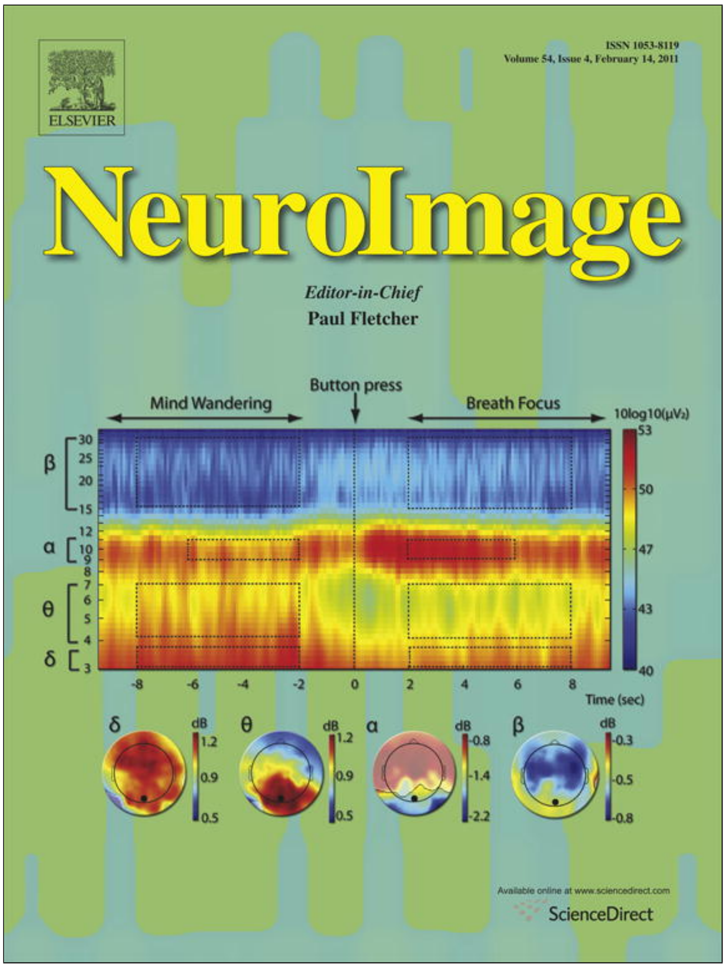
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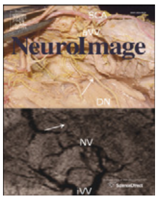

Electrophysiological correlates of retrieval orientation in reality monitoring

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ABSTRACT

Retrieval orientation describes the modulation in the processing of retrieval cues by the nature of the targeted material in memory. Retrieval orientation is usually investigated by analyzing the cortical responses to new (unstudied) material when different memory contents are targeted. This approach avoids confounding effects of retrieval success. We investigated the neural correlates of retrieval orientation in reality monitoring with event-related potentials (ERPs) and assessed the impact of retrieval accuracy on obtained ERP measures. Thirty-two subjects studied visually presented object names that were followed either by a picture of that object (perceived condition) or by the instruction to mentally generate such a picture (imagine condition). Subsequently, subjects had to identify object names of one study condition and reject object names of the second study condition together with newly presented object names. The data analysis showed that object names were more accurately identified when they had been presented in the perceived condition. Two topographically distinct ERP effects of retrieval orientation were revealed: From 600 to 1100 ms after stimulus representation, ERPs were more positive at frontal electrode sites when object names from the imagine condition were targeted. The analysis of response-locked ERP data revealed an additional effect at posterior electrode sites, with more negative ERPs shortly after response onset when items from the imagine condition were targeted. The ERP effect at frontal electrode sites, but not at posterior electrode sites was modulated by relative memory accuracy, with stronger effects in subjects who had lower memory accuracy for items of the imagine condition. The findings are suggestive for a contribution of frontal brain areas to retrieval orientation processes in reality monitoring and indicate that neural correlates of retrieval orientation can be modulated by retrieval effort, with stronger activation of these correlates with increasing task demands.

Introduction

Retrieval of episodic information is a core function of human behavior, with disturbances of these retrieval processes having vast consequences for life, as for example observed in dementia. Successful retrieval of episodic information depends also on the integrity of processes preceding and succeeding retrieval attempts. Pre-retrieval processes include what Tulving (1983) has conceptualized as retrieval mode. This term describes that a rememberer needs to be in an appropriate cognitive state in order to treat a stimulus as an episodic retrieval cue and to retrieve episodic information. Thus, the word "France" might or might not lead to the retrieval of episodic information, depending on the cognitive state.

Furthermore, the processing of retrieval cues is assumed to be modulated by the nature of the targeted material in memory. This modulation of retrieval processes by the retrieval goal has been conceptualized as retrieval orientation (Rugg and Wilding, 2000). Thus, this concept is more specific than the concept of retrieval mode and also underlines that retrieval of episodic information is of particular importance in goal directed behavior.

In order to study neural correlates of retrieval orientation with event-related potentials (ERPs), usually the cortical responses to correctly rejected new items under different retrieval goals are compared, as for this class of items confounding effects of retrieval success are avoided to most extent. In the majority of studies, retrieval orientation was investigated in memory exclusion tasks (Jacoby, 1991). This kind of task requires differentiating between subsets of studied items during retrieval: only a subset of previously studied items represents the target category, while other studied items together with new (non-studied) items have to be rejected as nontargets. Switching the target and nontargets category in a second retrieval condition creates two retrieval conditions which ideally differ only with regard to the targeted material.

The exclusion task requires, however, some differentiation of studied items as targets and nontargets. This differentiation might be based on core item characteristics, such as item material (e.g. pictures of objects vs. names of objects), or more on context features of the study phase (e.g. object names spoken in male voice or female voice). In many ERP studies on retrieval orientation, the differentiation was based on the item material (Duverne et al., 2009; Herron and Rugg,

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2003; Hornberger et al., 2004; Johnson and Rugg, 2006; Morcom and Rugg, 2004; Robb and Rugg, 2002; Stenberg et al., 2006), while studies of the second type are rarer (Dzulkifli and Wilding, 2005; Herron and Wilding, 2004; Wilding, 1999; Wilding and Nobre, 2001).

A classical case for the examination of retrieval orientation is the reality monitoring task, i.e. a task requiring the differentiation of self-generated information vs. externally perceived information. Within the source memory framework it is proposed that the origin of information is not tagged and read out of memory (Johnson et al, 1993). Rather, the attribution to an external or internal source is the result of a decision process that works on the basis of qualitative characteristics of the memory trace. Thus, perceptual richness of memories might be diagnostic for external sources, whereas memories for cognitive operations might be diagnostic for internally generated memory contents (Johnson et al., 1993).

