recorded by Brain Products Recorder (BrainAmp amplifiers) at sampling rate 500 Hz. A reference-free montage was used. The resistance of individual electrodes was kept below 5 kΩ. Built-in filters were used during recording (low cut-off frequency at 0.016 Hz and high cut-off frequency at 250 Hz).

EEG analysis

Channels were visually inspected and any channels with inappropriate resistance and/or artefacts were excluded from further analysis (approximately 1–6/128 channels per subject) to prevent contamination of other channels through average reference computation. Next, the EEG signal was re-referenced to the average reference.

EEG signal was divided in 4 s epochs of maintenance periods to be compared with 4 s epochs of rest periods. These periods are suitable for analysis in frequency domain, as they are stationary and long enough to enable the necessary frequency resolution.

We analysed the following frequency bands: theta (4–8 Hz), alpha (8–12 Hz), beta 1 (12–20 Hz), beta 2 (20–30 Hz) and gamma (30–60 Hz). Here, we emphasize the results in theta and gamma frequencies, which both play a pivotal role in working memory.

Task-related power spectrum analysis

Power spectrum of the signal was computed with Welch periodogram method using 256 samples wide Hamming window and 50 % of overlapping between segments and averaged for each task of a subject. The EEG signals of each subject were normalized with their standard deviations in order to minimize the inter-subject baseline differences for grand average computation.

Task-related coherence analysis

Coherence was calculated with mscohere function in Matlab, using 256 samples long signal sections windowed with Hamming window and 50 % overlapping. Paired coherence values for each maintenance (correct trials only) and the following rest period were collected in two vectors $CoH_{maintenance}$ and CoH_{rest}. Each vector consisted of 566 coherence values per electrode pair, representing the sum of all correct trials of all subjects. $TRCoH_{maintenance-rest}$ was calculated as a difference of $TRCoH_{maintenance}$ and $TRCoH_{rest}$.

Statistical analysis of task-related coherence Non-parametric Wilcoxon rank-sum test was used to identify significant differences in median values of $CoH_{maintenance}$ and CoH_{rest}. The p values were computed for all electrode pairs' coherences resulting in set of p values for each task and frequency band. The p value of the first percentile of the p values distribution became the significance level α. Such estimation of α from the data is an alternative to Bonferroni correction for multiple comparisons; however, it takes into account dataset properties [23]. The method was first applied to individual subjects; however, when inter-subject similarity was demonstrated, the data of all subjects were combined and analysed as one dataset.

Inter-subject similarity The similarity of $TRCoH_{maintenance-rest}$ patterns between subjects was estimated separately for each task and frequency band using methods from graph theory [33]. The networks were compared according to node and connection similarity. For connection similarity, a binary matrix representing significant electrode pairs' coherences with ones and non-significant coherences with zeros was constructed for each subject, task and frequency band for positive values of $TRCoH_{maintenance-rest}$. Significant and non-significant electrode pairs' coherences were estimated as described in the

statistical analysis of task-related coherence. The pairwise Hamming distances [33] between the binary matrices were calculated. Random significant coherence patterns were also generated, and the pairwise Hamming distances were computed between the random and the real matrices. Distances between inter-subject TRCoH $_{maintenance-rest}$ patterns and distances between TRCoH $_{maintenance-rest}$ and random patterns for each task and frequency band were then compared by using Wilcoxon test (the null hypothesis: equal median distances of the two distance groups; alternative hypothesis: the inter-subject distances are lower than subject-to-random patterns distances). The significance under $\alpha = 0.05$ would suggest higher than random inter-subject similarity. For node similarity, we constructed and compared node positions of significant electrode pairs' connections. The procedure of defining significant and non-significant electrode pairs' coherences was the same as for the connections similarity assessment; however, the connections were represented by their unique nodes. The nodes that were present in at least one significant connection were represented by ones and the remaining nodes were represented by zeros. The rest of the procedure was the same as for connections similarity assessment.

All the numerical analyses were performed in Matlab R2009b, The Mathworks inc. Natick, Massachusetts, U.S.A.

Results

Behavioural

The submaximal load for V and S tasks among subjects was ranging from 5 to 7 items. The correct response rate of subjects was 86 ± 4 % for V task and 83 ± 5 % for S task.

