The posterior parietal cortex and subjectively perceived confidence during memory retrieval

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Functional neuroimaging studies suggest a role for the left angular gyrus (AG) in processes related to memory recognition. However, results of neuropsychological and transcranial magnetic stimulation (TMS) studies have been inconclusive regarding the specific contribution of the AG in recollection, familiarity, and the subjective experience of memory. To obtain further insight into this issue, 20 healthy right-handed volunteers performed a memory task in a single-blind within-subject controlled TMS study. Neuronavigated inhibitory repetitive TMS (rTMS) was applied over the left AG and the vertex in a randomized and counterbalanced order. Prior to rTMS participants were presented with a list of words. After rTMS participants were shown a second list of words and instructed to indicate if the word was already shown prior to rTMS (“old”) or was presented for the first time (“new”). In addition, subjectively perceived memory confidence was assessed. Results showed that recollection was unaffected following inhibitory left AG rTMS. In contrast, rTMS over the left AG improved both familiarity and the subjectively perceived confidence of participants that demonstrated low baseline memory recognition. Our study highlights the importance of taking into account individual differences in experimental designs involving noninvasive brain stimulation.

The distinction between recollection and familiarity has also been demonstrated by functional magnetic resonance imaging (fMRI) studies showing ventrolateral posterior parietal cortex (PPC) activity during recollection and activity of the dorsolateral PPC during familiarity (Ciaramelli et al. 2008; Vilberg and Rugg 2008; Rugg and King 2017). In addition to the unique regional involvement, there is considerable overlap in cortical activity during recollection and familiarity (Skinner and Fernandes 2007; Vilberg and Rugg 2008; Horn et al. 2016; Rugg and King 2017). In particular, the left angular gyrus (AG) of the ventrolateral PPC shows increased activity during both recollection (Skinner and Fernandes 2007; Vilberg and Rugg 2008) and familiarity (Skinner and Fernandes 2007; Horn et al. 2016). Unfortunately however, the correlational nature of functional neuroimaging techniques makes it difficult to make strong inferences about whether or not the left AG is directly implicated in these aspects of memory.
recollection (Yazar et al. 2014). In a more recent study, cTBS over the left AG did not disrupt item and source memory (Bonni et al. 2015). Unfortunately, subjectively perceived memory confidence was not examined in this study. Another study reported that inhibitory rTMS over the left AG reduced the level of detail of episodic memories and altered the subjective experience of these memories (Thakral et al. 2017a).

While results from neuroimaging studies point to a role for the left AG in recollection and familiarity, lesion and TMS studies hint to a link with the subjective memory experience, such as perceived confidence. To this end, we applied inhibitory rTMS to healthy volunteers in a single-blind crossover design to further explore the role of the left AG in recollection, familiarity, and subjectively perceived memory confidence. Given the role of the left AG in the subjective experience of memories, we hypothesized that inhibitory rTMS over the left AG would lower subjectively perceived memory confidence. Specifically, we expected a lower rate of high-confident responses in the left AG rTMS condition. In addition, based on previous TMS studies (Yazar et al. 2014; Bonni et al. 2015), we did not anticipate a change in familiarity following inhibitory rTMS over the left AG. Finally, a negative effect on recollection in response to the left AG rTMS condition was expected.

Results

The rTMS procedure was well tolerated by all participants and no adverse effects occurred. At the end of the second session, nine participants indicated that they did not notice any differences between the stimulation of the target (AG) and control (VE) site. The 11 participants that did notice a difference indicated that the stimulation location differed over sessions (N = 2), that they had more sensations during VE stimulation (N = 1) or left AG stimulation (N = 4), or that they performed better after VE stimulation (N = 1) or left AG stimulation (N = 3). A binomial test showed that the probability of observing 11 out of 20 participants that reported a difference between sessions was not significantly different from a 50% chance level (P = 0.82).

Memory recognition
No significant test-retest effects were found on memory recognition as d-prime (M = 1.37, SD = 0.70) did not differ significantly between the first and second session (t18 = 0.73, P = 0.48). In addition, d-prime did not differ significantly between angular gyrus and vertex stimulation (t18 = 0.79, P = 0.44).