Retrieval orientation in a reality monitoring task has hardly been investigated so far. To our knowledge, there is one single study of Leynes et al. (2005) dealing with retrieval orientation in reality monitoring. In this study, subjects encoded words in two conditions. In a reality monitoring condition, subjects heard words in a male voice or they had to generate words themselves. In an external source monitoring condition, subjects heard words in a male or female voice. Subjects were subsequently tested in a source memory task. Leynes et al. (2005) found more positive ERP deflections at frontal electrode sites between 1000 and 1200 ms for new items in the reality monitoring condition, as compared to the external source monitoring condition.

It might be tempting to speculate that the frontally distributed ERP difference reflects activation of frontal brain areas involved in the retrieval of self-generated information: Recent functional magnetic resonance imaging (fMRI) studies have indeed shown that this kind of retrieval is associated with activation of rostral medial prefrontal brain areas Vinogradov et al., 2008) and left-lateral prefrontal structures (Lundstrom et al., 2003). However, Leynes et al. (2005) themselves were somewhat reluctant in interpreting their results (“it is unclear exactly what these differences signify”, p. 520). Knowledge about the neural correlates of retrieval orientation in reality monitoring is of high importance for a better understanding of dysfunctional reality monitoring, as e.g. observed in schizophrenia (e.g. Vinogradov et al., 2008) or Alzheimer's disease (Mammarella and Fairfield, 2006).

The interpretation of neural correlates of retrieval orientation is hampered by the limited knowledge about the potential influence of retrieval effort on these correlates. Retrieval effort refers to the level of processing resources deployed in service of a retrieval attempt (Rugg and Wilding, 2000). Since retrieval effort cannot be measured directly, it is usually operationalized by task difficulty, as measured by performance accuracy or reaction time. Empirical findings on the relation between retrieval effort and retrieval orientation vary.

In an early study, ERP effects of task difficulty and targeted material were reported to be temporally dissociated and not interacting (Robb and Rugg, 2002), with task difficulty manipulated intraindividually by varying the length of the study list. Effects of task difficulty on ERPs were restricted to the first 300 ms after stimulus onset, while ERP differences between different retrieval orientations were seen between 300 and 1800 ms. In a second study, effects of task difficulty and of targeted material were found to be independent as well, but were temporally overlapping (Morcom and Rugg, 2004).

Two other studies found effects of performance accuracy on ERP correlates of retrieval orientation, albeit in opposite directions: In a study of Dzulkifli et al. (2004), participants had to identify items of one study condition by a button press, while items of a second study condition as well as new items did not require a response. The average hit rate differed between the two target designations. A low relative difficulty group and a high relative difficulty group were defined by means of a median split on the basis of the difference between the two hit rates. ERP correlates of retrieval orientation were found at frontal sites, but only in the high relative difficulty group (i.e. only in subjects with relatively low accuracy).

A second study of the same lab compared the ERP correlates of retrieval orientation between subjects with high memory accuracy and subjects with low memory accuracy. ERP correlates of retrieval orientation were found only in subjects with high memory accuracy (Bridger et al., 2009). Although the extracted performance measures differ between the two aforementioned studies (accuracy differences between conditions vs. average accuracy), their findings support different notions: The study of Bridger et al. (2009) supports the view that a more effective usage of retrieval cues, as reflected in the ERP correlate of retrieval orientation, leads to better retrieval performance. The study of Dzulkifli et al. (2004) is more suggestive for retrieval orientation as a compensatory mechanism that needs to be engaged with increasing task difficulty.

The current study aimed at investigating the neural correlates of retrieval orientation in reality monitoring by means of ERP measures and at assessing the impact retrieval effort on these correlates. In contrast to Leynes et al. (2005), we investigated retrieval orientation in reality monitoring in the visual modality: Subjects studied objects names that were either followed by a picture of the denoted object or followed by the instruction to imagine a picture of the named object. Subsequently, subjects were tested in a memory exclusion task: they had to identify object names of one condition and to reject object names of the second condition together with unstudied, new object names as nontargets. In order to specify the neural correlates of retrieval orientation, ERPs to new object names were compared between conditions (perceived vs. imagined objects as targets). To anticipate the results, the ERPs differed between conditions, but also the response speed and retrieval accuracy varied depending on the targeted material: subjects were slower to respond and less accurate when imagined items were targeted. As one consequence, we analyzed additionally response-locked ERPs in order to eliminate the possibility that the findings on stimulus-locked ERPs were due to differences in the response speed between conditions. As second consequence of the performance differences between conditions, for assessing the relationship between retrieval effort and retrieval orientation, ERP effects of retrieval orientation could be correlated not only with the memory accuracy in each retrieval condition (absolute difficulty) but also with its between-condition difference (relative difficulty).

Methods

Participants

Thirty-two volunteers (16 female), ranging in age from 18 to 32 years (mean age 22.9 years) took part in the experiment. All participants were students at Saarland University and reported to be of good health with no history of neurological illness. Only German native speakers were included. All subjects were right handed and had normal or corrected-to-normal vision. All subjects were informed about the procedure of the experiment and gave written consent for participation. Participation was compensated with 8 €/hour.

Experimental procedure

The experimental set-up was adopted from Johansson et al. (2002), with the difference that it was designed as a memory exclusion task instead of a source memory task. The experiment consisted of two phases, a study phase and a test phase: During the study phase, object names were presented, followed by a picture of the object (perceived item condition) or followed by the instruction to create mentally such a picture (imagined item condition). Trials started with the presentation of a fixation cross for 500 ms.

Thereafter, object names were presented for 1500 ms. After each object name, either a coloured picture of the object with a white rectangle as background (perceived item condition) or a white rectangle without a picture (imagined item condition) were shown for 6000 ms. In the perceived item condition, subjects had to examine the picture and to assess at the end of its presentation whether the graphic distinctiveness was good, fair or bad. In the imagined item condition, subjects had to imagine a drawing of the named object and project this mental image onto the white rectangle on the screen. At the end of these trials, subjects had to rate whether the graphic distinctiveness of the imagined item was good, fair or bad. All ratings were made by button press on the numerical part of computer key board (with 1 for good, 2 for fair, and 3 for bad graphic distinctiveness), as soon as a question mark appeared on the screen. The next trial did not start before a response had been made. Perceived and imagined items were presented in random order within the same block, with the restriction that more than three items of one condition did not occur in succession.

In the test phase, trials started with a fixation cross, lasting for 100 ms and followed by an empty screen for 400 ms. Object names were presented for 200 ms. In one test condition, subject had to identify object names which had been presented as pictures (perceived item target condition) and to reject object names of the second study condition together with new object names. In the second test condition, subjects had to identify object names for which they had to produce mental images and to reject other object names (i.e. old object names presented together with pictures and newly presented object names). Participants were tested in both conditions, with a change of the target category after half of the test. Subjects were instructed to respond as fast and accurately as possible. There was a time limitation of 3800 ms for giving a response. No response feedback was provided. Subjects responded by pressing the letters “C” and “M” on a computer keyboard with the left and right index finger. The assignment of the key to the response category (Targets vs. Nontargets) varied from subject to subject and the order of target conditions was balanced across subjects.