The strategy used for V task was uniform for all subjects—subvocal rehearsal of the presented items. For S task, the most common strategy among subjects was drawing an imaginary line between the presented positions.

Electrophysiological

Inter-subject similarity

For all tasks, the inter-subject Hamming distances for networks of connections were statistically significantly smaller than the subject-to-random Hamming distances (p values below 5.5×10^{-6}) with the median distance values from 0.0055 to 0.011 for inter-subject distance and 0.013 to 0.016 for subject-to-random difference depending on task and frequency band. The median Hamming distances of the inter-subject node patterns vs. subject-to-random patterns were comparable for all tasks and

frequency bands (0.4 vs. 0.5, respectively) with p values below 0.006. The analysis shows some real inter-subject similarity; however, comparison of networks with variable node and connection numbers can be biased, regardless of the method [33]. The analysis results and visual inspection of individual network patterns showed the level of similarity which allowed pooling of all input data into a single block to be analysed together.

Theta (4–7 Hz) synchronization, desynchronization and power spectrum

The derivations involved in theta synchronization for V task (TRCoH with p values $\leq 4.1 \times 10^{-18}$) and S task (TRCoH with p values $\leq 3.1 \times 10^{-23}$) are represented in Figs. 1a and 2a, respectively. TRCoH values were 0.040–0.136 for V and 0.051–0.156 for S task, respectively.

For V and S tasks, there was also a similar pattern of decrease of theta TRCoH between interhemispheric prefrontal pairs of electrodes (Figs. 1b, 2b), again with similar absolute coherence values (0.005–0.117 for V and 0.007–0.131 for S task, respectively).

The greatest changes in theta power spectrum for V task were observed between electrodes FCC1h, FZ and FCC2h, corresponding to frontal midline regions (Fig. 1c), and between electrodes CPP2h and CPZ for S task, corresponding to centroparietal regions (Fig. 2c).

Gamma (30–60 Hz) synchronization

Synchronization in gamma frequency range in V task ($p < 4.6 \times e^{-7}$) was found among left lateral frontal derivations, left central derivations and left parietal derivations. In S task ($p < 6.1 \times e^{-6}$), the task-related gamma synchronization was occurring bilaterally over centroparietal regions with TRCoH = 0.013–0.045. The desynchronization in gamma band was wide-spread, including most derivations.

In the gamma power spectrum, there was an increase in gamma power in the bilateral fronto-temporoparietal regions and a decrease in the midline region.