Recollection and familiarity
No main effect of rTMS condition was observed on recollection (F1,18 = 0.10, P = 0.92, ηp² = 0.001) and familiarity (F1,18 = 0.47, P = 0.50, ηp² = 0.025, see Fig. 1). Recent findings suggest that behavioral effects of noninvasive brain stimulation can depend on individual differences in baseline performance (Ridding and Ziemann 2010; Sarkar et al. 2014; Benwell et al. 2015; Klaus and Schutter 2018), therefore we explored in an ad hoc fashion whether baseline memory recognition interacted with the rTMS intervention. To this end we divided the participants into a “low” and a “high” memory recognition group, based on a median split of d-prime scores during VE stimulation. This group categorization was used as a between-subject factor in analyses that explored the interaction between individual differences in memory recognition and the rTMS intervention.

The three-way interaction between stimulation (AG, VE), memory measure (recollection, familiarity), and group (high, low) was significant (F1,17 = 9.62, P = 0.006, ηp² = 0.36). Post-hoc analysis did not reveal an interaction effect between stimulation condition and individual differences on recollection scores (F1,17 = 0.21, P = 0.66, ηp² = 0.012). However, a significant interaction effect between rTMS condition and individual differences on familiarity scores was found (F1,17 = 6.98, P = 0.017, ηp² = 0.29). Post-hoc t-tests revealed that in the low memory recognition group familiarity was enhanced after left AG rTMS as compared to VE rTMS (t9 = 3.16, P = 0.013), whereas the high memory recognition group did not show a significant effect of rTMS on familiarity, (t9 = 1.07, P = 0.31, see Fig. 1B).

Inclusion of the between-subject factor did not considerably alter the main effect of rTMS on recollection (F1,17 = 0.015, P = 0.91, ηp² = 0.001) and familiarity (F1,17 = 0.86, P = 0.37, ηp² = 0.048).

Subjectively perceived confidence
No main effect of rTMS was found for subjectively perceived confidence in “old” (F1,18 = 2.57, P = 0.13, ηp² = 0.13) and subjectively perceived confidence in “new” responses (F1,18 = 0.69, P = 0.42, ηp² = 0.037; see Fig. 2). The three-way interaction between stimulation (AG, VE), memory measure (subjectively perceived confidence in “old” responses, subjectively perceived confidence in “new” responses), and group (high, low) was significant (F1,17 = 7.59, P = 0.014, ηp² = 0.31). Post-hoc analysis showed that individual differences in memory recognition did not interact with rTMS condition on the subjectively perceived confidence in “new” responses (F1,17 = 2.03, P = 0.17, ηp² = 0.11).

Figure 1. (Top) Mean recollection and familiarity estimates per stimulation condition. (Bottom) Mean recollection and familiarity estimates for low and high performing participants, based on a d-prime median split. Error bars represent standard errors of the mean. A statistical significant difference (P < 0.05) is indicated by a star.
contrast, a significant interaction effect between rTMS condition and individual differences on the subjectively perceived confidence in “old” responses was found \((F_{1,17} = 5.94, P = 0.026, \eta^2 = 0.26)\). Post-hoc t-tests revealed that in the low memory recognition group subjectively perceived confidence in “old” responses was enhanced after left AG rTMS as compared to VE rTMS \((t_{8.1} = 2.62, P = 0.031)\). The high memory recognition group did not show a significant effect of rTMS on subjectively perceived confidence in “old” responses \((t_{8.0} = 0.43, P = 0.68\), see Fig. 2A).

Inclusion of the between-subject factor did not considerably change the main effect of rTMS on subjectively perceived confidence in “old” responses \((F_{1,17} = 3.75, P = 0.070, \eta^2 = 0.18)\) and “new” responses \((F_{1,17} = 0.86, P = 0.37, \eta^2 = 0.048)\).

Time course of the rTMS effect
Since rTMS effects have been shown to decay over time (Thut and Pascual-Leone 2010), it is worthwhile to examine whether stimulation-related adjustments in performance change as a function of time. To this end, we split up retrieval in three equally sized phases of 300 trials. A GLM was performed with phase (early, mid, late), measurement (recollection, familiarity, subjectively perceived confidence in “old” responses, subjectively perceived confidence in “new” responses), and stimulation (AG, vertex) as within subject variables. Of main interest was the three-way interaction between phase, measurement, and stimulation, which was not significant \((F_{3,07,35,29.1} = 0.98, P = 0.41, \eta^2 = 0.052)\). This indicates that stimulation-related changes did not vary as a function of time during retrieval.