In addition to the behavioural task, subjects filled out the Vividness of Visual Imagery Questionnaire (VVIQ, Marks, 1973) in order to test whether memory performance was modulated by the visual image vividness. The VVIQ was conducted during the preparation for the EEG recording. The whole experimental set-up took between 2 and 2.5 hours (including preparation time for EEG recording).

Stimuli

Words were presented on a 17 inch monitor in white 18 pt Courier New font on a black background. The frame was a white rectangle defined to have a size of 75% of screen height and width. Likewise the pictures displayed within the frame were 75% of the dimensional size of the frame. All displays were centred in the middle of the computer screen, with subjects sitting 60-80 cm in front of it.

The stimulus material consisted of coloured painted drawings (Rossion and Pourtois, 2004), originating from the picture set of Snodgrass and Vanderwart (1980). Those drawings were preceded by the German name of the depicted object. The criteria for the selection of the stimuli were the same as in the study of Johansson et al. (2002): Only object names with a word length between 3 and 10 characters and a word frequency ranging from 1 to 475 occurrences per million were included. Word frequency was checked with the Celex linguistic database by Baayen et al. (1993). Ambiguous object names were excluded, too. Based on these criteria, 184 object names were selected as material for the study phase. Study material (words and pictures) was grouped into two lists of 92 items. One list was assigned to the perceived item condition and the second list to the imagined item condition. The list assignment to the study conditions was counter-balanced across subjects. Furthermore, the word length and word frequency of the two lists did not differ between lists and their halves. In each of the test conditions, there were 46 targets to be identified, and 46 old items of the second study condition (in the following labelled as nontargets), together with 46 new items that had to be rejected.

EEG recordings

Prior to the study phase, elastic caps (Easycap, Herrsching, Germany) with 58 embedded silver/silverchloride EEG electrodes were attached to the subject heads. Electrode locations in these caps are based on an extended 10-20 system (10-10 system). EEG was continuously recorded, referenced to the left mastoid. In addition, electroocular activity was recorded by a pair of electrodes affixed to the outer canthi and by a pair of electrodes placed below and above the right eye. Data were sampled with 500 Hz and filtered online from 0.016 Hz (time constant 10 sec) to 250 Hz. Electrode impedances were kept below 5 kΩ.

Offline, data were digitally filtered from 0.1 Hz to 40 Hz (48 dB), with an additional notch filter in order to suppress line activity, and re-referenced to linked mastoids. The impact of eye movements and blinks on EEG activity was eliminated by a correction algorithm implemented in the analysis tool (VisionAnalyzer 2.01, Gilching, Germany), based on an independent component analysis (ICA). After down-sampling to 200 Hz, data were exported to EEGLab (Swartz Center for Computational Neuroscience, University of California San Diego, USA). Here, a second ICA was run in order to eliminate the impact of muscular, electrocardiographic, and technical artifacts. Data were segmented into epochs of 3000 ms duration, including a 500 ms baseline. Data were baseline corrected and screened for artifacts, which remained undetected by the ICA procedure. Trials with EEG activity exceeding ±100 μV, exhibiting abnormal trends, or being abnormally distributed (± 5 SD from the mean) were excluded. Only correct responses to new items were considered for the current analysis. Average ERPs were calculated for correct rejections of new items, separately for each of the two conditions. ERPs to new items in the perceived item target condition (NEW_{PT}) were based on 41.4 trials (SD 2.8) and ERPs to new items in the imagined item target condition (NEW_{IT}) were based on 39.8 trials (SD 4.6). In addition to stimulus-locked ERP data, response-locked ERP data were analyzed as well. Segments of 1500 ms (1000 ms before response onset) were extracted from the baseline corrected stimulus-locked data. No further baseline correction was conducted for these response-locked ERP data sets. Since response-locked ERPs were extracted from the stimulus-locked data, trials with $RT<500$ ms and $RT>2500$ ms were not included for this analysis. The total number of trials for calculating the ERPs was only mildly affected by the exclusion of these trials: the response-locked ERPs to new items in the perceived item target condition were based on 39.8 trials (SD 3.2) and in the imagined item target condition on 38.0 trials (SD 4.8). All single subjects ERPs contained >20 trials.

Data analysis

Behavioral data

The discrimination index (Pr) was quantified as difference between the hit rate (P_target) and the false alarm rate to (old) nontargets (P_false alarm), for each target condition separately (Snodgrass and Corwin, 1988). (E.g. $Pr_{PT} = P\_target_{PT} - P\_false\ alarm_{PT}$, whereby the index PT refers to the perceived item target condition; accordingly, IT refers to the imagined item target condition). Behavioral responses were compared between the two conditions by means of paired *t*-tests and repeated measure analysis of variance (ANOVA). Covariation of behavioral measures was assessed by calculation of Pearson correlation coefficients (*r*).

The total sample was split twice in two subgroups in order to study the impact of memory accuracy on ERP correlates of retrieval orientation: First, the groups of high and low performers were defined by the median split of the averaged Pr of both conditions ($\mathrm{Pr}_{\mathrm{mean}} = ½\ [\mathrm{Pr}_{\mathrm{IT}} + \mathrm{Pr}_{\mathrm{PT}}]$). Secondly, the high and low relative difficulty groups were defined by the median Pr difference between the two conditions ($\Delta\mathrm{Pr} = \mathrm{Pr}_{\mathrm{IT}} - \mathrm{Pr}_{\mathrm{PT}}$). In addition to ERP measures, reaction times and the ratings of the study phase were compared between these groups.

ERP data

The mean amplitudes of stimulus-locked ERPs were quantified for 100-ms bins from 200 to 2000 ms after stimulus presentation and the mean amplitudes of response-locked ERPs from 500 ms before to 500 ms after response onset. In order to specify ERP correlates of retrieval orientation, ERPs to correctly rejected new items were compared between the two conditions (perceived item target condition and imagined item target condition) by paired t-tests for each of the 58 scalp electrodes. In order to take the spatial and temporal expansion of the ERP effects into account, for this comparison, P values of $p<0.05$ but $p>0.01$ were regarded as significant only if neighboring electrodes or neighboring time windows showed a significant condition effect at $p<0.01$. This approach provides a better understanding of the overall distribution of the retrieval orientation effect than a conservative correction of the significance level.

