Frontal and Parietal Cortices Show Different Spatiotemporal Dynamics across Problem-solving Stages

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Abstract

■ Arithmetic problem-solving can be conceptualized as a multistage process ranging from task encoding over rule and strategy selection to step-wise task execution. Previous fMRI research suggested a frontal–parietal network involved in the execution of complex numerical and nonnumerical tasks, but evidence is lacking on the particular contributions of frontal and parietal cortices across time. In an arithmetic task paradigm, we evaluated individual participants' "retrieval" and "multistep procedural" strategies on a trial-by-trial basis and contrasted those in time-resolved analyses using combined EEG and MEG. Retrieval strategies relied on direct retrieval of arithmetic facts (e.g., 2 + 3 = 5). Procedural strategies required multiple solution steps (e.g., 12 + 23 = 12 + 20 + 3 or 23 + 10 + 2). Evoked source analyses revealed independent activation dynamics within the first second of problem-solving in brain areas previously described as one network, such as the frontal–parietal cognitive control network: The right frontal cortex showed earliest effects of strategy selection for multistep procedural strategies around 300 msec, before parietal cortex activated around 700 msec. In time–frequency source power analyses, memory retrieval and multistep procedural strategies were differentially reflected in theta, alpha, and beta frequencies: Stronger beta and alpha desynchronizations emerged for procedural strategies in right frontal, parietal, and temporal regions as function of executive demands. Arithmetic fact retrieval was reflected in right prefrontal increases in theta power. Our results demonstrate differential brain dynamics within frontal–parietal networks across the time course of a problem-solving process, and analyses of different frequency bands allowed us to disentangle cortical regions supporting the underlying memory and executive functions. ■

INTRODUCTION

Everyday problem-solving such as mental arithmetic requires the coordination of a number of complex cognitive operations, including choosing an initial problem-solving strategy and monitoring the execution of this strategy as well as retrieving rules and facts from memory. These operations may be conceptualized in a framework of temporally and functionally distinct problem-solving stages (Anderson, 1983, 1993; Newell, Shaw, & Simon, 1958). Aspects of the corresponding executive functions and memory processes have been associated with distinct brain networks in past research. For example, a frontal–parietal network has been linked to working memory and executive functions (Cole et al., 2013; Duncan, 2010; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008), and a frontal–temporal declarative and semantic memory network may support the controlled retrieval of task-relevant facts or rules (Barredo, Öztekin, & Badre, 2013; Badre & Wagner, 2007; Bunge, Kahn, Wallis, Miller, & Wagner, 2003). However, the potentially different functional roles of regions within these networks, across stages of a complex cognitive process, are still not established (Duncan, 2010).

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Here, we analyzed neural correlates on different temporal stages of an abstract problem-solving process in combined EEG–MEG source estimates. We contrasted two types of arithmetic strategies, chosen on the basis of our participants' individual ratings (Tschentscher & Hauk, 2014, 2015): "retrieval" strategies, that is, solutions are retrieved directly from memory (e.g., "2 × 3"), and "procedural" strategies, for which several solution steps are required (e.g., "12 × 11 → 10 × 12 + 12"). Contrasting complex with easy problems can reveal neural networks related to executive and memory functions in specific time windows: In a sequential model of problem-solving, complex strategies pose higher demands on strategy selection and structuring of solution steps in early time windows, whereas easy problems rely on memory retrieval processes (Figure 1). Complex multistep procedural strategies are also likely to involve higher strategy execution demands in later time windows.

Previous neuroimaging studies have shown that a set of frontal and parietal regions is involved in numerical as well as nonnumerical reasoning (Arsalidou & Taylor, 2011; Duncan & Owen, 2000), whereas evidence on the specific contributions of these regions to the temporal stages of a complex cognitive process is still lacking. Computational accounts of problem-solving have already proposed different roles for frontal and parietal areas, such as

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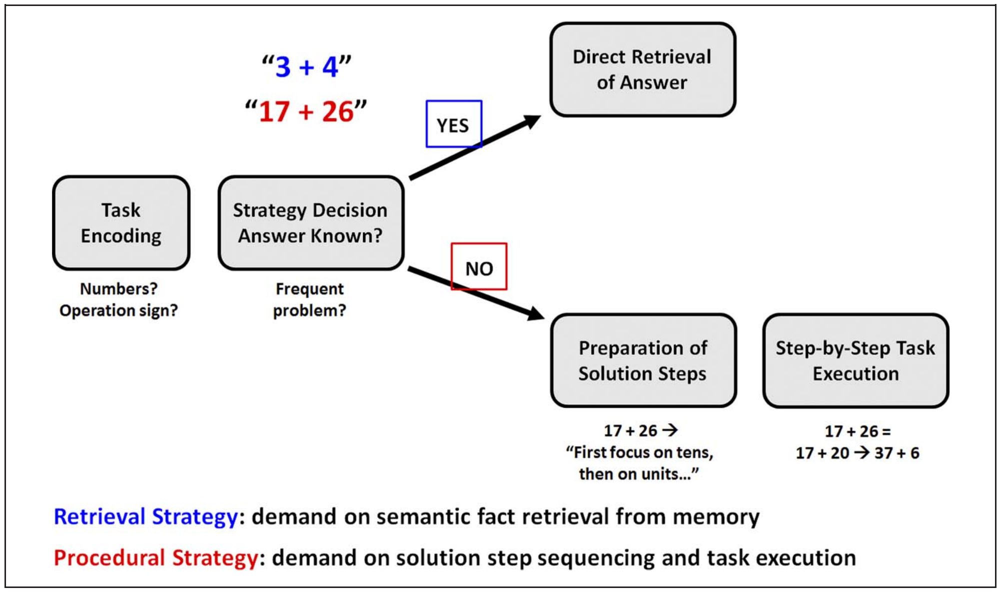

Figure 1. Model on the different stages of an arithmetic problem-solving process for easy and complex mental calculation tasks.

the ACT-R approach to arithmetic equation solving, in which intraparietal sulcus has been linked to maintaining a representation of the problem state and frontal cortex has been linked to the retrieval of problem-relevant facts from declarative memory (Anderson, Qin, Jung, & Carter, 2007).

The role of frontal cortex in the controlled retrieval of abstract rules and strategies is supported by several fMRI studies (Barredo et al., 2013; Bunge et al., 2003). Furthermore, fMRI evidence suggests that frontal cortex engages in the early development of a solution strategy as well as in the control and coordination of a multistage cognitive process (Fuster, 2001; Damasio, Everitt, & Bishop, 1996; Chao & Knight, 1995; Goldman-Rakic, 1995). In particular, posterior lateral frontal cortex has been associated with the temporal integration of multiple demands in a specific task context (Koechlin & Summerfield, 2007; Koechlin & Jubault, 2006). However, no spatiotemporal evidence exists so far on frontal cortex's role in cognitive control during early phases of human problem-solving. In contrast, parietal areas have been frequently associated with maintenance of attention as well as maintenance of a representation of the problem state in previous fMRI and ERP research (Stocco, Lebiere, O'Reilly, & Anderson, 2012; Bode & Haynes, 2009; Anderson et al., 2007; Brass, Ullsperger, Knoesche, von Cramon, & Phillips, 2005; Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002).