Discussion
Our results show that inhibitory rTMS over the left AG, as compared to inhibitory rTMS over the vertex, does not significantly influence recollection and the subjectively perceived confidence in “new” responses. However, we did find that left AG TMS increased familiarity and subjectively perceived confidence in “old” responses, which are more involved in binding episodic representations, which influence the richness of retrieved memories (Eichenbaum 2001; Bergmann et al. 2012; St-Laurent et al. 2014, 2016). The hippocampal formation and the AG are both part of a complex neural network associated with memory (Hayama et al. 2012; Thakral et al. 2017b). A close interaction within this memory network could perhaps explain the increased activation in the left AG during recollection (Skinner and Fernandes 2007; Vilberg and Rugg 2008), even though the left AG might not be directly involved in recollection-related processes. Alternatively, recollection-related left AG activity could actually be due to the involvement of the PPC in factors, such as subjectively perceived memory confidence, which are strongly related to episodic memory and hard to dissociate (Schoo et al. 2011).

Even though the AG has been implicated in familiarity (Skinner and Fernandes 2007; Horn et al. 2016), AG activity is typically linked to recollection (Ciaramelli et al. 2008; Vilberg and Rugg 2008; Rugg and King 2017). We speculate that the rTMS effect on familiarity in our study may, at least in part be due to the recruitment of the left AG in subjectively perceived memory confidence. This speculation is based on the similar effect we found for subjectively perceived memory confidence in “old” responses. In addition, the familiarity estimates are generated with the confidence ratings of the participants. Future studies are needed to confirm this speculation.

According to dual-process theories, recollection and familiarity are considered to involve independent retrieval processes. While recollection is characterized by a step-wise (Boolean) process that is accompanied by high levels of subjectively perceived memory confidence, familiarity is proposed to have a linear relation with subjectively perceived memory confidence (Mandler 1980; Yonelinas 2002). In contrast, strength theories assume that memory recognition is based on a single dimension of memory strength. In the latter theory, both recollection and familiarity are proposed to lie on a continuum that can be understood in terms of a varying degree of subjectively perceived confidence (Wixted 2007; Mickes et al. 2009). In concordance, it has been shown...
that activation patterns patterns in the parietal cortex are better explained by strength theories (Hayes et al. 2011). Our results concur with the proposed link between the parietal cortex and strength theories.

Both subjectively perceived memory confidence in “old” responses and familiarity were affected by left AG rTMS, but only in participants with relatively low memory recognition. It has been reported before that the effects of noninvasive brain stimulation vary across individuals (Daskalakis et al. 2006; Pena-Gomez et al. 2011; Berryhill and Jones 2012). Here, we speculate that high performing participants may have already reached an optimal level of performance, resulting in a ceiling effect, while in low performing participants there was still room for improvement (Krause and Cohen Kadosh 2014). Not taking into account individual differences in baseline performance may provide a possible explanation for previous studies that did not find group-level effects of left AG TMS on item memory (Yazar et al. 2014; Bonni et al. 2015). Our findings further illustrate the importance of taking individual variability into account in studying the effects of rTMS on behavioral and neurophysiological indices.

Importantly, our rTMS protocol was intended to disrupt left AG function and worsen performance, but instead we found an increase in subjectively perceived confidence and familiarity. The apparent paradox may imply that inhibition of physiological activity does not mean a decrease in functionality per se (Bonni et al. 2015). Indeed, it has been reported before that inhibitory rTMS does not necessarily lead to disruptive effects on behavior (Thut and Pascual-Leone 2010; Caparelli et al. 2012; Strigaro et al. 2016). Also, on the neurophysiological level inhibitory rTMS protocols may cause facilitatory effects that are state-dependent (Ridding and Ziemann 2010).

