

# Distinct Generation of Subjective Vividness and Confidence during Naturalistic Memory Retrieval in Angular Gyrus

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## Abstract

■ Our subjective experience of remembering guides and monitors the reconstruction of past and simulation of the future, which enables us to identify mistakes and adjust our behavior accordingly. However, what underlies the process of subjective mnemonic experience remains incompletely understood. Here, we combined behavior, repetitive TMS, and functional neuroimaging to probe whether vividness and confidence are generated differently during retrieval. We found that preretrieval repetitive TMS targeting the left angular gyrus (AnG) selectively attenuated the vividness efficiency compared with control stimulation while keeping metacognitive efficiency and objec-

tive memory accuracy unaffected. Using trialwise data, we showed that AnG stimulation altered the mediating role of vividness in confidence in the accuracy of memory judgment. Moreover, resting-state functional connectivity of hippocampus and AnG was specifically associated with vividness efficiency, but not metacognitive efficiency across individuals. Together, these results identify the causal involvement of AnG in gauging the vividness, but not the confidence, of memory, thereby suggesting a differentiation account of conscious assessment of memory by functionally and anatomically dissociating the monitoring of vividness from confidence. ■

## INTRODUCTION

According to Endel Tulving (Tulving, 1972, 1985), the conception of episodic memory is identified with autonoetic awareness, which gives rise to remembering of personally experienced events. The process of explicitly remembering a specific previous event is often accompanied by a subjective sense of recollection, which enables us to monitor experiences, identify mistakes, and guide future behavior accordingly. It is therefore crucial to understand what underlies the subjective mnemonic experiences, such as subjective vividness of the memory and confidence in the memory decisions. In memory research, vividness and confidence are often used interchangeably under the umbrella of “subjective experience.” However, an important and intriguing idea is that the processes of generating vividness and confidence operate differently during memory retrieval. Specifically, confidence is often used as a measure of the capacity to evaluate one’s own cognitive processes, referred to as metacognition (Metcalf & Shimamura, 1994), which has been studied across a range of task domains, including perceptual, memory, social, and value-based decisions (Morales, Lau, & Fleming, 2018; Ye, Zou, Lau, Hu, & Kwok, 2018; Bang et al., 2017; McCurdy et al., 2013; De Martino, Fleming, Garrett, &

Dolan, 2012). By comparison, vividness is a relatively specific measure of episodic memory recollection, which has been used to assess the degree to which the retrieved content is rich and detailed. On this basis, we reasoned that the computation of vividness should be partially, if not fully, independent from confidence of memory.

In this way, vividness and confidence of memory could be mediated by distinct neural mechanisms and even in different brain regions. A candidate region thought to differently support these two subjective mnemonic components is left lateral parietal cortex, in particular, the angular gyrus (AnG). The left AnG is widely thought to play an important role in subjective experience of remembering. For example, a number of human neuroimaging studies have shown that activity in AnG is associated with subjective reports of vividness (Bonnici, Richter, Yazar, & Simons, 2016; Kuhl & Chun, 2014) and confidence (Qin, van Marle, Hermans, & Fernández, 2011) during episodic memory retrieval. Consistently, disruption of left AnG processing by TMS has been found to selectively reduce confidence but leaving objective retrieval success intact (Wynn, Hendriks, Daselaar, Kessels, & Schutter, 2018; Yazar, Bergström, & Simons, 2014; but also see Branzi, Pobric, Jung, & Lambon Ralph, 2021). These results, however, have focused primarily on the level of confidence or vividness rating during memory retrieval, thereby leaving unanswered whether this region supports the ability to faithfully monitor subjective sense of remembering (i.e.,

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the correspondence between objective memory performance and subjective memory reports). Furthermore, the left AnG has been proposed to be involved in the integration of mnemonic features into a conscious representation that enables the subjective experience of remembering (Humphreys, Ralph, & Simons, 2021; Bonnici et al., 2016), which is analogous with the definition of the vividness of memory rather than a general subjective sense of confidence in memory decisions. Although it is difficult to completely rule the AnG out in confidence processing, we are inclined to theories asserting that confidence signal is modulated by metalevel information, above and beyond integration of multisensory information (Shekhar & Rahnev, 2018; De Martino et al., 2012). To our knowledge, no study has provided evidence for the involvement of AnG in metacognitive processing. We thus reasoned that the left AnG might exhibit disproportional engagement in the computation of vividness relative to confidence. It is important to note that we are interested in the degree to which confidence and vividness are related to objective memory performance, namely, metacognitive (confidence) efficiency and vividness efficiency, instead of the level of subjective ratings.

Here, we aimed to ask two key questions: (i) Are vividness and confidence dissociable subjective components during episodic memory? (ii) Does the AnG support the subjective assessment of memory quality? We addressed these questions by using both TMS and MRI methods. Specifically, to temporarily manipulate AnG function, we administered an inhibitory repetitive TMS (rTMS) protocol to the left AnG as well as to a control site (vertex) in a within-subject design. Following a 20-min rTMS protocol, we asked participants to report the vividness of mental replay of a target scene before the memory judgments and confidence ratings. Of note, to ensure that vividness and confidence ratings are based on the same segment of a piece of memory within a trial, we set to test participants' objective memory that largely depends upon the quality of the preceding mental replay. Accordingly, in the memory judgments, participants were asked to perform a temporal proximity judgment between two scenes with respect to the target scene. The temporal proximity judgment task requires participants to compare the temporal distance of two chunks of a specific episode, which demands participants to mentally replay the cue-related scenes for successful memory retrieval. Given the nature of our temporal proximity task, a correct memory response will be dependent on precise recollection of all three of these scenes. We expected that recollection is in turn related to participant's subjective evaluation of recall (i.e., subjective vividness). For an accurate comparison between these subjective experiences, we quantified the efficiencies of the two subjective memory ratings by computing the trial-by-trial correspondence between objective memory performance and subjective reports (Fleming & Daw, 2016; Maniscalco & Lau, 2012). As the correspondence between objective and subjective memory reports

increases, subjective awareness of memory approaches ideal. Given the known involvement of hippocampus in memory recollection and the richness of reexperiencing (Ford & Kensinger, 2016; Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004), we also employed a functional connectivity approach to assess the relationship between functional architecture of these regions and both subjective evaluation abilities. If the aforementioned hypothesis is true, we would expect to see a dissociation between vividness and metacognitive efficiency, where TMS to the left AnG will selectively affect the vividness efficiency but not metacognitive efficiency.