In our paradigm, we therefore predicted an earlier engagement of frontal cortex during selection and organization of a complex solution strategy, before parietal cortex may engage into the maintenance of attention and task-relevant information during later strategy execution phases. So far, one study has investigated the differential time course of executive functions in frontal and parietal regions by using EEG. Evidence for a frontal-before-parietal time course within the frontal–parietal network was provided by dipole modeling of ERP data in a task-switching paradigm (Brass et al., 2005). However, it is unclear whether this result generalizes to executive functions involved in complex problem-solving, where dipole modeling may not be appropriate. Thus, we determined the differential time courses of frontal and parietal brain regions using distributed whole-brain source estimates derived from combined EEG–MEG measurements.

Furthermore, we analyzed the time–frequency characteristics of arithmetic problem-solving strategies in EEG–MEG source power analyses of theta, alpha, beta, and gamma frequency bands. On the basis of previous EEG sensor level evidence, we can make specific predictions for easy and complex arithmetic strategies: These studies observed reduced alpha power for complex arithmetic strategies, whereas memory retrieval-based strategies showed power increases in the theta band (Grabner & De Smedt, 2012; De Smedt, Grabner, & Studer, 2009). However, the neural sources underlying those arithmetic strategy effects have not been investigated so far. We therefore further predict that memory retrieval strategies are reflected in theta power increases within frontal–temporal networks, whereas the executive demands related to procedural strategies should be reflected in alpha power decreases within frontal–parietal networks.

Studies on nonnumerical higher cognition partly support our time–frequency predictions for arithmetic problem-solving but also present a more complex picture. Several studies have suggested a link between aspects of memory processes and modulations in theta rhythm (Benchenane et al., 2010; Klimesch, Freunberger, Sauseng, & Gruber, 2008; Sato & Yamaguchi, 2007; Bastiaansen & Hagoort, 2003; Klimesch, 1999). A recent MEG study on episodic memory retrieval revealed phase synchronizations in the theta range between frontal and temporal sources as a function of memory retrieval demands (Guitart-Masip et al., 2013). Executive functions have been associated with modulations in alpha and beta bands (Reinhart & Woodman, 2013; Klimesch, 2012; Sadaghiani et al., 2012; Brookes et al., 2011; Palva & Palva, 2011) and have been related to a frontal–parietal network based on resting state studies (Sadaghiani et al., 2012; Brookes et al., 2011). However, we are cautious with respect to a simple one-to-one mapping of cognitive functions and frequency ranges. Although some authors have suggested that activity in certain frequency ranges may be "spectral fingerprints" for specific neural computations (Siegel, Donner, & Engel, 2012), memory and executive functions have been associated with effects in a broad range of different frequency bands (Hanslmayr, Matuschek, & Fellner, 2014; Guitart-Masip et al., 2013; Bonnefond & Jensen, 2012; Hanslmayr, Staudigl, & Fellner, 2012; Brookes et al., 2011; Hanslmayr et al., 2011; Engel & Fries, 2010; Jensen & Mazaheri, 2010; Hanslmayr, Spitzer, & Bäuml, 2009; Gross et al., 2004; Klimesch et al., 1996). In this study on complex problem-solving, we tested whether time–frequency analyses of combined EEG–MEG data allow us to disentangle brain networks involved in the underlying memory and executive functions based on differential neural frequency characteristics.

METHODS

Participants

Data were analyzed from 23 participants (15 women). The mean age was 26 years (*SD* = 5 years) in both male and female participants. They were all right-handed, had normal or corrected-to-normal vision, were educated in Western cultures (e.g., United States or Europe), and reported no history of neurological or psychiatric disorders. The mean IQ of participants was 120 (*SD* = 16.2; women: 123, *SD* = 17.3; men: 117, *SD* = 14.1). Before their selection, all participants indicated in an e-mail questionnaire that they could solve the type of arithmetic problems employed in this study within about 4 sec. Participants' IQ was assessed at the day of testing by using the Culture Fair Test, Scale 2 (Cattell & Cattell, 1960). Handedness was confirmed by a 10-item version of the Edinburgh Handedness Inventory (Oldfield, 1971). Participants received about £40 for their participation, and ethical approval was obtained from the Cambridge local research ethics committee.

Stimuli and Procedure

Initially, we selected "easy" and "complex" stimuli based on number and problem sizes. For the final experiment, stimuli were assigned to the categories "procedural" and "memory retrieval" based on individual strategy ratings. Sixty trials were presented in each of the four conditions: easy and complex tasks of two operation types (addition and multiplication), respectively. The complex condition contained the combination of numbers 12–59 for addition tasks and the numbers 2–5 combined with the numbers 12–29 for multiplication tasks. The easy condition consisted of two 1-digit numbers for both operation types. Tasks within the four predefined conditions were carefully matched according to the following criteria: An equal amount of problems containing two even numbers, two odd numbers, and odd–even and even–odd number combinations were chosen. The position of the larger operand was matched across all tasks. Participants had to confirm the correct solution, which was presented together with a distractor. For problems containing two 1-digit numbers (easy condition), the distractor was within the range of ±2 of the correct solution. For complex problems, consisting either of combinations of 1-digit and 2-digit numbers or two 2-digit numbers, 50% of the distractors were either within a range of ±2 of the correct solution (e.g., 56 and 54) or ±10 of the correct solution (e.g., 42 and 52) each. Exceptions were made for multiplication trials including the number 5: Distractors in those trials were within a range of ±5 of the correct solution. The position of the correct solution on the screen was counterbalanced across all trials within each arithmetic task type. The maximum height of stimuli was 15 mm. Stimuli were presented within a visual angle of less than 4° in Calibri font.