Discussion

The spatial and process-specific characteristics of theta synchronization

The spatial pattern of theta synchronization

In both V and S tasks (Figs. 1a, 2a), there was a clear, almost identical spatial pattern of theta synchronization.
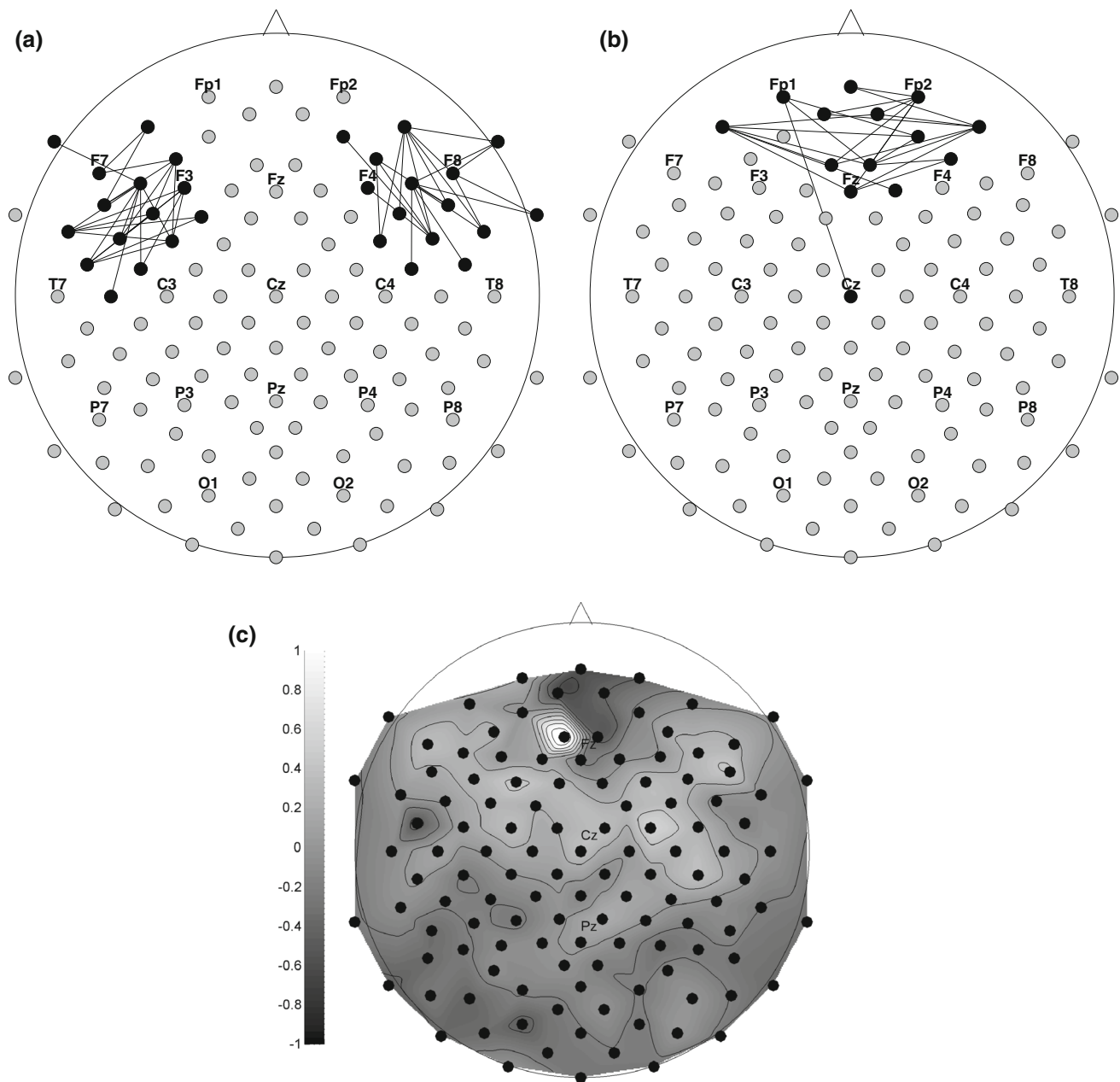
Fig. 1 a, **b**, **c** The spatial patterns of synchronization, desynchronization and power spectrum for V task in theta (4–7 Hz) frequency band. Grand average (GA) of all subjects. Theta synchronization among derivations corresponding to DLPFC and adjacent cortex (*a*), theta desynchronization between prefrontal midline regions (*b*) and a frontal midline increase in theta power (*c*)

The electrodes F3 and F4 in 10–20 International System in most subjects correspond to a part of DLPFC on medial frontal gyrus, while the anatomical centre of DLPFC is more anterior and inferior [23], so there is a good reason to believe that most connections occur within DLPFC and between ventral LPFC and DLPFC.

When reporting high coherence among anatomically adjacent areas, the biggest methodological concern would be neuronal activity spreading from truly engaged regions to adjacent regions by means of volume conduction [24].

However, as power increases and their gradients were independently positioned with respect to the areas of increased synchronization (Figs. 1a, 1c; 2a, 2c), the increases in coherence that are due to volume conduction can reliably be ruled out. Also, the use of average reference could inflate coherence, yet it would not exert any effect on TRCoH [9].