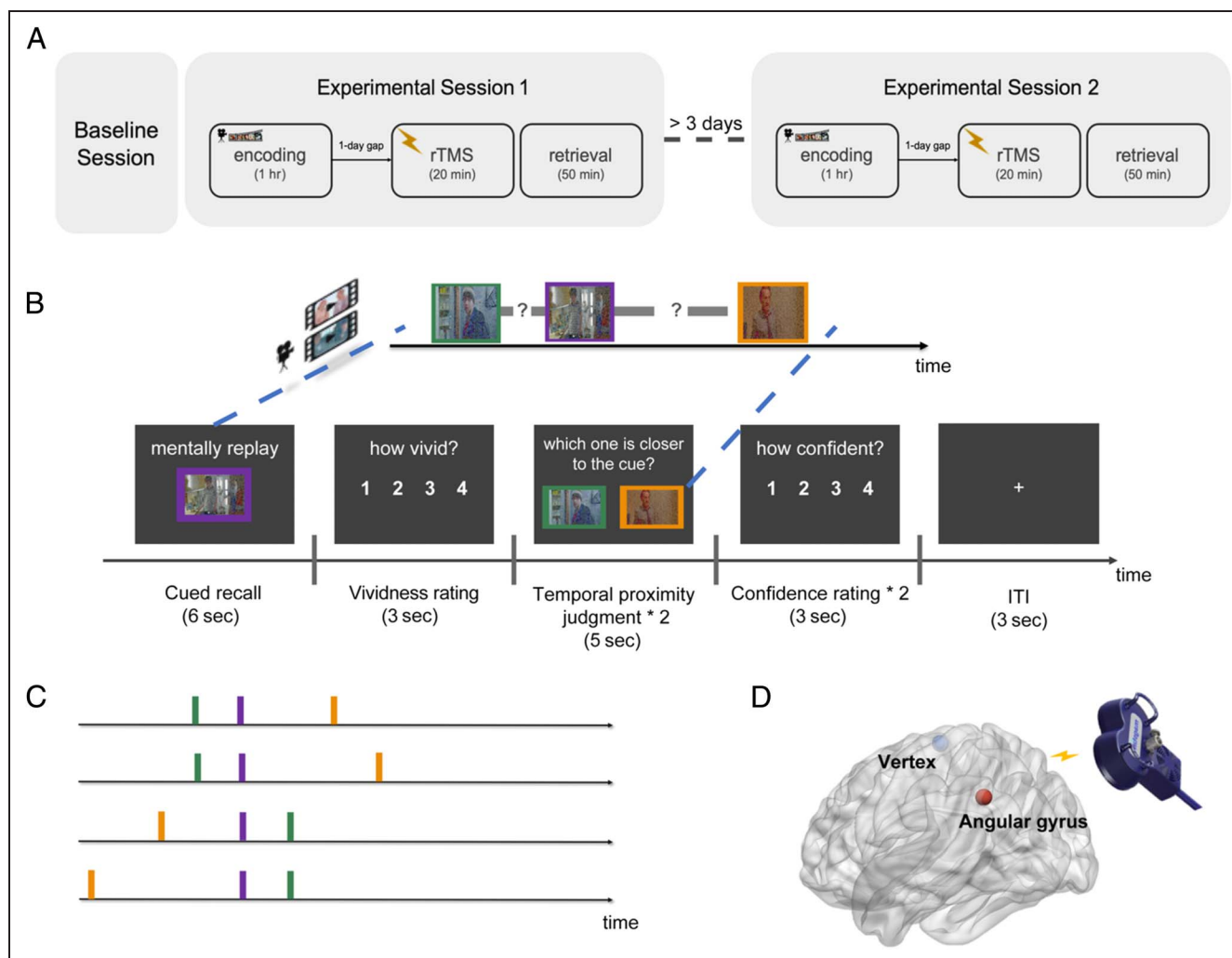
## METHODS

### Participants

Twenty healthy young adults took part in this study (11 women and 9 men, mean age = 22.70 years,  $SD = 2.8$  years, range = 18–26 years). The sample size was determined based on a power analysis ( $\alpha = .05$ , two-tailed, power = .8) performed on data from our previous TMS study probing the causal role of parietal cortex on memory metacognition (Ye et al., 2018). All participants were right-handed with normal or corrected-to-normal vision and had no contraindications for MRI or TMS. Each of them participated in two experimental sessions, giving us a within-subject comparison to assess the influence of TMS to AnG on memory. Data from three additional participants were excluded from data analyses: One participant did not complete the experiment because of anxiety, and the other two inadvertently hit the wrong response key throughout a whole test session. Participants were recruited from the East China Normal University undergraduate and graduate student population and compensated for their participation. The East China Normal University Committee on Human Research Protection approved the experimental protocol, and all participants gave their written informed consent. All participants self-reported to be native Chinese speakers and had not previously seen any episodes of *Black Mirror*.

### Overview of Experimental Design

Participants completed a baseline session and two experimental sessions on separate days in a within-subject design (Figure 1A). Following standard MRI and TMS safety screening, participants first underwent a baseline session where structural MRI scans and resting-state fMRI scans were obtained. The structural MRI scans were used to define the subjective-specific stimulation locations and enable accurate navigation. Each experimental session consisted of two phases separated by 1 day: an approximately 1-hr encoding session, during which participants watched one *Black Mirror* episode, and a retrieval session one day later, during which participants received either rTMS over the left AnG or over the vertex and completed



**Figure 1.** Experimental design. (A) Overview of task design. In each of the experimental sessions, participants viewed a 1-hr episode from *Black Mirror* at encoding. On the following day, participants received stimulation (over AnG or vertex) and performed a memory test. Episode and stimulation sites were assigned in a randomized and counterbalanced order. (B) Schematic overview of the memory test. Trial example: Participants mentally replay related scenarios while viewing an image cue from the episode and rated the vividness of their memory. Participants were then presented with another two still frames from the episodes and tested on their memory associated with the cued scene, followed by a confidence rating. Each cued recall was followed by two temporal proximity judgments. Episode stills in the figure are blurred for copyright reasons. (C) Triad of video stills selection criteria (purple: cue; green: the closer one to cue; orange: the further one to cue). (D) Stimulation sites: AnG (red, MNI coordinates:  $x = -43$ ,  $y = -66$ ,  $z = 38$ ) and vertex (blue, as control site).

a memory retrieval test. The retrieval began immediately after rTMS and lasted 50 min. In the retrieval phase, participants recalled relevant scenarios based on a cue image, rated their subjective vividness of the mental replay, made temporal proximity judgments, and rated their confidence of the memory judgments (Figure 1C).

### Memory Tests

In the memory test (Figure 1B), participants were first presented with an image cue abstracted from the episode and asked to mentally recall related scenarios in the episode with as much detail as possible for 6 sec. Participants were explicitly instructed to recall the full event related to the cue scene. They were instructed to replay details not only

from the point of the cued scene but also those preceding the cue. This served to ensure that the corresponding vividness ratings would be related to the full event segment encompassing the cue scene. Following the mental replay, participants were allowed 3 sec to rate their vividness of the memory by selecting a number from 1 to 4 (“not vivid” to “very vivid”). After the vividness rating, participants were presented with another two still frames from the episode and were asked to choose which of the two frames was temporally closer to the cue frame in the video. On each trial, the stimulus presentation and response window lasted for 5 sec. Each temporal proximity judgment was followed by a subjective confidence rating of their choice on a scale from 1 to 4 (“not confident” to “very confident”). Three seconds were allowed for confidence

ratings. There were two sets of temporal proximity judgment and confidence rating following each cued recall. No feedback was provided during the memory test.

### *Episode Scene Stimuli Used for Encoding, Cued Recall, and Temporal Proximity Judgment Tests*

Participants viewed two episodes of the British television series *Black Mirror* (Figure 1B; the first episode of Season 3, *Nosedive*, and the third episode of Season 3, *Shut Up and Dance*) with Chinese dubbing. Each episode was assigned to one of the experimental sessions. *Nosedive* was ~58 min long, and *Shut Up and Dance* was ~52 min long. For the subsequent memory retrieval test, 180 triads of still frames were extracted from each video based on the following criteria: (i) For each triad, one cue frame and two still images for temporal proximity judgments were from the adjacent scenes, and (ii) the absolute temporal distance between cue frame and temporally closer one to the cue was fixed. To further increase task difficulty, we selected the stimuli from four difficulty settings: hard/easy with left/right target (Figure 1C). The occurrence of event boundaries was identified using subjective annotations. Two external observers, who did not take part in the experimental sessions of the current study and had no knowledge of the experimental design, viewed each of the episodes and annotated with precision the temporal point at which they felt “a new event is starting; these are points in the episode when there is a major change in topic, location or time.” Participants were also asked to write down a short title for each event. With the participants’ boundary annotations, we looked for those boundary time points that were consistent across observers. This resulted in 50 scenes in *Nosedive* and 43 scenes in *Shut Up and Dance*. Given that event boundary can affect memory retrieval (DuBrow & Davachi, 2013), this procedure allowed us to control for this potential boundary effect and equate the memory task difficulty between stimulation sites. Episode and experimental sessions were assigned in a randomized and counterbalanced order across participants.

### *MRI Data Acquisition*

Participants were scanned in a 3-T Siemens Trio magnetic resonance imaging scanner with a 64-channel head coil. Structural MRI images were obtained using a T1-weighted multiecho MPRAGE protocol (field of view = 224 mm, repetition time = 2300 msec, echo time = 2.25 msec, flip angle = 8°, voxel size = 1 × 1 × 1 mm, 192 sagittal slices) to stereotactically guide the stimulation. Resting-state functional images were acquired with the following sequence: repetition time = 2450 msec, echo time = 30 msec, field of view = 192 mm, flip angle = 81°, voxel size = 3 × 3 × 3 mm.

### *rTMS*

In each experimental session, participants received rTMS to either the left AnG or vertex before the memory test. The stimulation site order was counterbalanced across participants. rTMS was applied using a Magstim Rapid2 magnetic stimulator connected to a 70-mm double air film coil. The structural data obtained from each participant were used in Brainsight 2.0, a computerized frameless stereotaxic system (Rogue Research), to identify the target brain regions on a subject-by-subject basis. The stimulation sites were selected in the system by transformation of the Montreal Neurological Institute (MNI) stereotaxic coordinates to participant’s normalized brain. The sites stimulated were located in the left AnG at the MNI coordinates  $x = -43, y = -66, z = 38$ , and in a control area on the vertex, which was identified at the point of the same distance to the left and the right preauricular, and of the same distance to the nasion and theinion (Figure 1D). The AnG coordinate was determined from a metareview of the parietal lobe and memory (Vilberg & Rugg, 2008). This coordinate has been adopted in several TMS studies studying subjective memory (Tibon, Fuhrmann, Levy, Simons, & Henson, 2019; Wynn et al., 2018; Bonnici et al., 2016; Yazar et al., 2014). To target the selected stimulation sites, four fiducial points located on the face were used to coregister the anatomical MRI to the participant’s head using an infrared pointer. The real-time locations of the TMS coil and the participant’s head were monitored by an infrared camera using a Polaris Optical Tracking System (Northern Digital).