The definition of strategy contrasts in EEG–MEG analyses was based on participants' individual strategy ratings of "memory retrieval" versus "multistep procedural" strategies, which were obtained together with RTs on a trial-by-trial basis after the EEG–MEG data acquisition. The exact 240 tasks (60 tasks per condition) were presented in the behavioral posttest, as in the MEG session. The MEG session, as well as behavioral posttest, was divided into eight blocks. To reduce effects of familiarity, all tasks in the MEG session and behavioral posttest were presented in different blocks. Each block contained easy and complex tasks of one operation type (i.e., either addition or multiplication), which resulted in four blocks per arithmetic operation. The duration of each block was approximately 7 min. Fifteen practice tasks were presented at the beginning of the EEG–MEG session and posttest. During the MEG session (Figure 2A), participants were requested to solve each presented problem within 4 sec (jittered exponentially between 3.7 and 5 sec to make it comparable with an fMRI version of this experiment [Tschentscher & Hank, 2014]) while the task stayed on the screen (e.g., "13 + 26"). After this period, a second operand (either plus or minus 1, 2, or 3) was presented with an exponentially jittered duration of 750 msec (time range of 0.5–2 sec), followed by a 2AFC result display, which was presented for 1750 msec. Participants indicated the correct solution by pressing a button as soon as the result display appeared. The fixation cross between tasks had a jittered SOA of 1.5–3.5 sec. The second task was included in the trial sequence to minimize response-related brain activation (cf. Tschentscher & Hauk, 2014; Jost, Khader, Burke, Bien, & Rosler, 2009). During the posttest (Figure 2B), RTs and arithmetic strategies were measured for all tasks of the EEG–MEG experiment. Trials consisted of the same arithmetic tasks as presented in the EEG–MEG sessions but were presented in a different order to reduce familiarity effects. Participants' strategy ratings were used

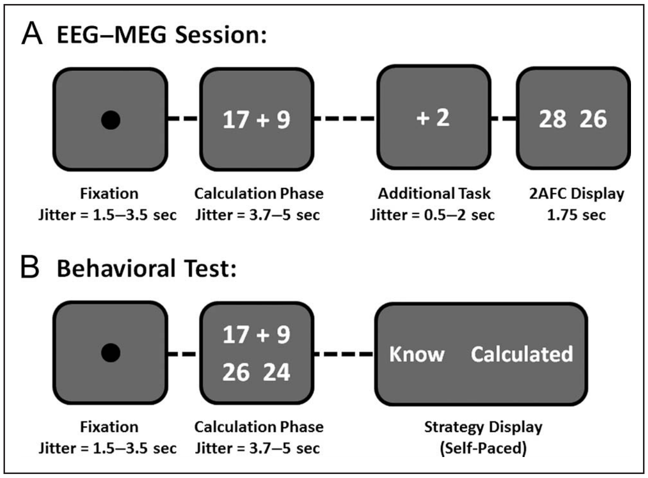

Figure 2. (A) Example for task procedure during the EEG–MEG session. The additional task was either plus or minus 1, 2, or 3. (B) Example for task procedure during the behavioral posttest on participants' individual arithmetic strategies. The relative sizes of stimuli and fixation dot have been changed for visualization purposes.

to define "retrieval" and "procedural" tasks in analyses of MEG data. In the posttest, tasks were presented in a 2AFC design together with two solution options for 4 sec each (jittered exponentially between 3.7 and 5 sec). Participants were instructed to respond as fast and accurately as possible. After solving each task, participants indicated whether they retrieved the answer from memory (i.e., by pressing a button for "known") or whether they used any kind of procedural calculation strategy ("calculated"). Participants were instructed to press "known" only when they immediately knew the answer and to press "calculated" when they needed several steps to calculate the answer (e.g., 26 + 34 = 26 + 30 + 4). Participants responded by pressing one of two buttons of a button box by using their index fingers. Finally, we determined participants' IQ and handedness.

Analysis of Behavioral Data

Error rates were analyzed for MEG sessions and posttest data, respectively. Mean RTs of each participant were extracted from posttest data for all arithmetic conditions and analyzed in a repeated-measures ANOVA with the factors Strategy (retrieval vs. procedural) and Operation (addition vs. multiplication).

EEG–MEG Recordings and Evoked Analysis

The continuously recorded MEG (306-channel Elekta Neuromag Vectorview system, Stockholm) and EEG data (70 electrodes) were digitally sampled at 1 kHz. The positions of five head position indicator coils, attached to the EEG cap, were digitized with a 3Space Isotrak II System (Fastrak Polhemus Inc., Colchester, VA) to determine the head position within the MEG helmet. Three anatomical landmark points (nasion and preauricular points) as well as 50–100 additional randomly distributed points (head shape) were digitized for an accurate coregistration with MRI data. The EOG was recorded bipolarly through electrodes placed above and below the left eye (vertical EOG) and at the outer canthi (horizontal EOG). Artifacts likely to be produced by sources distant to the sensor array were removed by means of the signal space separation method, which is implemented in the Neuromag Maxfilter software (Taulu & Kajola, 2005). The spatiotemporal variant of Maxfilter as well as the movement compensation was applied. EEG and MEG data were inspected visually, and interpolation of EEG channels was applied. Eye movement artifacts in EEG and MEG data were removed by using EEGLAB functions (http://sccn.ucsd.edu/eeglab/) implemented in SPM 5 (Delorme & Makeig, 2004), which were modified for MEG data. A temporal independent component analysis was applied to continuous data for magnetometers, gradiometers, and EEG scalp potentials separately to identify components whose time courses correlated with eye movement artifacts. Each data set was reduced to the largest 65 principal components, and the independent component analysis algorithm was applied (extended infomax algorithm). Component time courses were correlated with the vertical EOG to identify eye blink-related components. Eye blink components were then manually defined after inspection of their continuous waveforms, for visual comparison with the vertical EOG. Components that showed the highest correlation with the vertical EOG as well as a clear correspondence to the blink signal, were projected out of the data. Furthermore, the vertical and horizontal EOGs were tested for significant differences between experimental conditions within the analyzed time interval. No significant effect of task condition was observed in EOG at any point: Sample-by-sample paired t tests never exceeded a threshold of $p = .05$ uncorrected. Hence, eye movements can be excluded as potential cause for effects of task condition in evoked and time–frequency analyses.

Data were offline band-pass filtered between 0.1 and 30 Hz before averaging (see Supplementary Experimental Procedures). For each of the four conditions, epochs from −100 to 1000 msec after onset of the arithmetic task were averaged by using the MNE software package (Version 2.6; www.nmr.mgh.harvard.edu/martinos/userInfo/data/sofMNE.php) (Gramfort et al., 2013). Trials were rejected during averaging when the maximum–minimum amplitudes exceeded the following thresholds in the averaged interval: 120 μV in EEG, 3000 fT in magnetometers, and 2000 fT/cm in gradiometers. EEG data were rereferenced to average reference, and the mean amplitude of the 100-msec baseline interval was subtracted at all time points on each channel.

Source Estimation

Source estimates were derived from combined EEG and MEG data by using the MNE software package in combination with Freesurfer (Version 4.3.0; surfer.nmr.mgh.harvard.edu/). The noise covariance matrices for each data set were computed for baseline intervals of 300-msec duration before the onset of each arithmetic task. The noise covariance matrix is used to combine measurements from different sensor types (magnetometers, gradiometers, and EEG electrodes): All measures are transformed into signal-to-noise ratios (SNRs; "prewhitening") to suppress noise in the source estimates. For regularization, the default SNR in the MNE software was used (SNR = 3). EEG–MEG sensor configurations and MRI images were coregistered based on the matching of about 50–100 digitized points on the scalp surface. High-resolution structural T1-weighted MRI images were used, acquired in a 3-T Siemens Tim Trio scanner at the MRC Cognition and Brain Sciences Unit (UK) with a 3-D magnetization prepared rapid gradient-echo sequence, field of view = 256 mm × 240 mm × 160 mm, matrix dimensions = 256 × 240 × 160, 1-mm isotropic resolution, repetition time = 2250 msec, inversion time = 900 msec, echo time = 2.99 msec, and flip angle = 9°. The scalp surface of the MRI images was reconstructed by using the automated segmentation algorithms of the Freesurfer software. By using the traditional method for cortical surface decimation, the original triangulated cortical surface (consisting of several hundred thousand vertices) was down-sampled to a grid with an average distance between vertices of 5 mm, which resulted in approximately 10,000 vertices. A boundary element model containing 5120 triangles per surface was created including scalp, outer skull, and inner skull surfaces. Dipole sources were assumed to be almost perpendicular to the cortical surface, with some variation in the tangential plane (one fifth of the radial dimension, "loose" orientation constraint). Note that source distribution time courses are unaffected by the choice of EEG reference electrode. This is one of the advantages of source space compared with signal space analysis.