For evaluating the relationship between ERP correlates of retrieval orientation and memory performance, difference ERPs were calculated by subtracting the ERPs elicited by the two classes of new items ($\Delta\mathrm{ERP} = \mathrm{ERP}_{\mathrm{IT}} - \mathrm{ERP}_{\mathrm{PT}}$). As the use of single channel ERP data of 100-ms time bins for this purpose would have resulted in an inflationary number of correlation coefficients, dimensions of ERP data were reduced by a factor analysis with varimax rotation before calculating correlation coefficients. Data entered into the factor analysis were average difference ERPs of 200-ms time bins, with a focus on those 200-ms time bins showing the largest condition difference. Please note that extracted factors describe systematic variance in the difference ERPs, but not necessarily systematic condition differences. The individual scores of the first four factors derived from the factor analysis were then correlated with three performance measures (Pr in the two conditions and the difference between them, ΔPr). Kolmogorov–Smirnov *z* values were calculated for all variables in order to test for normal distribution of the data. The assumption of the normal distribution was not violated for any analyzed variable.

Results

Behavioral data study phase

The analysis of the rating data of the study phase was based on 31 subjects (data of one subject had to be excluded due to a technical failure). Ratings for the graphical distinctiveness did not differ between conditions (mean rating for perceived pictures = 1.60 ± 0.35 vs. mean rating for imagined pictures = 1.53 ± 0.31, $t_{30} = 0.907$, n.s.). Furthermore, ratings differed neither between high and low performers of the test phase nor between the high and low relative difficulty groups (all $t_{30} < 1.084$, n.s.).

Behavioral data test phase

The analysis of the behavioral data of the test phase revealed three major condition effects, indicating a poorer performance in the imagined item target condition. The Pr scores were lower, as well as reaction times for correctly rejected new items and correctly identified targets slower, as compared to the perceived item target condition.

Table 1

Mean accuracy of responses in the perceived item target condition (PT) and imagined item target condition (IT) (±SD): P_target (proportion of correctly identified targets), P_false alarms (proportion of false alarms to old nontargets), Pr (discrimination index), P_new (proportion of correctly rejected new items), P_no response (proportion of missed responses).

	PT	IT
P_target	0.81 ± 0.13	0.77 ± 0.13
P_false alarm	0.08 ± 0.05	0.11 ± 0.08
Pr	0.74 ± 0.16	0.65 ± 0.20
P_new	0.99 ± 0.02	0.96 ± 0.06
P_no response	0.002 ± 0.004	0.005 ± 0.011

In detail, the hit rate was lower ($t_{31} = 3.410$, $p = 0.002$) and the rate of false alarms was higher ($t_{31} = 2.902$, $p = 0.007$) for imagined item targets, resulting in a significant lower Pr value ($t_{31} = 4.481$, $p < 0.001$), as compared to the perceived item targets (Table 1). In addition, the proportion of correctly rejected new items was lower when imagined items were targets ($t_{31} = 2.040$, $p = 0.050$). Only on very few occasions subjects failed to respond to items, with no difference between retrieval conditions ($t_{31} = 1.651$, n.s.). The performance data for each subgroup are provided in Supplementary data (Table S1).

For reaction times (RTs), a repeated-measure ANOVA with ITEM (Target, Nontarget, New items) and CONDITION (PT, IT) as factors revealed significant main effects and an interaction (ITEM: $F_{2,\ 62} = 68.858$, $p < 0.001$, $\varepsilon = 0.801$; CONDITION: $F_{1,\ 31} = 12.064$, $p = 0.002$; ITEM*CONDITION: $F_{2,\ 62} = 9.281$, $p < 0.001$). Between conditions, reaction times differed for new items ($t_{31} = 3.365$, $p = 0.002$) and targets ($t_{31} = 4.350$, $p < 0.001$), with slower reaction times for these items in the imagined item target condition (Table 2). No difference between conditions was found for the reaction times to nontargets ($t_{31} = 1.171$, n.s.). The reaction times were always faster for new items than for both kinds of old items (Targets, Nontargets) in both conditions (all $t_{31} > 5.695$, $p < 0.001$). In the perceived item target condition, subjects responded faster to targets than to nontargets ($t_{31} = 3.595$, $p = 0.001$), while in the imagined item target condition these reaction times did not differ ($t_{31} = 1.692$, n.s.). Neither the groups of high and low performers nor the low and high relative difficulty groups differed in their RTs (all $t_{30} < 1.311$, n.s.), indicating that there was no speed-accuracy trade-off. The reaction times for each subgroup are provided in Supplementary data (Table S2).

In order to assess the relation of relative task difficulty (ΔPr) to other behavioral measures (ΔRT_new, ΔRT_target, $\mathrm{Pr}_{\mathrm{IT}}$, $\mathrm{Pr}_{\mathrm{PT}}$), correlation coefficients were calculated. This analysis showed that ΔPr was not associated with a slowing-down of reaction times ($r = -0.174$ for ΔRT_new and $r = 0.135$ for ΔRT_target, both n.s.), again indicating that there was no speed-accuracy trade-off with increasing relative task difficulty. ΔPr was found to be correlated with $\mathrm{Pr}_{\mathrm{IT}}$ ($r = 0.619$, $p < 0.001$) but not $\mathrm{Pr}_{\mathrm{PT}}$ ($r = 0.118$, n.s.). This indicates that high relative task difficulty (as reflected in more negative ΔPr scores) was driven primarily by a poorer accuracy in the imagined item target condition. In line with that, $\mathrm{Pr}_{\mathrm{IT}}$ differed between the low and high relative difficulty group (0.76 ± 0.17 vs. 0.56 ± 0.18, respectively, $t_{30} = 3.256$, $p = 0.003$), while $\mathrm{Pr}_{\mathrm{PT}}$ was equally high in both groups (0.76 ± 0.16 vs. 0.72 ± 0.15, respectively, $t_{30} = 0.631$, n.s.). A complete overview of

Table 2

Mean reaction times (± SD) for correctly identified targets (RT_target), correctly rejected old nontargets (RT_nontarget) and new items (RT_new) in the perceived item target condition (PT) and imagined item target condition (IT).

	PT	IT
RT_target	932.7 ± 201.3	1104.3 ± 271.7
RT_nontarget	1020.6 ± 213.5	1061.5 ± 235.9
RT_new	767.9 ± 150.6	842.7 ± 179.4

accuracy measures in the subgroups is provided in Supplementary data (Table S1).

Stimulus-locked ERPs

To examine ERP correlates of retrieval orientation, we contrasted ERPs to new items between the two conditions. The potential impact of the differential memory performance between conditions on ERPs was assessed by correlating ERP differences between conditions with performance measures. In addition, these ERP differences were compared between high and low performers and between the high and low relative difficulty groups.