The rTMS protocol was adopted from a similar study probing episodic memory metacognition (Ye et al., 2018). This stimulation protocol has also been used to induce inhibitory effect on the AnG in a similar task (Wynn et al., 2018). Specifically, rTMS was applied at 1-Hz frequency for a continuous duration of 20 min (1200 pulses in total) at 110% of active motor threshold, which was defined as the lowest TMS intensity delivered over the motor cortex necessary to elicit visible twitches of the right index finger in at least 5 of 10 consecutive pulses (Rossini et al., 2015). During stimulation, participants wore earplugs to attenuate the sound of the stimulating coil discharge. The coil was held to the scalp of the participant with a custom coil holder and the participant’s head was propped in a comfortable position. This particular stimulation magnitude and protocols of rTMS is known to induce efficacious intracortical inhibitory effects for over 60 min (Rossini et al., 2015; Thut & Pascual-Leone, 2010). Given that our task lasted 50 min, the TMS effects should have been long lasting enough for the task. Although these inhibitory effects are known to level off within hours by the end of the stimulation, for safety reasons and to avoid carryover effects of rTMS across sessions, Experimental Sessions 1 and 2 were conducted on separate days at least 3 days apart.



## Behavioral Data Analysis

Metacognition refers to one's subjective access to their own cognitive processes and is computed by estimating how accurate subjective ratings distinguish between correct and incorrect responses. For comparability with previous metacognition work (for a review, see Fleming & Lau, 2014), we estimated memory metacognitive ability using the confidence ratings. To assess whether participants' confidence ratings were reliably related to their objective memory performance, we computed meta- $d'$ , a metric that quantifies the metacognitive sensitivity and is independent of confidence bias, using a Bayesian model-based method (Fleming, 2017; Fleming & Lau, 2014). Given the metric, meta- $d'$  is expressed in the same units as  $d'$ , it allows a direct comparison between objective performance and metacognitive sensitivity. For example, if meta- $d'$  equals  $d'$ , it means that the observer is metacognitively ideal. Meta- $d'$  greater or less than  $d'$  indicates metacognition that is better or worse, respectively, than the expected given task performance. Here, we assessed metacognitive efficiency using the ratio meta- $d'/d'$ , which indexes a participant's metacognitive efficiency while adjusting for the influence of objective memory performance and response bias. Similarly, to quantify the extent to which participants' vividness ratings tracked their objective memory performance, we applied the same Bayesian framework of metacognitive efficiency but to vividness ratings and computed a metric termed vividness efficiency (vivid- $d'/d'$ ).

## Resting-state Functional Connectivity Analysis

For connectivity analysis of resting-state data, resting-state functional data were first converted to Brain Imaging Data Structure format and verified using the Brain Imaging Data Structure validator. Data preprocessing was performed using fMRIPrep (Esteban et al., 2019) with the default processing steps, including skull stripping, motion correction, brain tissue segmentation, slice time correction, and coregistration and affine transformation of the functional volumes to corresponding T1-weighted and subsequently to MNI space. For further details of the pipeline, please refer to the online documentation: <https://fmriprep.org/>.

To estimate connectivity between AnG and hippocampus, following previous studies studying AnG and episodic retrieval (Tibon et al., 2019; Bonnici et al., 2016), we defined the AnG ROI as a sphere of 6-mm radius (equivalent to 33 voxels) with its center at the stimulation site ( $x = -43$ ,  $y = 66$ ,  $z = 38$ ; Vilberg & Rugg, 2008). The hippocampal ROI was obtained from a medial-temporal lobe atlas (Ritchey, Montchal, Yonelinas, & Ranganath, 2015). ROI-ROI resting-state functional connectivity analysis was performed using the CONN toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012). Preprocessed functional data were first linearly detrended, and a commonly used bandpass filter (0.008–0.09 Hz) was

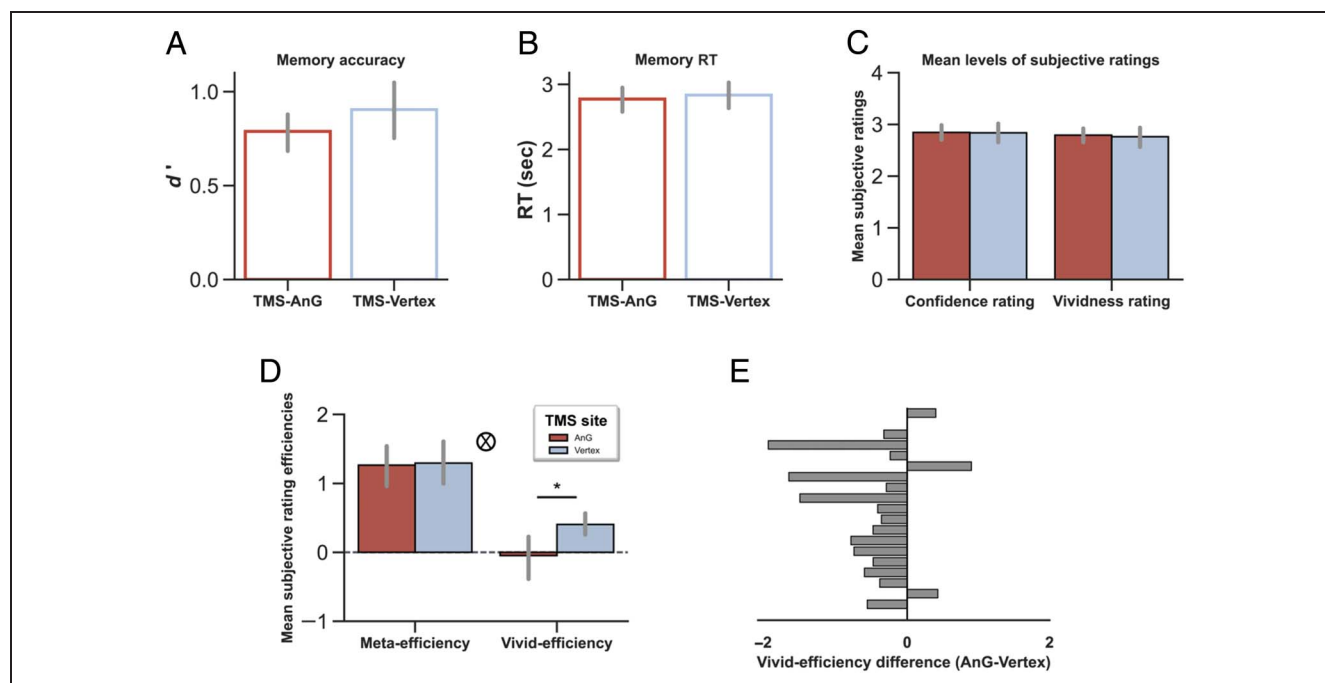
applied to isolate low-frequency fluctuations characteristic of resting-state fMRI and attenuate signals outside that range. White matter and CSF confound were removed using the aCompCor method. To ensure no voxels were included in mean estimates from outside ROIs, we performed all analyses using unsmoothed functional data.

## RESULTS

### Vividness Efficiency Is Causally Dependent on AnG

Although it is often assumed that both vividness ratings and confidence ratings during retrieval mediate subjective experience of remembering, our primary aim was to test whether these two components of subjective mnemonic experience during retrieval are dissociable. We operationalized this idea by developing a paradigm, in which participants watched episodes at encoding and performed a memory test immediately after receiving TMS inhibition to the AnG (Figure 1; see Methods for details). In the memory test, participants mentally replayed relevant scenes with an image cue and rated the vividness of their memory. Following the vividness rating, participants were asked to make a temporal proximity judgment related to the image cues and rated the confidence of their memory judgment. Importantly, the temporal proximity judgments demand participants to mentally replay the cue-related scenes for successful memory retrieval; thus, we are confident that vividness and confidence ratings were to be made on the same memory traces. The novel and critical manipulation in our experiment is that subjective evaluation efficiency computed by vividness rating and confidence rating are differentiable under the recollection of the same segment of memory within a trial.