Source estimates were computed for each participant and condition (rated retrieval and procedural tasks of both operation types, respectively). The results for each individual data set were morphed to the average brain across all participants. Time windows of interest for statistical analyses on EEG–MEG source estimates were defined based on the root mean square (RMS) of the SNR of combined EEG–MEG signal for all arithmetic tasks. Whole-brain t distributions for the contrasts of arithmetic strategy and operation type were obtained for each of the defined time windows by using MNE Python software 0.8 (Gramfort et al., 2014). Permutation-based whole-brain cluster-level statistics were applied by using a nonparametric cluster-level t test for spatiotemporal data (Maris & Oostenveld, 2007).

Second, four ROIs in bilateral frontal and bilateral parietal cortex of the averaged brain were extracted from parcellations of the cortical surface created by the neuroanatomical labels of the Freesurfer software. This is an automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest (Desikan et al., 2006). Two bilateral frontal and two bilateral parietal labels of the Freesurfer software were merged into one large frontal and one large parietal label within each hemisphere (i.e., the lateral orbito-frontal and rostral middle frontal labels of the Freesurfer software were merged as well as the superior parietal and inferior parietal labels). These labels were used instead of multiple adjacent labels within frontal and parietal cortices because the limited spatial resolution of EEG–MEG may not allow the separation of activity in these regions. We also present whole-brain corrected results, which show the distribution and location of peaks of our effects. Because these four defined ROIs are relatively far apart from each other, source estimations based on combined EEG–MEG data should be able to separate these sources (Hauk, Wakeman, & Henson, 2011; Molins, Stufflebeam, Brown, & Hämäläinen, 2008; Sharon, Hämäläinen, Tootell, Halgren, & Belliveau, 2007). The shape and size of the four ROIs are present in Figure 5.

We ensured that the ROIs captured regions of significant arithmetic strategy effects reported in previous fMRI literature (Tschentscher & Hauk, 2014) as well as executive control effects in regions of the multiple demands network (Duncan, 2010). For example, the fMRI study by Tschentscher and Hauk (2014) has used a very similar arithmetic task design and observed the strongest effects of arithmetic strategy (procedural vs. retrieval) in a frontal–parietal network including the ventro-lateral and orbito-medial pFC as well as the posterior superior parietal lobule and angular gyrus. These regions have been covered by our frontal and parietal ROI labels, respectively. However, we cannot be absolutely certain that the peaks of activity we see in our EEG–MEG source estimates correspond exactly to peaks in fMRI activation from previous studies.

Average source estimate amplitudes were computed within time windows and across vertices inside each of the ROIs. These were subjected to an ANOVA with the factors Strategy (procedural vs. retrieval strategy), Operation (addition vs. multiplication), Laterality (left vs. right hemisphere), and Caudality (anterior vs. posterior region), which was conducted for all time windows. For time windows that showed significant interaction effects, post hoc ANOVAs were conducted for each hemisphere including the factors Strategy (procedural vs. retrieval strategy), Operation (addition vs. multiplication), and Caudality (anterior vs. posterior regions) as well as post hoc t comparisons for Strategy and Operation effects on each ROI (Bonferroni-corrected for the number of analyzed ROIs, $N = 4$).

Time–Frequency Analyses

Data were band-pass filtered between 1 and 40 Hz to eliminate low- and high-frequency artifacts. MNE Python software 0.8 was used (Gramfort et al., 2013). The following artifact rejection thresholds were applied during epoching: 120 μV in EEG, 4000 fT in magnetometers, and 4000 fT/cm in gradiometers. Epochs for single events, that is, procedural and retrieval strategies of addition and multiplication tasks, were extracted from −500 up to 1000 msec, relative to the onset of the arithmetic task on screen. Four frequency bands were chosen: theta (3–6 Hz), alpha (8–12 Hz), beta (18–22 Hz), and gamma (25–40 Hz). These frequency bands were defined in line with previous EEG sensor level studies reporting a reduction in alpha power for complex arithmetic strategies and an increase in theta power for memory retrieval strategies (Grabner & De Smedt, 2012; De Smedt et al., 2009). The aim of the current study was to replicate and source localize those findings. Morlet wavelets were applied (cf. Hansen, Kringelbach, & Salmelin, 2010) to extract the time–frequency representation of induced power for a given time point and frequency. This was done by calculating the squared norm of the convolution of a Morlet wavelet to the signal, with frequency-dependent number of cycles, for theta power chosen as 2, for alpha power as 4, and for beta and gamma power as 7. The induced power was extracted for single participants on all vertices in combined EEG–MEG MNE source estimates. The same forward model as for computation of evoked EEG–MEG source estimates was used. Reconstructed cortical sources of induced power for individual participants were smoothed with a 10-mm FWHM Gaussian kernel and morphed onto the averaged brain template. Grand averages were computed across participants for each of the four conditions (addition retrieval, multiplication retrieval, addition procedural, and multiplication procedural) in source space. The power estimates in each frequency band were divided by the mean power of the interval −400 to 0 msec (which was chosen instead of the −500- to 0-msec interval to exclude edge effects caused by the Morlet wavelet). Time windows for statistical analyses were defined based on source induced power values for each frequency band from all arithmetic tasks, which were averaged across all vertices. Whole-brain t distributions were obtained for contrasts of strategy and operation type as well as permutation-based whole-brain cluster-level statistics (Maris & Oostenveld, 2007).

RESULTS

Behavior

Our behavioral data showed that all participants could solve the tasks accurately within 4 sec. The mean error rates were 10% (SD = 6%) in the MEG session and 9% (SD = 5%) in the behavioral posttest. Error trials from the MEG session were excluded from the corresponding analyses. The mean number of reorganized trials because of ratings across participants was 1.78 trials for addition and 12.39 trials for multiplication. After reorganization of trials because of ratings and removal of error trials, the mean number of retrieval trials for analyses was 126.30 (SD = 30.24), and the mean number of procedural trials was 90.91 (SD = 23.89). There was no significant correlation between IQ scores and the amounts of rated procedural (r = .25, p = .24) and retrieval (r = −.24, p = .26) strategies.