Unexpectedly, we demonstrated a decrease in theta synchronization between prefrontal midline electrodes. This is finding is in disagreement with other scalp EEG
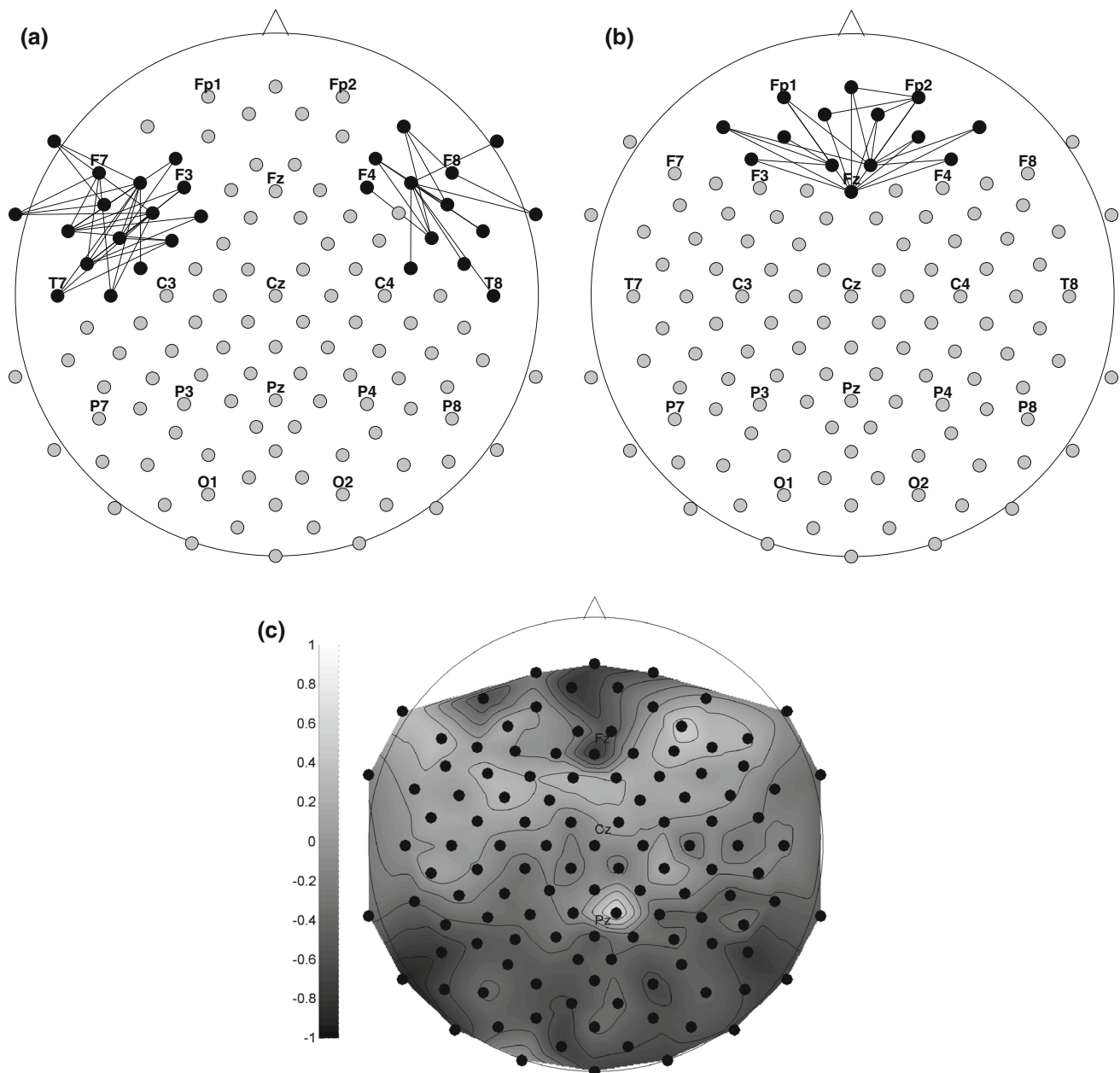
Fig. 2 a, b, c The spatial patterns of synchronization, desynchronization and power spectrum for S task in theta (4–7 Hz) frequency band. Grand average (GA) of all subjects. Theta synchronization among derivations corresponding to DLPFC and adjacent cortex (a), theta desynchronization between prefrontal midline regions (b) and a centroparietal midline increase in theta power (c). Note the similar, almost identical spatial patterns in V task

studies [14, 15, 20, 21], but it resonates well with fMRI connectivity studies, as the medial prefrontal cortex was shown to be anticorrelated with WM task [27]. While task-related changes undoubtedly occur in frontal midline structures, their specific role in WM processes less clear. For example, some data from functional neuroimaging suggest that activation of these regions in fact reflects a state of preparedness for selecting motor response based on the information held online [34]. Gevins et al. concluded

that ACC is involved in complex tasks that require constant attention [25]. Functional neuroimaging study has found a double dissociation—a greater engagement of ACC as a function of task difficulty with no change in DLPFC activation and greater engagement of DLPFC with increasing WM demand with no change in ACC activation [35]. Although in the present study we found marked theta power changes for V task in frontal midline regions, as demonstrated previously [25, 26], coherence analysis

provided no evidence that prefrontal midline structures take part in theta synchronization—and thus in binding or integration of the information between the WM subsystems.