The main findings of the comparison of ERPs to new items in the imagined and perceived target condition are displayed in Fig. 1, including mapped ERP differences and t values: ERPs started to diverge at ~600 ms at frontal electrodes, with ERPs being more positive in the imagined item target condition. Largest differences were found at the electrodes Fpz, AF3, Fz, F1, F2, F3, F5, and FC3 and between 600 and 800 ms, as highlighted by the mapped ERP differences. In contrast, ERPs did not differ between conditions at posterior electrodes. The statistical comparison of the mean ERP amplitudes by paired *t*-tests showed that the significant condition differences at frontal and frontocentral electrodes lasted up to 500 ms (600–1100 ms).

A factor analysis with varimax rotation was run on the difference ERP values between the conditions for the latency window from 600 to 800 ms. The first four factors explained 87.3% of the total variance. The second factor explained 31.9% of the total variance and loaded highly on ERP differences at frontal recording sites, at which the significant retrieval orientation effect had been revealed in the first step of ERP analysis. The individual scores of this factor correlated with ΔPr ($r_{31} = -0.453$, $p = 0.009$), but not with the Pr values of each condition. Furthermore, the individual scores of this factor tended to be larger for the high than the low relative difficulty group ($F_{1,31} = 3.645$, $p = 0.066$), but did not differ between high and low performers ($F_{1,31} = 0.734$, n.s.). No significant correlations or group differences were found for the other extracted factors. The factor loadings on each electrode are depicted in Supplementary data (Fig. S1).

To sum up, ERP to new items differed between conditions at frontal electrodes in the latency range from 600 to 1100 ms, with ERPs in the imagined item target condition being more positive. ERP differences between 600 and 800 ms at frontal electrodes were modulated by the relative difficulty of the two tasks (ΔPr), but not by the absolute difficulty ($\mathrm{Pr}_{\mathrm{mean}}$).

Response-locked ERPs

Main findings of the comparison of ERPs averaged to the responses to new items in the two conditions are displayed in Fig. 2. Very similar to the stimulus-locked ERP data, response-locked ERPs differed at frontal electrodes, with ERPs being more positive in the imagined item target condition. These differences were most pronounced shortly before response onset and ended shortly after it: *t*-tests revealed

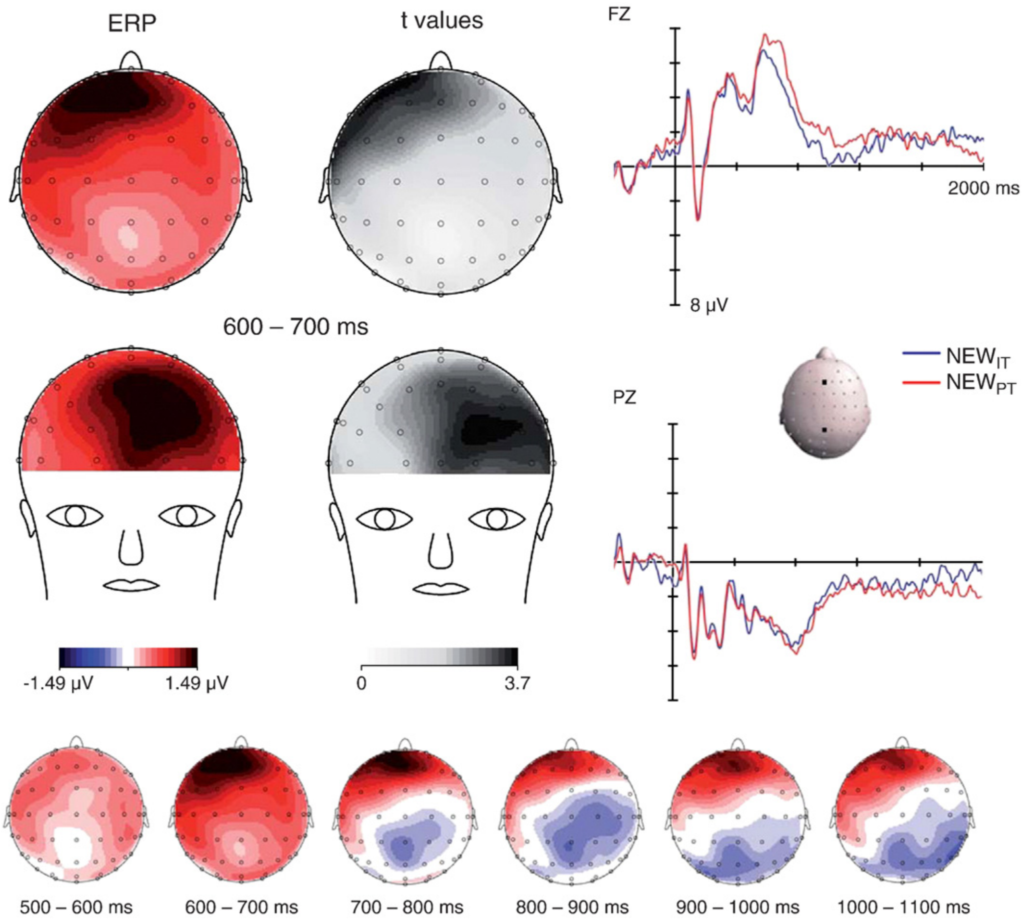

Fig. 1. Stimulus-locked ERPs of new items in the two target conditions: on the right side, data from the FZ and PZ electrodes are shown; ERPs to new items in the perceived item target condition are plotted as a blue line, ERPs to new items in the imagined item target condition as red line. On the left side, the difference potential between the conditions is depicted for the latency range 600-700 ms, when the ERP differences were largest. To the right of this, the according t values are mapped ($t_{31} > 2.044$ significant at $p < 0.05$; $t_{31} > 2.744$ significant at $p < 0.01$). The button row shows the time course of the difference potential between 500 and 1100 ms. Frontal differences were significant between 600 and 1100 ms.