As expected, posttest RTs for retrieval and procedural strategies showed a significant main effect of Strategy ($F(1, 22) = 987.93, p < .000$; mean retrieval addition = 1298 msec, SD = 223.03 msec; mean retrieval multiplication = 1378 msec, SD = 231.92 msec; mean procedural addition = 2456 msec, SD = 218.82 msec; mean procedural multiplication = 2423 msec, SD = 259.27 msec). We also found a significant Strategy × Operation type interaction ($F(1, 22) = 13.59, p = .001$), driven by a significant Operation type effect for retrieval tasks according to planned t-test comparisons ($t(22) = -3.37, p = .003$, addition > multiplication).

Evoked EEG–MEG Source Analyses: Frontal Cortex Activates Before Parietal Cortex

For EEG–MEG analyses, the classification of easy and complex tasks was accomplished on an individual basis, using the trial-by-trial strategy ratings from the behavioral post-MEG test. According to participants' ratings, tasks were classified as problems solved either by "direct memory retrieval" or by a "multistep procedural strategy."

The shortest behavioral responses in our retrieval tasks indicated that a comparison between retrieval and procedural tasks beyond 1000 msec would not have been meaningful. Taking into account previous ERP literature, we suggest that the time window up to 400 msec mainly reflects strategy selection (cf. El Yagoubi, Lemaire, & Besson, 2003) and latencies post 400 msec should reflect strategy execution (cf. Nunez-Pena, Honrubia-Serrano, & Escera, 2005). Visual inspection of the overall time courses of source power in four frequency bands (Figure 3B) further suggests a qualitative change in brain dynamics around 400 msec, with an increase compared with baseline for lower frequencies before and a decrease for higher frequencies after 400 msec. For a detailed analysis of evoked brain activation, we chose five time windows of interest based on peaks in the RMS curve of the SNR of all arithmetic tasks, in line with effects in previous evoked potential studies on mental arithmetic (Nunez-Pena, Cortinas, & Escera, 2006; Nunez-Pena et al., 2005; El Yagoubi et al., 2003): 100–120, 180–220, 250–300, 300–350, and 450–560 msec. A sixth time window of 700–1000 msec was chosen despite the absence of peaks in the RMS of SNR curve, to cover the remaining interval until up to the approximate end of the arithmetic process, indicated by the mean RTs for retrieval strategies from the posttest (Figure 3A for all time windows). Early numerical encoding was predicted to occur in the first two time windows (Dehaene, 1996), effects of early strategy selection (procedural vs. retrieval) in time windows around 300 msec (El Yagoubi et al., 2003), and effects of arithmetic strategy execution in the latest two time windows (Nunez-Pena et al., 2006).

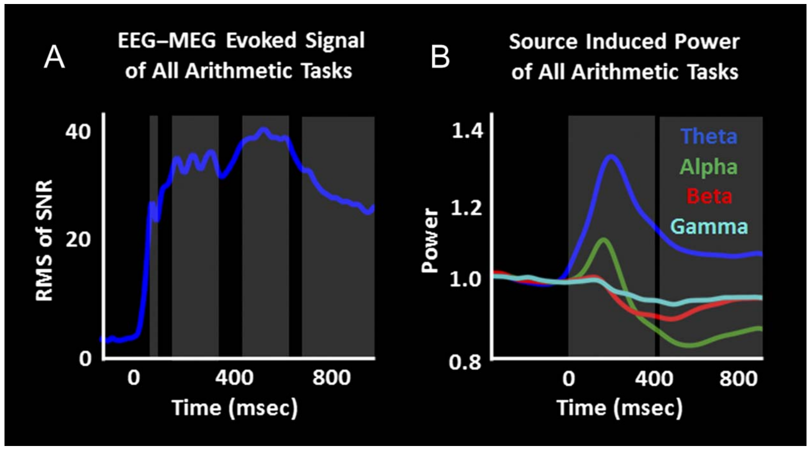

Figure 3. Overall activation time courses in the evoked and time–frequency data. (A) RMS of the SNR for combined EEG and MEG evoked signals of all arithmetic tasks. Gray areas indicate the time windows used for statistical analyses. (B) Mean source induced power across all vertices for all arithmetic tasks in different frequency bands, relative to baseline. Gray boxes indicate the time windows used for statistical analyses.

To determine whether frontal and parietal brain areas show different activation time courses, source estimates of combined EEG–MEG signal were analyzed in each of the six time windows. We computed whole-brain distributions of t values as well as whole-brain nonparametric cluster-level t tests that are presented together with significant effects from ROI analyses (Figure 4). The ROI time courses are presented in Figure 5. An ANOVA with the factors Strategy (procedural vs. retrieval strategy), Operation (addition vs. multiplication), Laterality (left vs. right hemisphere), and Caudality (anterior vs. posterior regions) was run on a set of bilateral frontal and bilateral parietal ROIs within each of the six time windows. Post hoc ANOVAs were conducted for each hemisphere separately as well as post hoc t comparisons for Strategy and Operation effects on each ROI (Bonferroni-corrected for the number of analyzed ROIs, $N = 4$).

We found an activation sequence of frontal-before-parietal cortex within the frontal–parietal network. Procedural strategies produced more activation compared with retrieval strategies from 250 msec onward, reflected in a Strategy × Caudality × Laterality interaction in the 250- to 300-msec ($F(1, 22) = 5.75$, $p = .025$) and 300- to 350-msec windows ($F(1, 22) = 6.28$, $p = .020$). No other significant main effect of Strategy or interaction occurred in any of the first four time windows. A post hoc ANOVA run for each hemisphere separately showed that the Strategy × Caudality × Laterality interaction in the 300- to 350-msec window was driven by early right frontal activations: A Strategy × Caudality interaction in the 300- to 350-msec window was only observed in the right hemisphere ($F(1, 22) = 7.58$, $p < .011$), but not in the left hemisphere. Post hoc t tests on ROI effects showed stronger activation for procedural than retrieval strategies in the right frontal ROI for the 300- to 350-msec window ($t(22) = 3.10$, $p = .005$; Figures 4A and 5). This ROI effect was confirmed in significant whole-brain cluster-level corrected statistics in right frontal regions within the same time window (Figure 4B). Post hoc tests on the 250- to 300-msec window did not reach significance.

In the last two time windows (450–650 and 700–1000 msec), main effects of Strategy emerged ($F(1, 22) = 7.24$, $p = .013$, and $F(1, 22) = 11.58$, $p = .002$, respectively) as well as a Strategy × Laterality interaction in the 700- to 1000-msec window ($F(1, 22) = 4.84$, $p = .038$). Post hoc ANOVAs for each hemisphere showed that the interaction in the 700- to 1000-msec window was driven by a significant main effect of Strategy in the left hemisphere ($F(1, 22) = 15.90$, $p = .006$), whereas no such effect was observed in the right hemisphere. Cluster-level whole-brain statistics revealed significant left parietal strategy effects in the latest time window (Figure 4B). Within the 450- to 650-msec window, no strategy effect was observed in cluster-level statistics. No other significant main effect or interaction involving the factor Strategy occurred in ROI analyses in the two latest time windows.