We first examined the effect of TMS to AnG on basic performance. As expected, TMS did not influence objective memory performance as measured by memory sensitivity  $d'$  (mean<sub>AnG</sub> = 0.79,  $SD_{AnG}$  = 0.23; mean<sub>vertex</sub> = 0.90,  $SD_{vertex}$  = 0.35;  $t(19) = 1.39$ ,  $p = .18$ , Cohen's  $d = 0.38$ ; Figure 2A) and RT (mean<sub>AnG</sub> = 2.78 sec,  $SD_{AnG}$  = 0.43; mean<sub>vertex</sub> = 2.84 sec,  $SD_{vertex}$  = 0.44;  $t(19) = 0.68$ ,  $p = .51$ , Cohen's  $d = 0.14$ ; Figure 2B). Moreover, a repeated-measures ANOVA with Subjective Rating Type (vividness/confidence) and TMS Site (AnG/vertex) for mean levels of subjective rating (confidence rating: mean<sub>AnG</sub> = 2.85,  $SD_{AnG}$  = 0.32; mean<sub>vertex</sub> = 2.84,  $SD_{vertex}$  = 0.42; vividness rating: mean<sub>AnG</sub> = 2.79,  $SD_{AnG}$  = 0.31; mean<sub>vertex</sub> = 2.76,  $SD_{vertex}$  = 0.43) did not reveal any significant main effects (rating type:  $F(1, 19) = 1.60$ ,  $p = .22$ ,  $\eta^2 = .08$ ; TMS:  $F(1, 19) = 0.13$ ,  $p = .72$ ,  $\eta^2 = .01$ ) nor an interaction ( $F(1, 19) = 0.21$ ,  $p = .66$ ,  $\eta^2 = .01$ ; Figure 2C). Of importance, we assessed whether inhibitory rTMS to the left AnG modulated the efficiency of subjective ratings during memory retrieval (meta-efficiency: mean<sub>AnG</sub> = 1.26,  $SD_{AnG}$  = 0.66; mean<sub>vertex</sub> = 1.29,  $SD_{vertex}$  = 0.72; vivid-efficiency: mean<sub>AnG</sub> = -0.05,  $SD_{AnG}$  = 0.70; mean<sub>vertex</sub> = 0.40,  $SD_{vertex}$  = 0.35) using two robust indices (vivid- $d'/d'$  and



**Figure 2.** TMS effect on behavioral performance. (A) Accuracy ( $d'$ ) and (B) RTs in the temporal proximity task. (C) Mean levels of confidence ratings and vividness ratings. (D) Metacognitive efficiency and vividness efficiency. (E) Change in vividness efficiency between AnG and vertex stimulation for each participant. Error bars represent *SEM*.  $\otimes$  indicates interaction of Subjective Reports Efficiency by Stimulation Site in a repeated-measures ANOVA.  $*p < .05$ .

meta- $d'/d'$ ; see Methods). A repeated-measures ANOVA with factors of Subjective Efficiency Type (vividness efficiency/metacognitive efficiency) and TMS Site (AnG/vertex) revealed a significant main effect of Efficiency Type,  $F(1, 19) = 69.23, p < .001, \eta^2 = .78$ , as well as an interaction,  $F(1, 19) = 5.88, p = .02, \eta^2 = .24$  (Figure 2D). Follow-up  $t$  tests revealed that participants showed significantly lower vividness efficiency following TMS to the left AnG compared with vertex,  $t(19) = 2.96, p_{\text{holm}} = .016$ , Cohen's  $d = 0.80$ , whereas no analogous decrement was found in metacognitive efficiency,  $t(19) = 0.12, p_{\text{holm}} = .91$ , Cohen's  $d = 0.04$ . To better characterize the effect of AnG stimulation on vividness, we performed a sign test to verify the extent of changes between TMS to AnG and vertex. Reductions in vividness efficiency were consistent across participants due to TMS to AnG (16/20 reduced; sign test:  $p < .001$ ; Figure 2E).

We further queried whether the vividness rating was reliably related to the temporal proximity memory performance using two additional analyses. First, we performed a permutation test to ensure the internal validity of the vividness efficiency index. Specifically, we randomly shuffled the vividness rating under TMS to vertex and recalculated the vividness efficiency score for each participant (permutation  $n = 1000$  per participant). Statistical significance was determined by comparing the true vividness efficiency to the null distribution of permutations for each participant. This analysis revealed that the vividness efficiency robustly quantifies the correspondence between vividness

and objective memory in every participant (all  $ps < .005$ ). Second, we assessed the efficiency of vividness on a trial-by-trial basis and tested the AnG TMS effect using a mixed-effects logistic regression model for objective memory performance against vividness ratings with the participant as a random effect for each stimulation site. Consistent with the observed TMS effect on vividness efficiency, we found that the vividness rating was a significant predictor of memory performance under TMS to vertex ( $\beta = 0.213, p < .001$ ), but not under the AnG TMS condition ( $\beta = 0.054, p = .761$ ). These two analyses show that vividness efficiency, albeit its relatively low value, is a valid indicator for memory performance, both as a trialwise and as a whole measure.

Subjective judgments (mainly metacognitive judgments) have been shown to exert a causal impact on the choice to collect more information (Desender, Boldt, & Yeung, 2018; Metcalfe & Finn, 2008). We next asked whether the AnG TMS would impose any effect on the trade-off between memory accuracy and speed (RT). To do so, we computed an inverse efficiency score (mean correct RTs/% correct) to index the speed-accuracy trade-off. We did not observe a significant TMS effect on this speed-accuracy efficiency score,  $t(19) = 0.30, p = .76$ , suggesting that the observed TMS effect on vividness efficiency could not be explained away by any speed-accuracy tradeoff. In addition, to test whether the vividness ratings might be biased by the order of the target scene, we applied a 2 (TMS: AnG, vertex)  $\times$  2 (Occurrence Order: before, after)

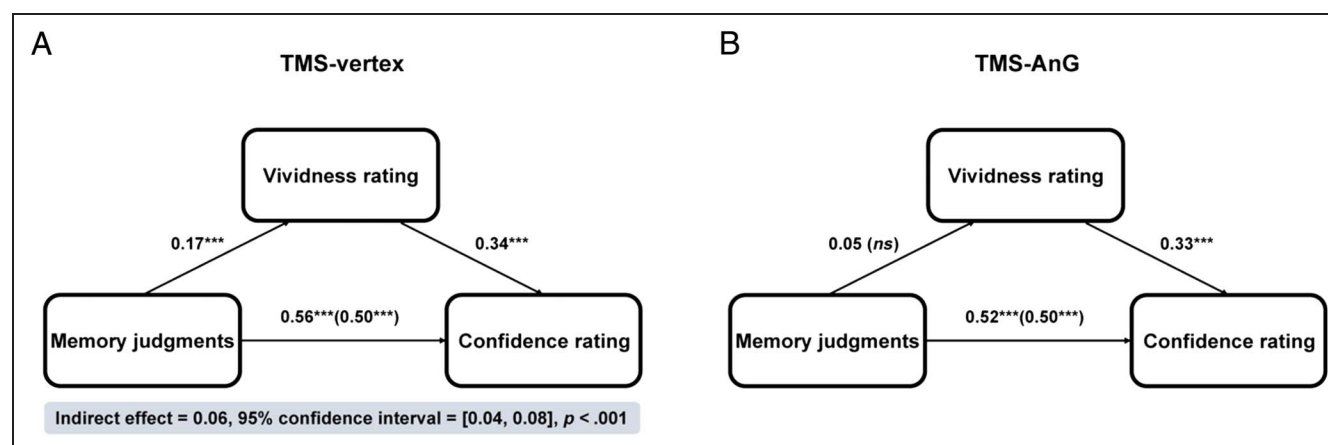
ANOVA to vividness efficiency and we found no significant interaction,  $F(1, 19) = 0.99, p = .33, \eta^2 = .05$ . This confirmed that the vividness ratings were not affected by the location of the target scene within the recalled segment. Moreover, to verify the lasting effects of TMS, we split the AnG TMS data into halves based on their time within the experiment (first vs. second half). To test whether the observed TMS effect was modulated by time, we reran the vividness efficiency analysis for each half and submitted the vividness efficiency to a 2 (TMS: AnG, vertex)  $\times$  2 (Time: first half, second half) repeated-measures ANOVA. This revealed no main effect of Time,  $F(1, 19) = 0.002, p = .96, \eta^2 < .001$ , and no interaction involving Time,  $F(1, 19) = 1.22, p = .28, \eta^2 = .06$ , suggesting that the TMS effect did not differ in the first or second half of the experiment.

Together, these results suggest that the AnG is engaged in the monitoring of vividness, and there might be a dissociation between vividness efficiency and confidence efficiency during episodic retrieval.