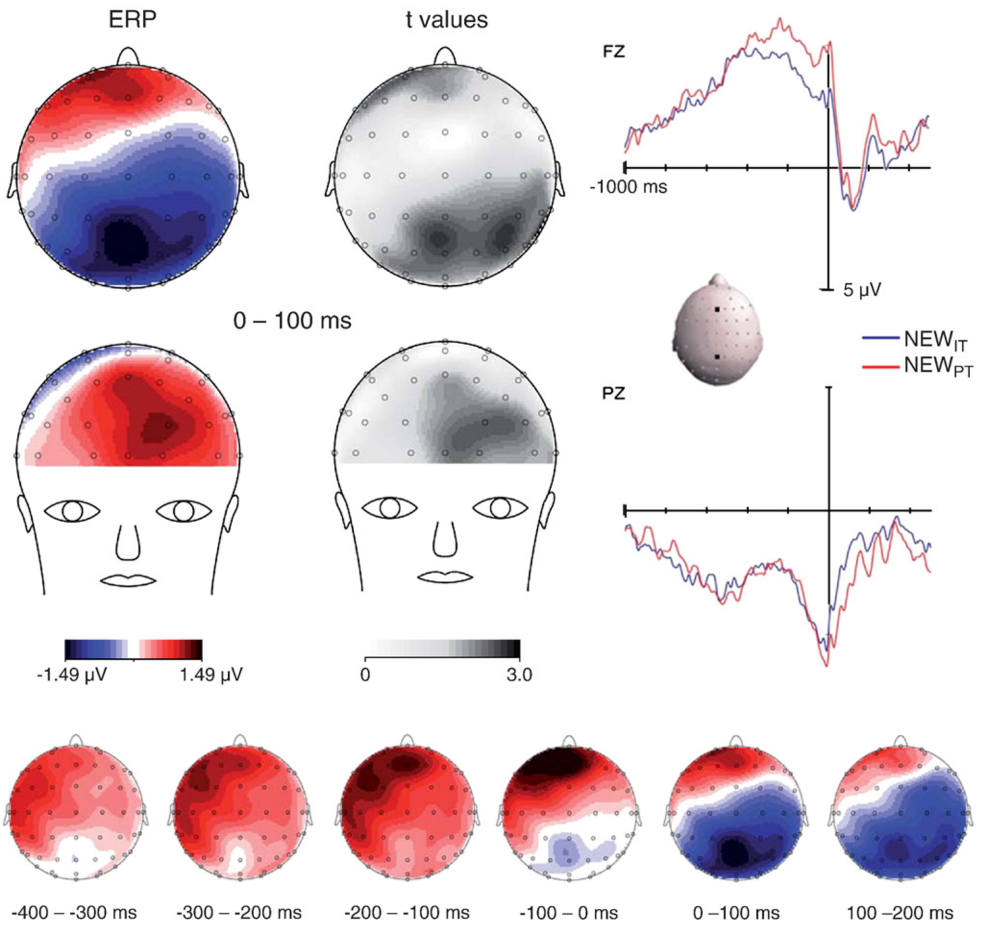

Fig. 2. Response-locked ERPs of new items in the two target conditions: on the right side, data from the FZ and PZ electrodes are shown; ERPs to new items in the perceived item target condition are plotted as a blue line, ERPs to new items in the imagined item target condition as red line. On the left side, the difference potential between the conditions is depicted for the latency range 0–100 ms, when in addition to frontal effects parietal ERP differences were observed. Right to it, the *t* values are mapped accordingly. The bottom row shows the time course of the difference potential from 400 ms prior to the response to 200 ms after it. Note, significant parietal effects were observed only in the response-locked data. Frontal differences were significant between −400 and 100 ms, parietal effects between 0 and 200 ms.

significant frontal differences from 400 ms before the response onset to 100 ms thereafter. In addition to the frontal effect seen in both response and stimulus-locked ERP data, response-locked ERPs displayed a second condition effect. At parieto-occipital electrodes, ERPs in the imagined item target condition were significantly more negative than in the perceived item target condition. Differences were strongest at electrodes PCz, P1, P2, P4, and Pz. As revealed by t-tests, they started with response onset and ended 200 ms thereafter.

The first four factors derived from the factor analysis, aggregating the ERP difference values between the conditions from −200 and 0 ms, explained 89.8% of the total variance. The second factor had high loadings on ERP differences at frontal electrodes where a significant retrieval orientation effect had been revealed in the first step of ERP analysis. This factor explained 31.1% of the total variance. The individual factor scores correlated with ΔPr on a trend level ($r_{31} = -0.336$, $p = 0.060$) and differed significantly between the high and low relative difficulty groups ($F_{1,31} = 5.215$, $p = 0.030$). In other words, the ERP difference between the imagined and perceived item condition is primarily seen in subjects with a large performance difference between the two conditions, which is in line with the marginally significant effect for the stimulus-locked data. The differential effect of retrieval orientation on frontal ERPs in the high and low relative difficulty groups is displayed in Fig. 3. No such difference was observed between high and low performers ($F_{1,31} = 0.187$, n.s.).

A second factor analysis aggregated the ERP difference values between 0 and 200 ms after response onset. The first four factors explained 85.9 % of the total variance. The factor analysis revealed a major factor for posterior ERP differences, where a significant retrieval orientation had been revealed in the first step of ERP analysis. This factor explained 40.9% of the total variance in this time range. The individual factor scores did not correlate with performance differences ΔPr ($r = 0.039$, n.s.) and did not differ between the high and low relative difficulty group ($F_{1,31} = 0.180$, n.s.). The scores of other factors in this time window did not differ between the two groups either. Furthermore, analysis did not reveal any differences between high and low performers.

To sum up, response-locked ERPs differed at frontal electrodes between conditions, similarly to the findings obtained by the analysis of stimulus-locked ERPs. As an additional effect, ERPs at parieto-occipital electrodes were more negative in the imagined item target condition shortly after the response onset. The frontal ERP effect again was larger for the high than the low relative difficulty groups, while the later parietal effect was not influenced by relative or absolute task difficulty.

Discussion

To sum findings up, two topographically distinct ERP effects of retrieval orientation were observed: the analysis of both stimulus-locked and response-locked ERP data revealed a difference at frontal electrode sites between conditions, with ERPs in the imagined condition being more positive than in the perceived condition. This frontal ERP difference was modulated by the relative task difficulty, i.e. the larger the difference in task performance the larger the frontal

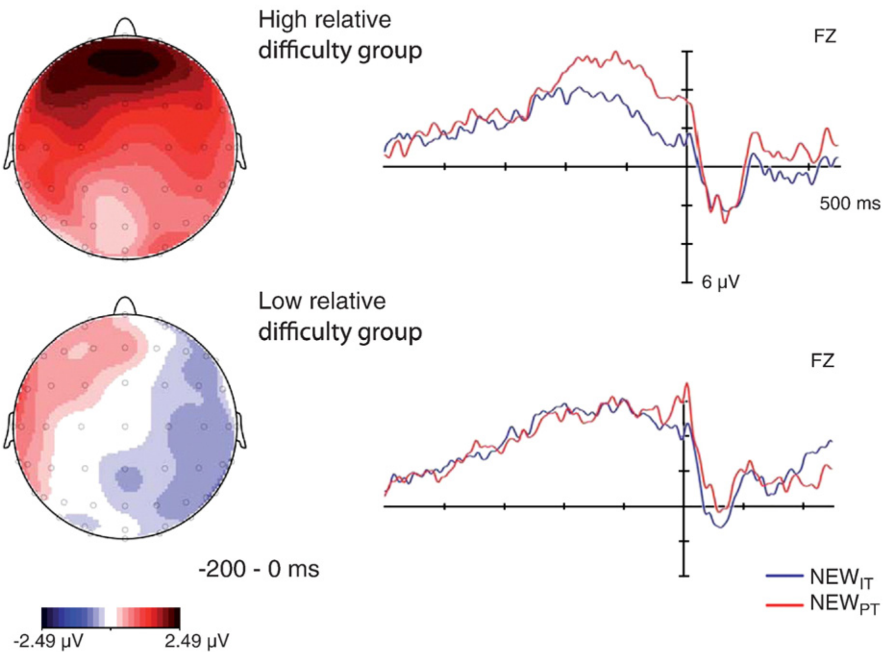

Fig. 3. Response-locked ERPs of new items in the two target conditions: on the right side, data from the FZ electrode are shown, separately for the high and low relative difficulty group; ERPs to new items in the perceived item target condition are plotted as a blue line, ERPs to new items in the imagined item target condition as red line. On the left side, the difference potentials between the conditions are depicted for the latency range −200 to 0 ms, separately for the two groups.