For example, according to the Bienensstock–Cooper–Munro (BCM) model (Bienensstock et al. 1982), neurons that are in a less excitable state prior to stimulation can be more susceptible to increased cortical excitability, even after inhibitory TMS. In keeping with fMRI studies that consistently show decreased AG activity during encoding (Huijbiers et al. 2011; Elman et al. 2013), subsequent inhibitory rTMS might in fact induce cortical facilitation and result in related functional improvement. In further support of this view, a previous study indeed showed that the application of inhibitory rTMS after memory encoding lead to an increased memory performance (Bonni et al. 2015). As previously discussed, the AG is part of a complex memory network that involves a variety of brain regions including the hippocampus (Hayama et al. 2012; Thakral et al. 2017b). In a recent study 1 Hz rTMS was found to increase functional connectivity between the left inferior PPC and the hippocampus (Eldaief et al. 2011). Increases in functional connectivity are typically interpreted as improved network functioning (Ranganath et al. 2005; Wang et al. 2010), and may hint toward a possible mechanism that can explain the present “paradoxical facilitation” of memory performance (Kapur 1996; Brem et al. 2014).

Several limitations of this study should be mentioned. First, due to the ad hoc nature of our analyses on individual performance differences, these analyses lack high statistical power. Even though the results concur with recent findings demonstrating state-dependent effects of performance on the efficiency of noninvasive brain stimulation (Sarkar et al. 2014; Benwell et al. 2015; Klaus and Schutter 2018), they should be interpreted with caution. Second, the dual-process signal detection model that we adopted is based on the general assumption that recollection is based on a threshold-like process while familiarity is more related to a continuous process (Yonelinas et al. 1996; Yonelinas 2002). As a consequence, our recollection and familiarity estimates do not hold if recollection, similar to familiarity, is conceptualized as a continuous process. Third, we localized the left AG on the basis of MNI coordinates from a meta-analytic neuroimaging study (Vilberg and Rugg 2008) while we used neuronavigation to position and hold the coil over the target site (Yazar et al. 2014, 2017). However, individual differences in brain anatomy as well as the physiological susceptibility of rTMS give rise to variability (Wild et al. 2017) that may have a negative impact on the effect size (Sack et al. 2009).

In conclusion, our study provides evidence that the left AG is involved in familiarity and subjectively perceived memory confidence, while the left AG does not appear to be involved in recollection. Our study further highlights the complex relationship between TMS-related physiological and behavioral changes, and the importance of taking into account individual differences in performance in experimental designs involving rTMS.

Materials and Methods

Participants

Twenty healthy adult right-handed volunteers (11 women) with a mean age of 23 (M = 23.05, SD = 3.41) participated in this study. All had normal or corrected-to-normal vision, were native Dutch speakers, nonsmokers and free from neurological or psychiatric conditions (self-report). All participants received written and oral information prior to participation, but remained naive about the aim of the study, and all provided written informed consent. Main exclusion criteria were: metal in their cranium; epilepsy or a family history of epilepsy; history of other neurological conditions or psychiatric disease; heart disease; use of psychoactive medication or substances; pregnancy. Stimulation parameters were in agreement with the International Federation of Clinical Neurophysiology safety guidelines (Rossi et al. 2009), and the study was approved by the medical ethics committee of the Radboud University Medical Center, Nijmegen, The Netherlands, and carried out in accordance with the standards set by the Declaration of Helsinki. One participant was excluded from data analyses due to an at chance level performance on the memory task.

Memory task

Stimuli were presented on a personal computer screen with a 21-inch monitor. Stimulus presentation and recording of responses were attained using PsychoPy (v1.80; Peirce 2007). The stimulus material consisted of 900 words per session, differing per participant, randomly chosen from a pool of 2038 words. This set was selected based on word frequency (Dutch logarithmic: M = 0.92 (SD = 0.71, range = [0, 3.66]), familiarity (M = 496.48 (SD = 73.61, range = [203, 657]), and concreteness (M = 527.97 (SD = 82.19, range = [204, 670]), from the MRC Psycholinguistic Database (http://websites.psychology.uwa.edu.au/school/MRCDatabase/uwa_mrc.htm) and translated to Dutch (Dutch word length: M = 6.44 (SD = 2.51, range = [2, 25]). In this way, participants were only presented with words that were relatively easy to imagine, which facilitates memory processes (Nittono et al. 2002; Fliessbach et al. 2006). Two parallel versions of word lists were generated per participant, one for each session.