We had no predictions for operation type (addition vs. multiplication) effects in the present analysis. Effects of operation type were observed in the 180- to 220- and 450- to 650-msec windows, whereas no effects of operation type occurred around 300 msec when early strategy selection effects were observed or during later phases of strategy execution from 700 msec. An Operation × Caudality × Laterality interaction occurred in ANOVAs on frontal–parietal ROIs in the 180- to 220-msec time window ($F(1, 22) = 11.34$, $p = .002$), driven by a significant post hoc Operation × Caudality interaction in the left hemisphere ($F(1, 22) = 9.94$, $p = .004$), whereas no operation type effects were observed in the right hemisphere. However, post hoc t tests on individual ROIs did not reach significance. A main effect of Operation emerged in the 450- to 650-msec time window ($F(1, 22) = 5.04$, $p = .035$).

Time–Frequency Analyses in EEG–MEG Source Space

Visual inspection of the time course for our time–frequency data revealed an early increase in induced power relative to the baseline, most pronounced in the theta band, until up to 400 msec, followed by a decrease in induced power that was strongest in the alpha band (Figure 3B). Therefore, we chose an early time window of 0–400 msec and a later time window of 400–1000 msec for our time–frequency analysis.

Whole-brain *t* value distributions for EEG–MEG source induced power values of theta, alpha, beta, and gamma bands were obtained together with permutation-based cluster-level statistics in the early (0–400 msec, strategy selection) and late (400–1000 msec, strategy execution) time windows. We only found whole-brain corrected significant effects in the late but not in the early time window. For the theta range, stronger power increase for retrieval in contrast to procedural strategies was observed in right frontal and temporal cortices (Figure 6A and B). Alpha and beta bands showed stronger power suppression for procedural in contrast to retrieval strategies in right parietal, frontal, and temporal regions (Figure 6A and B). Time–frequency representations for parietal, frontal, and temporal regions confirmed that strategy effects were driven by stronger theta power increase for retrieval strategies and stronger alpha and beta power suppression for procedural strategies (Figure 6C). No significant strategy or operation type effects were observed in gamma bands, and no significant effects of operation type were observed in any of the analyzed frequency bands.

DISCUSSION

We investigated the spatiotemporal dynamics of neural networks during arithmetic problem-solving in source estimates of evoked and time–frequency brain responses, derived from combined EEG–MEG data. Two categories

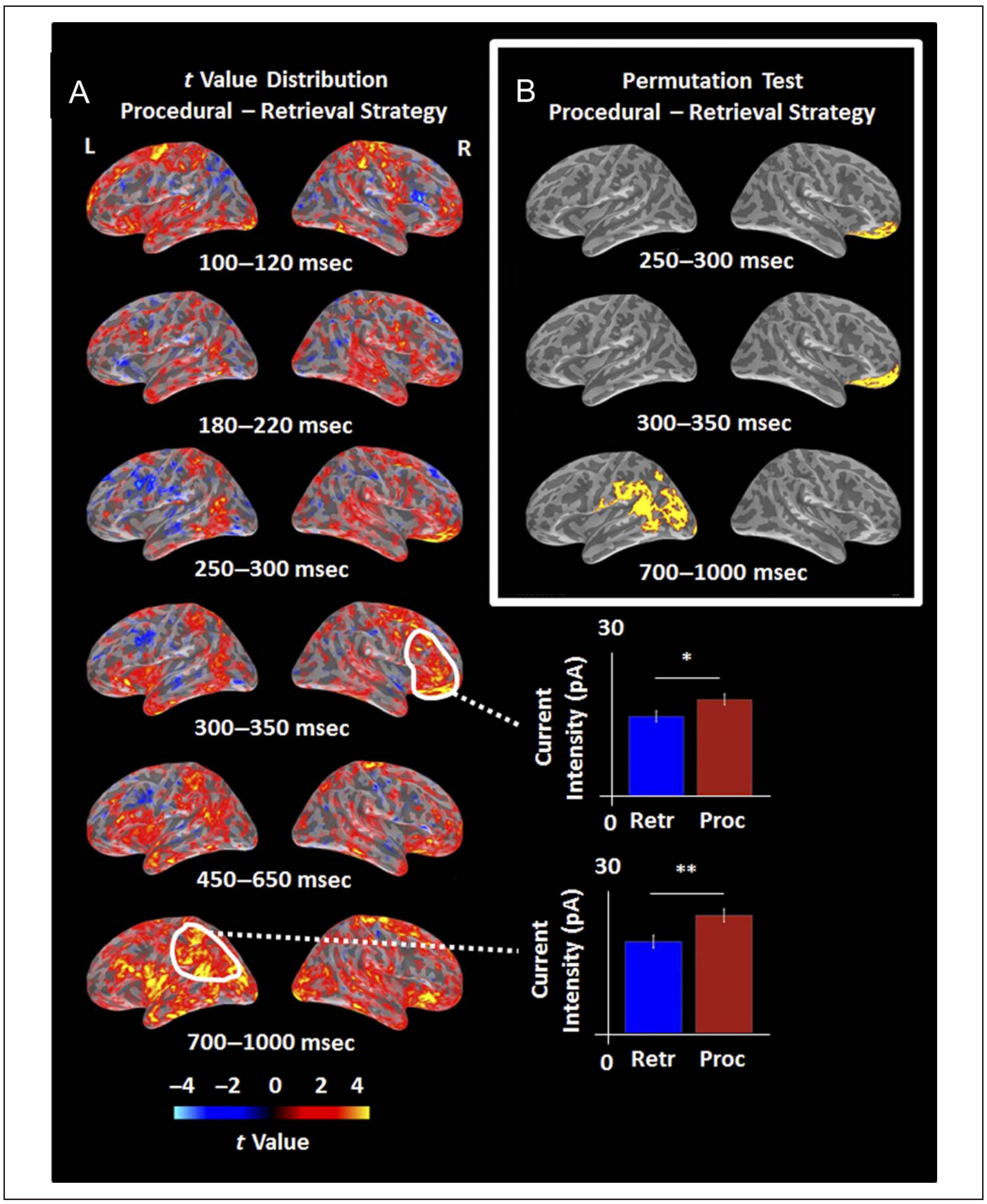

Figure 4. (A) *t*-Value distributions of evoked EEG–MEG minimum norm source estimates are presented for contrasts between procedural (Proc) and memory retrieval (Retr) arithmetic strategies, in each of the six analyzed time windows. Red color indicates more activation for procedural than retrieval strategies; and blue color, the reverse. Bar graphs show EEG–MEG source current intensities indicating significant main effects of strategy in analyses on frontal and parietal ROIs. Error bars indicate the *SEM* difference between conditions. (B) Significant clusters in evoked EEG–MEG minimum norm source estimates from permutation tests with spatial clustering.