ERP difference. In the response-locked ERP data, a parietal ERP effect was observed in addition. It took the form of more negative going ERPs in the imagined condition immediately after the response. This parietal effect was not associated with any behavioral measure of retrieval accuracy.

Frontal ERP effect

The finding of more positive ERPs at frontal recording sites in the imagined condition is in accordance with the only previous ERP study on retrieval orientation in reality monitoring: Leynes et al. (2005) described more positive ERPs to new items from 800 to 1200 ms in a reality monitoring condition, as compared to an external source monitoring condition. This retrieval orientation effect was found to be pronounced at frontal electrodes between 1000 and 1200 ms. The resemblance of this ERP effect in the two studies is remarkable, considering that Leynes et al. (2005) contrasted two retrieval conditions in the auditory domain, while we contrasted two retrieval conditions in the visual domain. This resemblance might indicate that the ERP effect at frontal electrode sites is associated with the retrieval orientation on self-generated information in general and does not depend on the sensory modality.

However, there was not a perfect match of the ERP effects between the two studies: We did not observe any tendency for more positive ERP deflections in the imagined item target condition at parietal electrodes, while in the study of Leynes et al. (2005) the ERPs differed at parietal sites, too. This difference might be of little surprise given that, in addition to the tested modality, there are other differences between the two study designs: While Leynes et al. (2005) used a source monitoring task, we used a memory exclusion task; while Leynes et al. (2005) contrasted an external source monitoring task and a reality monitoring task, we contrasted the retrieval of perceived and self-generated information; finally, as likely consequences from the described design differences, in the study of Leynes et al. (2005) subjects responded much slower to new test items (mean RT_new>1500 ms) and less accurately (P_new = 0.77), as compared to our study.

Although the response speed was much lower in the study of Leynes et al. (2005), as compared to our study, the latencies of the retrieval orientation effect in the stimulus-locked ERP data were approximately the same in both studies. Thus, the retrieval orientation effect in the stimulus-locked ERP data does probably not depend crucially on the timing of the motor response.

In our study, subjects responded slower to new items in the imagined item target condition than in the perceived item target condition. In order to eliminate the possibility that the findings on stimulus-locked ERPs could have been due to these differences in response speed, we also analyzed response-locked ERP data. This analysis revealed a very similar frontal ERP effect in the response-locked ERP data, as compared to the analysis of the stimulus-locked ERP data. Thus, the different response speed in the two conditions did not confound the results obtained by the analysis of the stimulus-locked ERP data. Of note, the lag between stimulus and response onset in our study showed little variation, as indicated by the relatively small interindividual variance of reaction times. We would predict that with increasing response speed variability the frontal retrieval orientation effect in response-locked ERP would be diminished.

The more positive frontal ERP deflections, when self-generated information is targeted, might indicate the activation of prefrontal brain areas involved in the retrieval of self-relevant information (Lundstrom et al., 2003; Vinogradov et al., 2008). The role prefrontal brain structures in reality monitoring is also underlined by a recent fMRI study on schizophrenia patients with auditory verbal hallucinations (Raij et al., 2009). The subjective reality of the hallucinations correlated with hallucination-related activation in the inferior frontal gyri.

Of note, in two other ERP studies on retrieval orientation more positive frontal ERP deflections to new items were found when items were targeted for which subjects had to reactivate self-relevant information from the study phase: Frontal ERPs were more positive for target conditions when during study subjects had to rate the number of functions they could generate for shown items, as compared to assessing the difficulty of an artist to draw the shown/named items (Johnson et al., 1997). Frontal ERPs were more positive for target conditions in which subjects judged the pleasantness or the animacy of study items, as compared to conditions when target material was defined by non-self relevant information, namely the item location on the monitor during study (Herron and Wilding, 2004).

Taken together, we revealed an ERP correlate of retrieval orientation in a reality monitoring task with more positive ERPs at frontal electrode sites between 600 and 1100 ms when imagined item were targeted, in accordance with previous results of Leynes et al. (2005).

Frontal ERP effect and retrieval effort

As outlined in the introduction, the modulation of ERP correlates of retrieval orientation by retrieval effort is still a matter of controversy, with conflicting empirical findings. One position is that an effective usage of retrieval cues is beneficial for retrieval processes. Following this position, a stronger activation of networks subserving retrieval orientation is associated with higher retrieval accuracy. Empirical evidence for this position was provided by the study of Bridger et al. (2009) who revealed *positive* correlations between ERP effects of retrieval orientation and retrieval accuracy. A second position is that retrieval orientation needs to be engaged to a greater extent with increasing difficulty of the retrieval task. Based on this position, the activation strength of neural networks subserving retrieval orientation should be *negatively* correlated with retrieval accuracy. Empirical evidence for this position was provided by the study of Dzulkifli et al. (2004) who found ERP correlates of retrieval orientation only in subjects whose performance was poorer in the more difficult task. Finally, there is the position that retrieval orientation and retrieval effort do not interact, based on the findings of Morcom and Rugg, 2004 and Robb and Rugg, 2002. This position implies that ERP correlates of retrieval orientation are not affected by varying degrees of retrieval effort and that retrieval effort is reflected in ERP correlates that differ in time course and/or scalp topography from ERP correlates of retrieval orientation.

The current study revealed that frontal ERP correlates of retrieval orientation increased in amplitude with increasing relative task difficulty. Thus, the current findings are in line with the observation of Dzulkifli et al. (2004). Furthermore, two other ERP studies on retrieval orientation have pointed into a similar direction. In these studies of Ranganath and Paller (1999, 2000), a general retrieval condition and a specific retrieval condition were contrasted. Pictures were studied and some of the studied pictures were manipulated in their aspects ratios or in their size when tested. In the general retrieval condition, study items had to be identified irrespective of whether items were manipulated or not. In the specific condition, old items had to be rejected when manipulated (Ranganath and Paller, 1999) or the kind of manipulation had to be classified (Ranganath and Paller, 2000). As expected, accuracy in the specific conditions was worse. In addition, ERPs at left-frontal electrode sites were more positive in the specific conditions. No correlations between the frontal ERP effect and retrieval accuracy were calculated, but the observed variation of the ERP with more positive ERPs at left-frontal electrode sites in the more difficult condition is line with the data provided by Dzulkifli et al. (2004) and the currently obtained results. Of note, response probabilities (Ranganath and Paller, 1999) and response options (Ranganath and Paller, 2000) were not adopted between the retrieval conditions in these studies. However, findings similar to Ranganath and Paller (1999, 2000) were also obtained by a more recent study of Werkle-Bergner et al. (2005) with verbal materials, in which response probabilities were equated across tasks.