Procedure

Participants received either rTMS over the left AG or vertex (VE) during two sessions in a randomized and counterbalanced order. Sessions were separated by exactly 1 wk and controlled for time of day. During both sessions, resting motor threshold (MT) for the right first dorsal interosseous hand muscle was determined for each participant (Schutter and van Honk 2006). Next, the participant’s head was coregistered to a standard brain using the Localite TMS Navigator (Localite GmbH) to guide TMS stimulation. After the MT was determined, participants were seated in front of a computer and instructed on the encoding phase of the memory task. In this phase of the memory task, trials began with
a 1-sec centrally presented fixation cross, followed by a 2-sec presentation of a word. Each participant performed 450 encoding trials, while making a semantic classification ("pleasant" or "unpleasant") regarding the presented word. The semantic classification of the stimuli ensured that participants kept attending to the stimulus presentations and aimed to deepen encoding (see Fig. 3; Demb et al. 1995; Fletcher et al. 2003).

When the encoding phase was completed, the eight-shaped coil (Cool-B65, Magventure A/S) was placed over the target (left AG: (MNI coordinates: −43, −66, 38; Vilberg and Rugg 2008) or control location (VE: (MNI coordinates: 0, −15, 74; Okamoto et al. 2004; see Figs. 4–5).

After the coil was positioned over the target location, volunteers received a 20 min 1 Hz train of rTMS (1200 pulses) over the left AG or VE at 90% of MT. The MTs (M = 49.20, SD = 9.78) did not differ significantly between sessions (t(19) = 0.85, P = 0.41).

During stimulation, the participant sat quietly in a chair while the TMS coil was held manually by the experimenter. The exact target location of the TMS coil relative to the head was monitored online and adjusted when there was a deviation greater than two millimeter from the target in any of the three dimensions. RTMS was administered intermediate the encoding and retrieval phase of the task in order to interfere with subsequent retrieval processes and to avoid distraction during encoding (Yazar et al. 2014; Bonni et al. 2015).

During the retrieval phase, participants performed a recognition task, including all 450 "old" words presented during encoding and 450 "new" words. In total, each participant performed 900 fixed-paced recognition trials, which started with a 1 sec fixation cross, followed by a 2 sec presentation of a word. During word presentation, participants classified the item as "old" or "new." When a response was made, the trial ended with a "confidence" screen presenting the question "how sure?" for one and a half seconds. During the "confidence" screen participants rated their confidence of their "old/new" classification on a three-point scale (see Fig. 3; Yonelinas et al. 1996).

To familiarize participants with the task, 20 practice trials preceded both the encoding and retrieval phase of the experiment. Stimuli used during the practice trials were not used in the experimental trials. Each trial consisted of a 2 sec word presentation, 1 sec fixation presentation, and one and a half seconds to make confidence judgements. After every 150 experimental trials there was a short break of at least one minute, resulting in 25 min of encoding and 75 min of retrieval. At the end of the second session volunteers were debriefed and received compensation for participation.

Data analyses
Data analyses were performed with the use of MATLAB (v2015b, MathWorks Inc.). Recollection and familiarity estimates, and d-prime were computed using the ROC toolbox for MATLAB (Koen et al. 2016). Subjectively perceived confidence was measured as the rate of high-confident responses, which was done separately for old trials and new trials.

Statistical analyses
General linear models (GLMs) for repeated measurements were used to test for significant differences in recollection, familiarity, or confidence, during both stimulation conditions. Previous studies have demonstrated significant inter-individual variability in the behavioral effects of noninvasive brain stimulation (Maeda et al. 2000; Siebner et al. 2009; Pena-Gomez et al. 2011; Klaus and Schutter 2018). To explore such an effect, a median split was made based on d-prime scores obtained during control VE stimulation as a measure of baseline memory recognition. This distinction between sample-based low and high performers was entered as a between-subject factor in the GLMs. Alpha level of significance
was set at 0.05 (two-tailed) and effect sizes (partial eta-squared; $\eta^2_p$) were computed for all analyses.

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