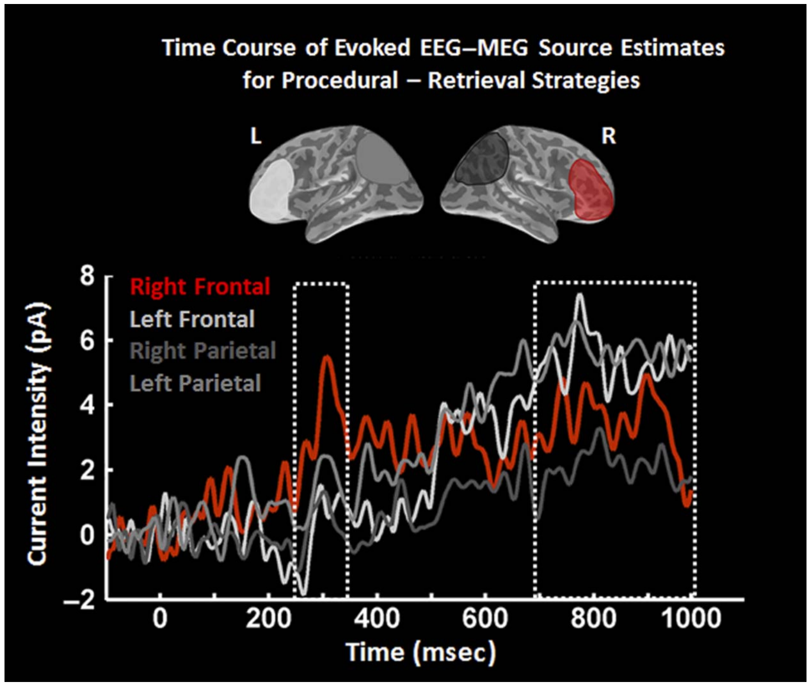

Figure 5. Time courses of evoked EEG–MEG source current intensities within the four analyzed ROIs for the contrast of procedural versus retrieval strategies. First effects of arithmetic strategy were observed in right frontal cortex around 300 msec (indicated by the dotted rectangle), followed by left parietal cortex from 700 msec onward.

of arithmetic problems were contrasted, chosen on the basis of our participants' individual ratings: "retrieval", that is, problems for which solutions are retrieved directly from memory, and "procedural" strategies, for which several solution steps are required. Procedural strategies pose higher demands on executive functions, whereas retrieval strategies mostly rely on memory processes. Our evoked analysis demonstrated differential temporal dynamics in frontal–parietal networks as a function of executive demands. In our time–frequency analyses, retrieval and procedural strategies could be dissociated by neural effects in different frequency bands. The increased theta power for retrieval strategies, as well as the reduced alpha and beta power for procedural strategies, suggests that theta and alpha/beta frequency bands are differentially sensitive to memory retrieval and executive demands, respectively.

Evoked EEG–MEG source estimates revealed separate dynamics of frontal and parietal cortices across stages of the problem-solving process: The right lateral frontal cortex showed first strategy effects in time windows around 300 msec, whereas later strategy effects occurred in left parietal regions from 700 msec onward. Thus, frontal activation preceded parietal activation, consistent with previous evidence for sequential activation of frontal and parietal cortices in a task-switching paradigm on the basis of dipole modeling of ERP data (Brass et al., 2005).

The time course of our strategy effects was in line with previous ERP studies and may suggest that early effects around 300 msec are due to aspects of strategy selection, whereas later effects from around 700 msec reflected strategy execution. Previous ERP studies on mental arithmetic reported specific effects because of strategy selection demands in brain responses around 300 msec after task onset (Uittenhove, Poletti, Dufau, & Lemaire, 2013; Uittenhove & Lemaire, 2012; El Yagoubi et al., 2003), whereas later strategy execution has been associated with a positive slow wave from 600 msec onward (Nunez-Pena, Gracia-Bafalluy, & Tubau, 2011; Nunez-Pena, 2008; Nunez-Pena et al., 2005, 2006; Pauli, Lutzenberger, Birbaumer, Rickard, & Bourne, 1996; Pauli et al., 1994).

Our localization of early strategy effects in frontal cortex is in line with fMRI and electrophysiological studies, suggesting its role in strategy selection (Bongard & Nieder, 2010) as well as in controlled rule retrieval (Bunge et al., 2003). Although our results are not inconsistent with the view of previous fMRI literature that a frontal–parietal network as a whole supports the execution of cognitively demanding tasks (Duncan, 2010; Dosenbach et al., 2008), our evoked analyses point to a special role of frontal brain areas within this network regarding early stages of strategy selection. This special role of frontal cortex in cognitive control and executive functions has already been suggested on the basis of neuropsychological and electrophysiological data (Fuster, 2001; Damasio et al., 1996; Goldman-Rakic, 1995), as well as in the ACT-R framework, applied to algebraic problem-solving (Anderson, Betts, Ferris, & Fincham, 2011; Anderson & Qin, 2008; Anderson, 2005). In particular, lateral frontal cortex has been associated with the temporal integration of multiple task requirements (Koechlin & Summerfield, 2007), and our analyses of the spatiotemporal brain dynamics suggest that the process of organization and solution step sequencing may occur already in early time windows around 300 msec.

We did not observe any stronger neural effects for retrieval strategies in contrast to procedural strategies in evoked EEG–MEG source estimates at any point in time. This may be explained by higher cognitive demands for more difficult tasks. Task difficulty in our paradigm means that a problem requires the organization and execution of a more complex solution strategy, and individual trial-by-trial strategy ratings may be the most precise measure of experienced task difficulty, that is, accounting for individual differences in skill levels, as shown by recent behavioral research (Tschentscher & Hauk, 2015). In line with this, we did observe not only a modulation of overall source amplitudes (e.g., "generally more activation for more difficult problem") but also more subtle effects on source topography and time course. In addition, our time–frequency analyses revealed differential effects for retrieval and procedural strategies in frontal and parietal regions within different frequency bands. This does suggest that the two types of arithmetic strategies rely on qualitatively different cognitive functions, whereas evoked source analyses were mostly sensitive to the amplitude differences related to general cognitive demands.