Synchronization occurs between the executive cortex and areas involved in temporary storage of information as reported previously [5]. Specifically, our spatial pattern of synchronization suggests the functional coupling between DLPFC and ventral LPFC. The dorsal subdivision is more active with higher class operations [28, 29] or when the task demands greater executive control. There are speculations that dorsal and ventral subdivisions are hierarchically organized, with information passing from ventral to dorsal LPFC, where it is additionally processed [17]. Our data imply that integration of information between ventral LPFC and DLPFC takes place in the form of theta synchronization.

The process-specific characteristics of theta synchronization

We found no evidence of task-related lateralization in theta synchronization, although the strategies described by subjects were highly congruent with concepts of phonological loop and visuospatial sketchpad. These findings imply that theta synchronization does not play part in the specific rehearsal mechanism, but is instead involved in processes that are common to both spatial and phonological rehearsal—the executive control, consistent with the literature [30–32].

What is the specific function of this executive control and how does theta synchronization reflect the functional cooperation between the WM subsystems?

One plausible explanation would be that theta synchronization supports the integration of information between central executive and its modality-independent storage, the episodic buffer. So far, the biological implementation of the episodic buffer has remained obscured. Very interestingly, Baddeley has hypothesized the synchronous nervous firing as a mechanism of its action and frontal lobes as its anatomical location [3].

The spatial and process-specific characteristic of gamma synchronization

As reported previously [6], task-related increases in gamma power were found over the extensive areas of frontal, parietal and temporal cortices. In the quoted study [6], only left hemisphere electrodes were placed. Our results show that gamma power is increased bilaterally. Task-related gamma synchronization in V task was, however, left lateralized. Only few derivations reached the statistical significance of the first percentile of distribution, the threshold

used for theta synchronization. When considering the third percentile of distribution ($p < 4.6 \times e^{-7}$), the functional network was revealed among the electrodes overlying left frontal cortex, left frontocentral region and left parietal cortex. As opposed to these findings, in the S task the gamma synchronization occurred bilaterally over centroparietal regions.

A closer look at the spatial pattern of gamma synchronization reveals two clusters of short-range connections. One of the two clusters is involving the electrodes overlying left DLPFC and Broca's area, while the other cluster with especially rich connections is centred on the electrode P3, which in most individuals overlies the left inferior parietal region [23]. These regions correspond well with the areas involved in subvocal rehearsal and phonological storage identified by fMRI studies [36, 37]. Both its spatial and process-specific characteristics thus suggest that the functional network in gamma frequency band could represent the electrophysiological correlate of the phonological loop by functionally coupling the areas engaged in phonological rehearsal and storage.

The interaction between theta and gamma frequencies

Although theta and gamma synchronization seem to correspond to different WM processes, in V task they also involve common cortical areas. The topology of functional networks in theta and gamma frequencies, however, exhibits distinct properties. While theta synchronization engages longer, mainly anterior to posterior connections, the functional network in gamma frequency band exhibits local clustering and short, mainly transverse paths among the nodes within each cluster. These patterns are consistent with the view that the lower frequencies preferably establish synchronization over longer distances, while higher frequencies are important for local precision of functional networks [7].

Also, it has been proposed that theta rhythm could represent a neural code in which gamma oscillations are represented in the different phase of the theta cycle, enabling parallel memory processes in the same neural network [38]. Moreover, a mathematical model was constructed that confirmed that the oscillatory buffer model in theta and gamma frequencies can account for the variety of data on the Sternberg task [38].

Conclusions

The high-density EEG has provided a closer look on the landscape of synchronized regions surrounded by areas of inhibition. These detailed spatial patterns of

synchronization are a contribution of our high-density EEG study and imply that the synchronized activity is limited to highly specialized areas. In theta synchronization, two coherent networks involving DLPFC and adjacent cortex, specifically engaged in active maintenance of modality-free information were elucidated. In gamma synchronization, another functional network was revealed, coupling the areas involved in phonological rehearsal and storage. Thus, an important step has been made towards the electrophysiological correlates of the episodic buffer and the phonological loop.

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