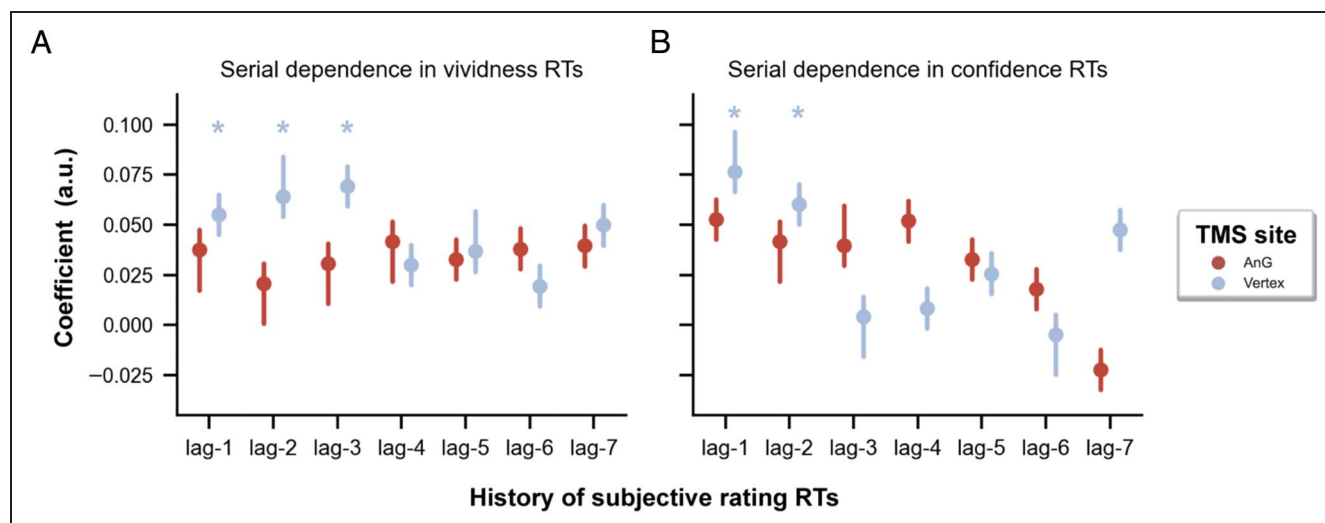
### AnG Stimulation Alters the Mediating Role of Vividness in Confidence in the Accuracy of Memory Judgment

To examine how objective memory accuracy and the two subjective ratings of memory are interrelated in a single statistical framework, we conducted a mediation analysis using objective memory performance as the independent variable and vividness rating as the mediator variable under each TMS condition separately. We hypothesized that the link between objective memory response and confidence might be mediated by the vividness of memory. Under TMS to vertex, as expected, objective memory performance was significantly associated with both

vividness ratings ( $\beta = 0.17, p < .001$ ) and confidence ratings ( $\beta = 0.56, p < .001$ ), indicating that both subjective ratings are meaningful in tracking the success of the same memory judgments. This is important because it allows us to test for the dissociation between vividness and confidence under the same TMS intervention. After adding vividness ratings as a simultaneous predictor, the relationship between objective memory performance and confidence ratings remained intact ( $\beta = 0.50, p < .001$ ). The trialwise mediation analysis revealed that vividness ratings partially mediated the association between objective memory performance and confidence ratings (indirect effect = 0.06,  $p < .001$ , 95% CI [0.04, 0.08]; Figure 3A). Most importantly, by contrast, the vividness ratings did not mediate the relationship between objective memory and confidence ratings following AnG stimulation. The AnG stimulation altered the association between objective memory performance and vividness ratings ( $\beta = 0.05, p = .149$ ; Figure 3B). Neither the relationship between confidence ratings and memory performance ( $\beta = 0.52, p < .001$ ) nor the relationship between confidence and vividness ratings ( $\beta = 0.33, p < .001$ ) was interrupted by AnG TMS. There was also a significant association between vividness ratings and confidence ratings ( $\beta = 0.34, p < .001$ ), which was not affected by AnG TMS. These findings indicate that, although both vividness ratings and confidence ratings were independently associated with objective memory performance under control site stimulation, AnG stimulation selectively impacted the association between vividness ratings and objective memory. These results provide further support to our main results (see Figure 2D and E) and revealed a mediation between memory performance and confidence through the subjective vividness of memory.



**Figure 3.** Mediation analysis between TMS conditions. (A) The mediation path diagram (vertex TMS condition) shows significant relationships between memory performance and vividness ratings, vividness ratings and confidence ratings, memory performance and confidence ratings, and a significant mediation effect of vividness on the relationship between memory performance and confidence ratings. (B) AnG TMS altered the association between objective memory performance and vividness ratings, while leaving the relationship between vividness ratings and confidence ratings, and memory performance and confidence ratings unimpacted.  $^{***}p < .001$ ;  $ns$  = not statistically significant.



**Figure 4.** Serial dependence in subjective reports RTs. (A) Autocorrelation in vividness RTs was observed up to lag-3 under TMS to vertex (all  $p$ s < .05; blue dots). No reliable autocorrelation was found in vividness RTs after TMS to AnG (red dots). (B) Autocorrelation was found in confidence RTs up to lag-2 under TMS to vertex (all  $p$ s < .05). Such autocorrelation in confidence RT was also not found after TMS to AnG. \* $p$  < .05.

### AnG Stimulation Eradicates Serial Dependence Effect in Both Subjective Ratings RTs

We have thus far revealed differential TMS effects on the accuracy of two subjective ratings and their interrelationship with objective memory performance. We next sought to investigate whether the subjective evaluation mechanisms might share similarity in terms of how they incorporate past information into the current decision or otherwise known as serial dependence effect (Rahnev et al., 2020; Rahnev, Koizumi, McCurdy, D'Esposito, & Lau, 2015; Fischer & Whitney, 2014). Given that RT is a defining element of the trade-off between speed and accuracy that characterizes decisions, the presence of serial dependence on RT can provide important insights into the nature of subjective awareness generation. To test for serial dependence in vividness RTs and confidence RTs separately, we performed a series of mixed regression analyses predicting subjective rating RTs with fixed effects for the recent trial history up to seven trials back and random intercepts for each participant. We also explicitly tested for any different involvement of AnG in generating subjective estimation during memory retrieval. We found that there was autocorrelation in vividness RTs up to lag-3 (all  $p$ s < .05; Figure 4A) under TMS to vertex. Following TMS to AnG, such serial dependence was no longer found. Furthermore, we also observed autocorrelation in confidence RTs up to lag-2 (all  $p$ s < .05; Figure 4B) under TMS control condition and such serial dependence effect was also reduced by AnG stimulation. These results replicated the existence of serial dependence in confidence RT and revealed serial dependence in vividness rating RTs, and both are modulated by AnG stimulation. The findings of such serial spill-over bias in both subjective estimations and their susceptibility to AnG stimulation might suggest

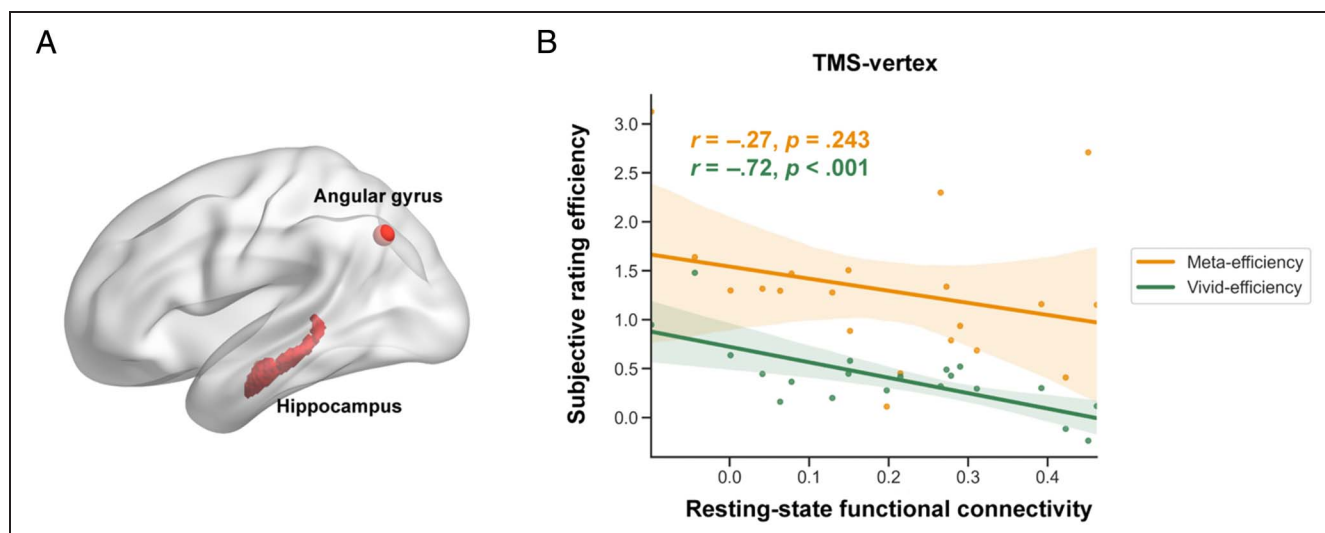
their similarity in terms of subjective experience generations during memory retrieval.