Why have some studies failed to observe an impact of relative or absolute task difficulty on ERP correlates of retrieval orientation or reported a conflicting pattern? First, it should be noted that in principle ERP studies on retrieval orientation have only in common that ERP responses to newly presented items are compared when different kinds of information have to be retrieved. As initially suggested by Johnson et al. (1997), differences between ERPs evoked by classes of unstudied words reflect the different ways in which memory traces are probed for these different kinds of information. This might be achieved by processes that enhance the processing of retrieval cues (cue bias) or by processes that directly act on memory representations and modulate their accessibility (target bias) (Anderson and Bjork, 1994; Dzulkifli and Wilding, 2005; Mecklinger, 2010). According to the reinstatement hypothesis, retrieval of a prior episode involves the reinstatement of processes or representations that were active when the episode was encoded (Rugg et al., 2008). As consequence, the neural correlates of retrieval orientation are likely to vary, depending on which retrieval conditions are contrasted.

Indeed, the timing and the topography of retrieval orientation effects vary considerably between studies: E.g. the retrieval orientation effect described by Bridger et al. (2009) showed e.g. a left parieto-occipital distribution, while the retrieval orientation effect described by Dzulkifli et al. (2004) as the one found in the present study was maximal at frontal electrode sites, indicating that the neural correlates of retrieval orientation vary between these studies. Although the determination of neural generators on the basis of the scalp topography is far from being trivial, it is rather unlikely that activation of the same set of neural generators result in qualitatively distinct scalp topographies. One tentative explanation for the differing findings on the interaction of retrieval orientation and retrieval effort might be that this interaction depends to some degree on the neural network involved in the processing of retrieval cues and memory representations.

In Bridger et al. (2009), subjects were asked to say aloud a function of a named object (function task) or were asked to rate verbally how difficult it would be to draw a named object (drawing task). Creation of conceptual details of named objects was more likely encouraged by the function task, while creation of visual details was more likely to occur in the drawing task. Thus in all likelihood, the created information associated with an object name differed considerably between the study conditions. For the retrieval of e.g. object names from the function task, suppression of visual-perceptual networks and/or activation of semantic networks might be regarded as beneficial and would lead to better memory accuracy. Indeed, Bridger et al. (2009) revealed that larger ERP effects of retrieval orientation were associated with better memory accuracy. In contrast, in both of our study conditions, object names were associated with visual information. Under such conditions, the increasing fontal activity with increasing retrieval effort might reflect a stronger engagement of prefrontal structures in order to control the similar and therefore competing memory traces (Mecklinger, 2010).

Secondly, retrieval effort probably encompasses multiple cognitive processes: consequently, increasing retrieval effort by an experimental manipulation might not necessarily interact with other dimensions of retrieval effort. In the two studies reporting no interaction between retrieval orientation and task difficulty, subjects studied object pictures and word names and were later tested with object names as retrieval cues (Robb and Rugg, 2002; Morcom and Rugg, 2004). Task difficulty was manipulated within subjects by varying the length of the study list. Increasing the length of study lists leads to a longer duration of study blocks, but also to a higher memory load and a higher likelihood of interferences in the memory contents. Thus, the introduced task difficulty refers more or less to the strength of memory representations. Presenting test words when pictures were studied, however, means that there is no nonconceptual overlap between retrieval cues and memory representations and mere recapitulation will not suffice (Hornberger et al., 2004). In this case, retrieval cues have to be processed on a conceptual level that poses an additional demand to subjects, as compared to test situation when the retrieval cue and test item do have a nonconceptual overlap. The needed cognitive resources for a processing of picture items on a conceptual level might indeed be relatively independent of manipulations of the memory strength.

In neuroimaging studies, the impact of retrieval effort on retrieval orientation has hardly been investigated and findings as yet are not fully conclusive. In an event-related fMRI study, Ranganath et al (2000) contrasted a general and specific retrieval condition for unstudied items, highly similar to the ERP study of Ranganath and Paller (1999). In well accordance to this ERP study, a larger left frontal activity was found for the specific, as compared to the general retrieval condition. However, even at a very liberal statistical threshold, Rugg et al. (2003) did not find such difference in their study when contrasting an exclusion and inclusion task.

Taken together, the modulation of the ERP retrieval orientation effect at frontal recording sites by relative task difficulty is well in line with the studies of Dzulkifli et al. (2004) and Ranganath and Paller (1999, 2000) and point towards the view that processes of retrieval orientation need to be engaged to a greater extent with increasing relative difficulty. The lack of an interaction reported by some other studies (Morcom and Rugg, 2004; Robb and Rugg, 2002) might be explained by the quality of experimental manipulation of task difficulty. Conditions under which retrieval orientation effects in the ERP are associated with better accuracy (Bridger et al., 2009) warrant further investigations.

Parietal ERP effect

In addition to a frontal retrieval orientation effect, a parietal retrieval orientation effect was observed in the response-locked ERP data only. This effect was not modulated by any measures of retrieval accuracy and occurred after the response onset. To our knowledge, response-locked ERP data has not been investigated for the study of retrieval orientation effects in any previous study. However, in their review paper on the Late Posterior Negativity (LPN) Johansson and Mecklinger (2003) report larger response-locked posterior negativities during recognition conditions characterized by high response conflict, as for example, when old items have to be discriminated from lures that share common features. They interpreted this effect as a result of the increased action monitoring demands. As the timing and the topography of the response-locked ERPs reviewed by Johansson and Mecklinger (2003) are similar to the currently observed parietal ERP effect, it might be interpreted as an LPN. It is conceivable that action monitoring demands were higher for new items in the imagined condition because of the higher task difficulty in this condition, further supporting this interpretation.

Conclusions

The findings suggest a contribution of frontal brain areas to retrieval orientation processes in reality monitoring. Furthermore, findings indicate that neural correlates of retrieval orientation can be modulated by retrieval effort, with stronger activation of these correlates with increasing task demands. However, no such modulation was found for the retrieval orientation effect at posterior electrode sites in the response locked ERP data. Furthermore, the modulation of retrieval orientation by retrieval effort is likely to depend on contrasted retrieval conditions.

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2010.10.068.

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