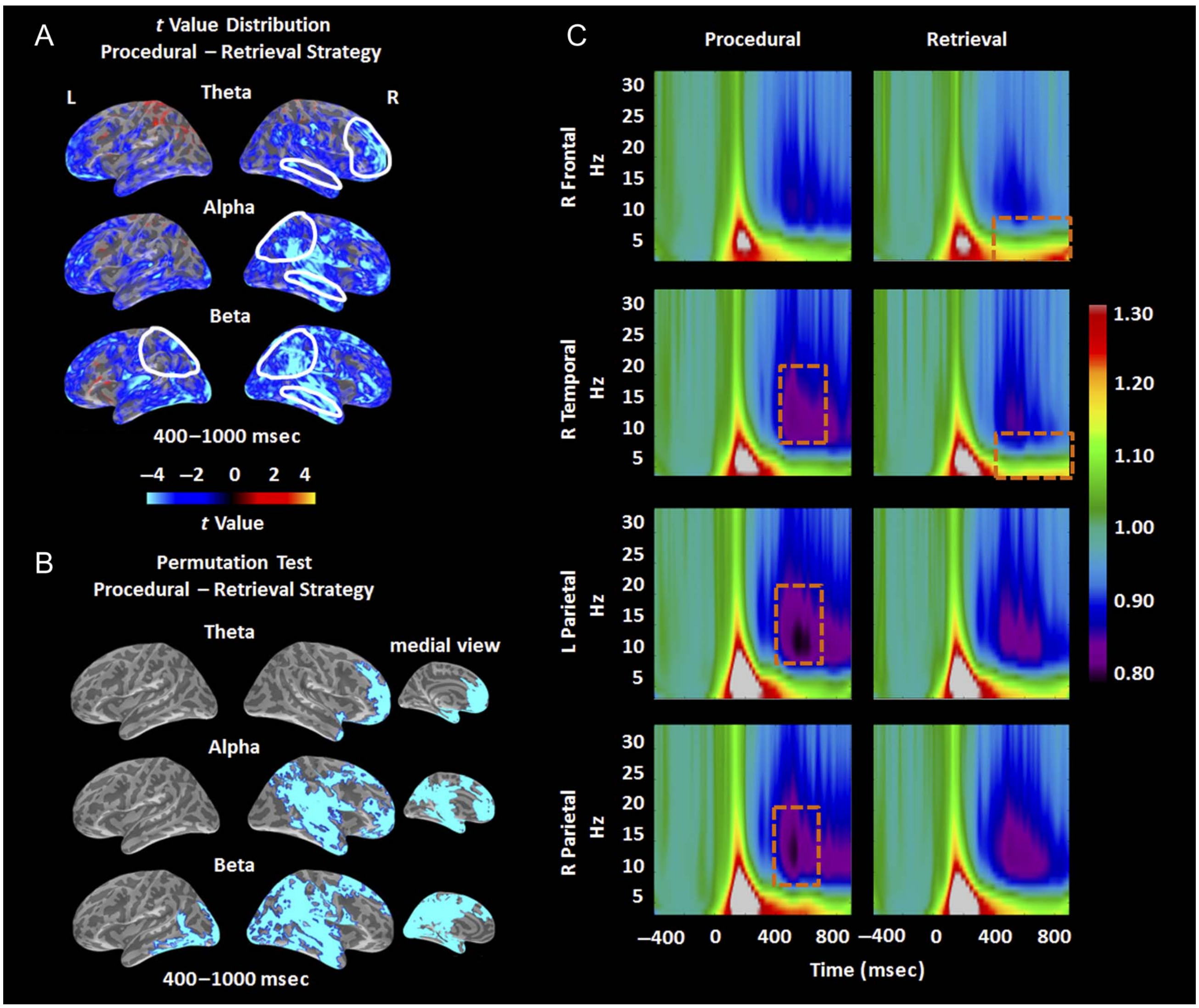

Figure 6. (A) Whole-brain t value distributions of EEG–MEG source induced power for the contrast of procedural versus retrieval strategies. Whole-brain-corrected results were only significant in the late time window for theta, alpha, and beta bands. (B) Significant clusters in EEG–MEG source induced power for the contrast of procedural versus retrieval strategies from permutation tests with spatial clustering. (C) Time–frequency representations (3–35 Hz, as ratio to baseline) for frontal, temporal, and parietal source space ROIs that were selected based on significant effects in whole-brain estimates for the contrast procedural versus retrieval strategies (indicated by white frames in A). Time–frequency representations show that effects in A and B were driven by stronger enhancement in theta power for retrieval compared with procedural strategies in right frontal and right temporal ROIs (orange rectangles) and stronger suppression in alpha and beta power for procedural compared with retrieval strategies in bilateral parietal ROIs and in the right temporal ROI. L = left; R = right.

Our time–frequency results are consistent with previous EEG sensor level analyses reporting theta power enhancement for memory retrieval strategies in arithmetic task paradigms, whereas multistep procedural strategies were reflected in reduced alpha power (Grabner & De Smedt, 2012; De Smedt et al., 2009). We here provide novel evidence on the localization of these effects within frontal, parietal, and temporal cortices. A stronger induced power decrease in alpha- and beta-frequency ranges was observed for procedural in contrast to retrieval strategies in right frontal, parietal, and temporal regions. A stronger increase in right frontal and temporal theta power was observed for retrieval strategies. The topography of these effects in source estimates supports the view that procedural strategies more strongly rely on a frontal–parietal executive control network (Cole et al., 2013; Duncan, 2010). Retrieval strategies mostly rely on arithmetic fact retrieval from memory, and our results confirm the previously suggested role of prefrontal regions in deliberate long-term memory retrieval of specific rules and facts in interaction with medial–temporal and hippocampal regions (Barredo et al., 2013; Anderson et al., 2007; Badre & Wagner, 2007; Donohue, Wendelken, Crone, & Bunge, 2005; Bunge et al., 2003).

Although our results speak for differential time–frequency characteristics of memory and executive functions in a given task environment, we are cautious regarding the generalization of these effects to other higher-level executive control and memory processes (Jensen & Bonnefond, 2012; Siegel et al., 2012; Grabner & De Smedt, 2011; Benchenane et al., 2010; De Smedt et al., 2009; Klimesch et al., 2008; Sato & Yamaguchi, 2007; Bastiaansen & Hagoort, 2003; Salinas & Sejnowski, 2001; Klimesch, 1999). Our results are encouraging in so far as different frequency bands allowed us to disentangle brain areas also reported to be involved in memory and executive processes in a broad range of metabolic neuroimaging studies. This separation of brain dynamics based on neural frequencies is not possible with metabolic neuroimaging methods. However, the particular role of different frequency bands in higher cognitive functions may depend on the experimental paradigm and the temporal characteristics of cognitive processes involved. We therefore hope that future studies will be able to use this approach to characterize the "networks" subserving memory and executive functions previously described in the neuroimaging literature in more detail.

In conclusion, our results demonstrate specific temporal dynamics of brain activation already within the first second of the problem-solving process. We could provide evidence for a frontal-before-parietal activation pattern as a function of executive demands, that is, multistep procedural strategies in contrast to retrieval strategies. Our results suggest a special role of right frontal cortex in early structuring of a demanding solution process. Thus, disentangling the contributions of different brain regions at different stages of the problem-solving process requires the temporal resolution of EEG and MEG measurements. The current analyses suggest that specific neural frequency bands reflect distinct cognitive functions in a multicomponent problem-solving process, such as executive functions in alpha and beta power decreases within frontal and parietal regions, and memory functions in right frontal theta power enhancement. EEG and MEG will be essential to characterize the regions and networks involved in cognitive control and executive functions in more detail.

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