### Resting-state Functional Connectivity between Hippocampus and AnG Specifically Relates to Vividness Efficiency

Having demonstrated that the AnG modulated the efficiency of vividness ratings, we then explored whether the intrinsic functional communication among brain regions was associated with subjective reports efficiencies. Specifically, we examined the relationship between intraindividual variability in subjective report efficiency and the resting-state functional connectivity between the AnG and hippocampus (Figure 5A). These two regions have previously been shown to be related to memory metacognition (Baird, Smallwood, Gorgolewski, & Margulies, 2013). Interestingly, we observed a dissociation in this functional connection between efficiency of vividness and confidence. The functional connectivity of AnG–hippocampus was significantly correlated with vividness efficiency ( $r = -.72$ ,  $p < .001$ ; Figure 5B), but not metacognitive efficiency ( $r = -.27$ ,  $p = .243$ ; comparison between correlations:  $z = 1.876$ ,  $p = .03$ ), suggesting that the vividness and confidence during memory retrieval may be mediated by distinct neural substrates. Moreover, TMS to AnG reduced the correlation between functional connectivity of AnG–hippocampus and vividness efficiency ( $r = -.31$ ,  $p = .189$ ; comparison between TMS sites:  $z = 3.201$ ,  $p = .001$ ). Consistent with our prediction, these results revealed that the self-monitoring of vividness and confidence is not only functionally but also neurally dissociable.

In summary, consistent with our predictions, these findings establish a specific role of AnG, its mediating effects,





**Figure 5.** Resting-state functional connectivity analysis. (A) ROIs (hippocampus and AnG). (B) Vividness efficiency, but not metacognitive efficiency, is significantly correlated with AnG–hippocampal functional connectivity.

and its functional connection with the hippocampus in subserving our perceived vividness of memory retrieval. The direct comparison with the metacognitive counterpart (indexed by confidence ratings) suggested functional and anatomical dissociation between the two subjective efficiencies in these mnemonic processes.

## DISCUSSION

How do we obtain accurate assessment of our memory performance? Much of what we know about subjective aspects of memory comes from experimental work measuring the relationship between the level of confidence or vividness rating and neural activity during memory retrieval. However, the ability to accurately monitor subjective mnemonic experience has remained poorly understood. Here, we asked the question of whether subjective confidence and vividness of memory reflect distinct introspective capacities. By administering noninvasive preretrieval stimulation to the left AnG, a candidate region supporting the subjective components of memory (Humphreys et al., 2021), we provide evidence for a causal involvement for AnG specifically in vividness efficiency. Critically, we show evidence that the ability of monitoring vividness of memory is indeed functionally and anatomically dissociable from confidence during episodic memory retrieval.

One of the novel aspects of this work is that we isolate the processes underlying vividness and confidence reports during episodic memory retrieval. We observed that temporary disruption of the AnG leads to difference in the efficiency of vividness ratings while leaving the efficiency of confidence ratings intact, suggesting that vividness and confidence of memory are two separable subjective experiences. These results are compatible with prior

findings that the AnG is involved in the subjective experience of remembering (Kuhl & Chun, 2014; Yazar et al., 2014) but not in confidence-related metacognition. One possibility is that vividness of memory reflects something akin to the perception of past events, analogous to the “attention to memory” account (Hutchinson, Uncapher, & Wagner, 2009; Cabeza, 2008; Ciaramelli, Grady, & Moscovitch, 2008). Retrieval from long-term memory demands selection between specific memories competing for recall (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005). Previous theories have advanced the analogies between selection in the perceptual domain and selection during memory retrieval (Cabeza, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). Accordingly, the “attention to memory” account proposes that the parietal mechanisms (including AnG) support goal-directed attention toward the maintenance of mnemonic cues as well as facilitate the monitoring of episodic memory retrieval (Kwok & Macaluso, 2015; Hutchinson et al., 2009). In light of this view, the subjective sensed vividness during memory recall may thus represent a product of internal attentional processes rather than a subjective evaluation of memory quality, such as confidence. It is then plausible that the TMS to the AnG disrupts the shifting and allocation of attention to internal representations, resulting in less accurate perceived vividness of memory. A potential future direction following this work is to examine the degree of anatomical and functional convergence between the vividness rating and reflective attention.

Previous studies have linked activity in AnG with rated vividness (Bonnici et al., 2016; Kuhl & Chun, 2014) and reported that patients with lateral parietal lesions show diminished vividness or confidence of their memories (Hower, Wixted, Berryhill, & Olson, 2014; Simons, Peers, Mazuz, Berryhill, & Olson, 2010; Berryhill, Phuong,

Picasso, Cabeza, & Olson, 2007). In the same vein, some other TMS studies have reported that AnG stimulation reduced confidence ratings of memory (Wynn et al., 2018; Yazar et al., 2014). Here, however, we did not observe any TMS effect on the overall reported vividness or confidence. One explanation for the discrepancy is that, in our study, the participants encoded a naturalistic story per session and made memory judgments about the temporal proximity of two scenes, whereas in previous studies, they used words and recognition task. As noted in Yazar et al. (2014), the observed TMS effect on mean confidence rating was specific to source recollection, while having cued recall confidence unimpaired, suggesting that differences in the types of task and stimuli might be responsible for producing differential AnG stimulation effects on mean subjective ratings across studies. Rather, instead of using the reported vividness, here we applied the concept of using performance and confidence correspondence (a quantitative measure of metacognition) to derive the degree of correspondence between rated vividness and objective memory accuracy. This approach enables us to estimate the TMS effect on the vividness efficiency independently from the level of vividness and objective memory performance. We asked participants to rate the vividness of the mental replay before any mnemonic decision, which allows for an uncontaminated assessment of the richness of mental experience before any memory judgment (Siedlecka, Paulewicz, & Wierchoń, 2016). Our findings add to this limited literature by demonstrating a causal role for the AnG in vividness efficiency. One interpretation of these results is that the AnG may act as an accumulator in service of mnemonic decisions (Wagner et al., 2005). It has been previously proposed that memory retrieval is accomplished by a diffusion process during which evidence for a memory decision is accumulated (Ratcliff, 1978), and the parietal cortex, including AnG, is thought to play a role in the integration of sensory information (Gold & Shadlen, 2007; Shadlen & Newsome, 2001). This hypothesis is compatible with our data, accommodating the finding that TMS to AnG affected the correspondence between vividness and memory performance, but not the mean level of rated vividness and objective memory performance. Our findings clarify a role for AnG to accurately gauging the vividness of memory and support the notion that AnG participates in accumulating and integrating information in support of mnemonic processes.

In addition, intrinsic individual differences in functional connectivity between brain structures have informed our understanding of the varied ability to introspect about self-performance (Ye et al., 2019; Baird et al., 2013; Fleming, Weil, Nagy, Dolan, & Rees, 2010). Here, we found that resting-state functional connectivity of hippocampus and AnG is specifically associated with vividness efficiency, but not metacognitive efficiency, across individuals. This dissociation between functional connections between vividness and confidence efficiency is in line with our behavioral results that vividness and confidence may

depend on dissociable neural substrates, suggestive of a differentiation account of subjective assessments of memory by functionally and anatomically dissociating the monitoring of vividness from confidence. A number of studies have shown AnG is causally involved in episodic memory tasks (Tambini, Nee, & D'Esposito, 2018; Bridge et al., 2017; Wang et al., 2014). Regarding the influence of AnG TMS, we found that the relationship between vividness efficiency and AnG–hippocampal connectivity was eliminated under AnG TMS, consistent with the notion that the AnG TMS would distally modulate the function of hippocampus for memory processes (Wang et al., 2014). To put the results into a broader perspective, AnG is a key node within the default mode network, a set of brain regions that are consistently activated during rest and deactivated during task (e.g., Buckner, Andrews-Hanna, & Schacter, 2008; Fox et al., 2005; Raichle et al., 2001). Interestingly, our finding revealed a negative relationship between vividness efficiency and AnG–hippocampal resting-state functional connectivity under vertex TMS. The negative correlation might be consistent with the proposal that suppression of the default mode network (including the AnG) is critical to success in some cognitive task performance (Anticevic, Repovs, Shulman, & Barch, 2010). Future work combining TMS with fMRI could be used to examine to what extent TMS to AnG affect the interconnection between AnG and hippocampus during subjective memory processes.

Furthermore, we observed a phenomenon of serial dependence in both subjective memory measures. These results extend previous demonstration of serial dependence in metacognitive judgments in perceptual tasks (Rahnev et al., 2020) to vividness and confidence judgments in an episodic memory task, suggesting that this phenomenon might be represented in a generic, task-independent format. We also showed that such effect was modulated by AnG stimulation, suggesting that the impact of AnG inhibition might go beyond subjective evaluation related to memory strength alone. Future studies should test whether this serial dependence phenomenon is domain-general and what factors might affect serial dependence in subjective evaluation judgments. In the literature on perceptual metacognition, theories of confidence generation posit that the central processing of evidence leading to a perceptual decision also establishes a level of confidence (Sanders, Hangya, & Kepecs, 2016; Fetsch, Kiani, Newsome, & Shadlen, 2014). Some argue that confidence rating is corrupted by a metalevel noise (Shekhar & Rahnev, 2018; De Martino et al., 2012). In contrast, it remains less studied for the origins of confidence in the context of episodic memory decisions. Here, in an elucidation of the relationship between vividness, confidence, and objective memory performance, we found that vividness mediates the association between confidence and objective performance. This indicates that the sensed vividness of memory is instrumentally used for the computation of confidence.

Consideration of the relative contribution of subjective feeling of vividness in generating confidence, especially for naturalistic paradigms involving continuous streams of multisensory information and mnemonic experiences, is thus paramount. Although the issue of deriving the best model for memory confidence is not our focus here, we hope that our findings provide some new insights into the confidence generation in episodic memory decision for future work. A critical avenue for future studies is to exploit what other information beyond subjective vividness is being used for confidence generation in episodic memory.

In closing, we demonstrate the contribution of AnG to vividness processing in terms of its mediating effect and its regional (by TMS) and cross-regional connectivity characteristics (by resting-state MRI). These findings suggest conscious mnemonic experiences could be elucidated by taking memory vividness, their relationship with confidence, and their anatomical profile into consideration.

## Acknowledgments

This research received support from Science and Technology Commission of Shanghai Municipality (grant no. 201409002800), the National Natural Science Foundation of China (grant no. 32071060), internal funding from School of Psychology and Cognitive Science (East China Normal University), and Jiangsu Qinglan Award (S. C. K.).

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Futing Zou: Conceptualization; Formal analysis; Investigation; Methodology; Software; Visualization; Writing—Original draft; Writing—Review & editing. Sze Chai Kwok: Conceptualization; Funding acquisition; Resources; Supervision; Writing—Review & editing.

## Funding Information

Sze Chai Kwok, National Natural Science Foundation of China (<https://dx.doi.org/10.13039/501100001809>), grant number: 32071060, Science and Technology Commission of Shanghai Municipality (<https://dx.doi.org/10.13039/501100003399>), grant number: 201409002800, Open Research Fund of the State Key Laboratory of Cognitive Neuroscience and Learning (Beijing Normal University), internal funding from School of Psychology and Cognitive Science (East China Normal University), and Jiangsu Qinglan award.

## Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were  $M(\text{an})/M = .407$ ,  $W(\text{oman})/M = .32$ ,  $M/W = .115$ , and  $W/W = .159$ , the comparable proportions for the articles that these authorship teams cited were  $M/M = .549$ ,  $W/M = .257$ ,  $M/W = .109$ , and  $W/W = .085$  (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be as follows:  $M/M = .652$ ,  $W/M = .239$ ,  $M/W = .022$ , and  $W/W = .087$ .

## REFERENCES

- Anticevic, A., Repovs, G., Shulman, G. L., & Barch, D. M. (2010). When less is more: TPJ and default network deactivation during encoding predicts working memory performance. *Neuroimage*, 49, 2638–2648. <https://doi.org/10.1016/j.neuroimage.2009.11.008>, PubMed: 19913622
- Badre, D., Poldrack, R. A., Paré-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron*, 47, 907–918. <https://doi.org/10.1016/j.neuron.2005.07.023>, PubMed: 16157284
- Baird, B., Smallwood, J., Gorgolewski, K. J., & Margulies, D. S. (2013). Medial and lateral networks in anterior prefrontal cortex support metacognitive ability for memory and perception. *Journal of Neuroscience*, 33, 16657–16665. <https://doi.org/10.1523/JNEUROSCI.0786-13.2013>, PubMed: 24133268
- Bang, D., Aitchison, L., Moran, R., Herce Castanon, S., Rafiee, B., Mahmoodi, A., et al. (2017). Confidence matching in group decision-making. *Nature Human Behaviour*, 1, 1–7. <https://doi.org/10.1038/s41562-017-0117>
- Berryhill, M. E., Phuong, L., Picasso, L., Cabeza, R., & Olson, I. R. (2007). Parietal lobe and episodic memory: Bilateral damage causes impaired free recall of autobiographical memory. *Journal of Neuroscience*, 27, 14415–14423. <https://doi.org/10.1523/JNEUROSCI.4163-07.2007>, PubMed: 18160649
- Bonnici, H. M., Richter, F. R., Yazar, Y., & Simons, J. S. (2016). Multimodal feature integration in the angular gyrus during episodic and semantic retrieval. *Journal of Neuroscience*, 36, 5462–5471. <https://doi.org/10.1523/JNEUROSCI.4310-15.2016>, PubMed: 27194327
- Branzi, F. M., Pobric, G., Jung, J., & Lambon Ralph, M. A. (2021). The left angular gyrus is causally involved in context-dependent integration and associative encoding during narrative reading. *Journal of Cognitive Neuroscience*, 33, 1082–1095. [https://doi.org/10.1162/jocn\\_a\\_01698](https://doi.org/10.1162/jocn_a_01698), PubMed: 34428784
- Bridge, D. J., Gagnon, E. P., Vanhaerents, S. A., Voss, J. L., Nilakantan, A. S., Bridge, D. J., et al. (2017). Stimulation of the posterior cortical-hippocampal network enhances precision of memory recollection. *Current Biology*, 27, 465–470. <https://doi.org/10.1016/j.cub.2016.12.042>, PubMed: 28111154



- Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*, 1124, 1–38. <https://doi.org/10.1196/annals.1440.011>, PubMed: 18400922
- Cabeza, R. (2008). Role of parietal regions in episodic memory retrieval: The dual attentional processes hypothesis. *Neuropsychologia*, 46, 1813–1827. <https://doi.org/10.1016/j.neuropsychologia.2008.03.019>, PubMed: 18439631
- Ciaramelli, E., Grady, C. L., & Moscovitch, M. (2008). Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia*, 46, 1828–1851. <https://doi.org/10.1016/j.neuropsychologia.2008.03.022>, PubMed: 18471837
- De Martino, B., Fleming, S. M., Garrett, N., & Dolan, R. J. (2012). Confidence in value-based choice. *Nature Neuroscience*, 16, 105–110. <https://doi.org/10.1038/nn.3279>, PubMed: 23222911
- Desender, K., Boldt, A., & Yeung, N. (2018). Subjective confidence predicts information seeking in decision making. *Psychological Science*, 29, 761–778. <https://doi.org/10.1177/0956797617744771>, PubMed: 29608411
- DuBrow, S., & Davachi, L. (2013). The influence of context boundaries on memory for the sequential order of events. *Journal of Experimental Psychology: General*, 142, 1277–1286. <https://doi.org/10.1037/a0034024>, PubMed: 23957281
- Esteban, O., Markiewicz, C. J., Blair, R. W., Moodie, C. A., Isik, A. I., Erramuzpe, A., et al. (2019). fMRIPrep: A robust preprocessing pipeline for functional MRI. *Nature Methods*, 16, 111–116. <https://doi.org/10.1038/s41592-018-0235-4>, PubMed: 30532080
- Fetsch, C. R., Kiani, R., Newsome, W. T., & Shadlen, M. N. (2014). Effects of cortical microstimulation on confidence in a perceptual decision. *Neuron*, 83, 797–804. <https://doi.org/10.1016/j.neuron.2014.07.011>, PubMed: 25123306
- Fischer, J., & Whitney, D. (2014). Serial dependence in visual perception. *Nature Neuroscience*, 17, 738–743. <https://doi.org/10.1038/nn.3689>, PubMed: 24686785
- Fleming, S. M. (2017). HMeta-d: Hierarchical Bayesian estimation of metacognitive efficiency from confidence ratings. *Neuroscience of Consciousness*, 3, 1–14. <https://doi.org/10.1093/nc/nix007>, PubMed: 29877507
- Fleming, S. M., & Daw, N. D. (2016). Self-evaluation of decision performance: A general Bayesian framework for metacognitive computation. *Psychological Review*, 124, 1–59. <https://doi.org/10.1037/rev0000045>, PubMed: 28004960
- Fleming, S. M., & Lau, H. (2014). How to measure metacognition. *Frontiers in Human Neuroscience*, 8, 1–9. <https://doi.org/10.3389/fnhum.2014.00443>, PubMed: 25076880
- Fleming, S. M., Weil, R. S., Nagy, Z., Dolan, R. J., & Rees, G. (2010). Relating introspective accuracy to individual differences in brain structure. *Science*, 329, 1541–1543. <https://doi.org/10.1126/science.1191883>, PubMed: 20847276
- Ford, J. H., & Kensinger, E. A. (2016). Effects of internal and external vividness on hippocampal connectivity during memory retrieval. *Neurobiology of Learning and Memory*, 134, 78–90. <https://doi.org/10.1016/j.nlm.2015.12.007>, PubMed: 26778653
- Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Essen, D. C. V., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences, U.S.A.*, 102, 9673–9678. <https://doi.org/10.1073/pnas.0504136102>, PubMed: 15976020
- Gilboa, A., Winocur, G., Grady, C. L., Hevenor, S. J., & Moscovitch, M. (2004). Remembering our past: Functional neuroanatomy of recollection of recent and very remote personal events. *Cerebral Cortex*, 14, 1214–1225. <https://doi.org/10.1093/cercor/bhh082>, PubMed: 15166099
- Gold, J. I., & Shadlen, M. N. (2007). The neural basis of decision making. *Annual Review of Neuroscience*, 30, 535–574. <https://doi.org/10.1146/annurev.neuro.29.051605.113038>, PubMed: 17600525
- Hower, K. H., Wixted, J., Berryhill, M. E., & Olson, I. R. (2014). Impaired perception of mnemonic oldness, but not mnemonic newness, after parietal lobe damage. *Neuropsychologia*, 56, 409–417. <https://doi.org/10.1016/j.neuropsychologia.2014.02.014>, PubMed: 24565734
- Humphreys, G. F., Ralph, M. A. L., & Simons, J. S. (2021). A unifying account of angular gyrus contributions to episodic and semantic cognition. *Trends in Neurosciences*, 44, 452–463. <https://doi.org/10.1016/j.tins.2021.01.006>, PubMed: 33612312
- Hutchinson, J. B., Uncapher, M. R., & Wagner, A. D. (2009). Posterior parietal cortex and episodic retrieval: Convergent and divergent effects of attention and memory. *Learning & Memory*, 16, 343–356. <https://doi.org/10.1101/lm.919109>, PubMed: 19470649
- Kuhl, B. A., & Chun, M. M. (2014). Successful remembering elicits event-specific activity patterns in lateral parietal cortex. *Journal of Neuroscience*, 34, 8051–8060. <https://doi.org/10.1523/JNEUROSCI.4328-13.2014>, PubMed: 24899726
- Kwok, S. C., & Macaluso, E. (2015). Exogenous features versus prior experiences modulate different subregions of the right IPL during episodic memory retrieval. *Scientific Reports*, 5, 11248. <https://doi.org/10.1038/srep11248>, PubMed: 26057929
- Maniscalco, B., & Lau, H. (2012). A signal detection theoretic approach for estimating metacognitive sensitivity from confidence ratings. *Consciousness and Cognition*, 21, 422–430. <https://doi.org/10.1016/j.concog.2011.09.021>, PubMed: 22071269
- McCurdy, L. Y., Maniscalco, B., Metcalfe, J., Liu, K. Y., de Lange, F. P., & Lau, H. (2013). Anatomical coupling between distinct metacognitive systems for memory and visual perception. *Journal of Neuroscience*, 33, 1897–1906. <https://doi.org/10.1523/JNEUROSCI.1890-12.2013>, PubMed: 23365229
- Metcalfe, J., & Shimamura, A. P. (Eds.). (1994). *Metacognition: Knowing about knowing*. Cambridge, MA: MIT Press. <https://doi.org/10.7551/mitpress/4561.001.0001>
- Metcalfe, J., & Finn, B. (2008). Evidence that judgments of learning are causally related to study choice. *Psychonomic Bulletin & Review*, 15, 174–179. <https://doi.org/10.3758/PBR.15.1.174>, PubMed: 18605499
- Morales, J., Lau, H., & Fleming, S. M. (2018). Domain-general and domain-specific patterns of activity supporting metacognition in human prefrontal cortex. *Journal of Neuroscience*, 38, 3534–3546. <https://doi.org/10.1523/JNEUROSCI.2360-17.2018>, PubMed: 29519851
- Qin, S., van Marle, H. J. F., Hermans, E. J., & Fernández, G. (2011). Subjective sense of memory strength and the objective amount of information accurately remembered are related to distinct neural correlates at encoding. *Journal of Neuroscience*, 31, 8920–8927. <https://doi.org/10.1523/JNEUROSCI.2587-10.2011>, PubMed: 21677175
- Rahnev, D., Desender, K., Lee, A. L. F., Adler, W. T., Aguilar-Lleyda, D., Akdoğan, B., et al. (2020). The confidence database. *Nature Human Behaviour*, 4, 317–325. <https://doi.org/10.1038/s41562-019-0813-1>, PubMed: 32015487
- Rahnev, D., Koizumi, A., McCurdy, L. Y., D'Esposito, M., & Lau, H. (2015). Confidence leak in perceptual decision making. *Psychological Science*, 26, 1664–1680. <https://doi.org/10.1177/0956797615595037>, PubMed: 26408037
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of



- brain function. *Proceedings of the National Academy of Sciences, U.S.A.*, 98, 676–682. <https://doi.org/10.1073/pnas.98.2.676>, PubMed: 11209064
- Ratcliff, R. (1978). A theory of memory retrieval. *Psychological Review*, 85, 59–108. <https://doi.org/10.1037/0033-295X.85.2.59>
- Ritchey, M., Montchal, M. E., Yonelinas, A. P., & Ranganath, C. (2015). Delay-dependent contributions of medial temporal lobe regions to episodic memory retrieval. *eLife*, 4, e05025. <https://doi.org/10.7554/eLife.05025>, PubMed: 25584461
- Rossini, P. M., Burke, D., Chen, R., Cohen, L. G., Daskalakis, Z., Di Iorio, R., et al. (2015). Non-invasive electrical and magnetic stimulation of the brain, spinal cord, roots and peripheral nerves: Basic principles and procedures for routine clinical and research application. An updated report from an I.F.C.N. Committee. *Clinical Neurophysiology*, 126, 1071–1107. <https://doi.org/10.1016/j.clinph.2015.02.001>, PubMed: 25797650
- Sanders, J. I., Hangya, B., & Kepecs, A. (2016). Signatures of a statistical computation in the human sense of confidence. *Neuron*, 90, 499–506. <https://doi.org/10.1016/j.neuron.2016.03.025>, PubMed: 27151640
- Shadlen, M. N., & Newsome, W. T. (2001). Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey. *Journal of Neurophysiology*, 86, 1916–1936. <https://doi.org/10.1152/jn.2001.86.4.1916>, PubMed: 11600651
- Shekhar, M., & Rahnev, D. (2018). Distinguishing the roles of dorsolateral and anterior PFC in visual metacognition. *Journal of Neuroscience*, 38, 5078–5087. <https://doi.org/10.1523/JNEUROSCI.3484-17.2018>, PubMed: 29720553
- Siedlecka, M., Paulewicz, B., & Wierzbchoń, M. (2016). But I was so sure! Metacognitive judgments are less accurate given prospectively than retrospectively. *Frontiers in Psychology*, 7, 218. <https://doi.org/10.3389/fpsyg.2016.00218>, PubMed: 26925023
- Simons, J. S., Peers, P. V., Mazuz, Y. S., Berryhill, M. E., & Olson, I. R. (2010). Dissociation between memory accuracy and memory confidence following bilateral parietal lesions. *Cerebral Cortex*, 20, 479–485. <https://doi.org/10.1093/cercor/bhp116>, PubMed: 19542474
- Tambini, A., Nee, D. E., & D'Esposito, M. (2018). Hippocampal-targeted theta-burst stimulation enhances associative memory formation. *Journal of Cognitive Neuroscience*, 30, 1452–1472. [https://doi.org/10.1162/jocn\\_a\\_01300](https://doi.org/10.1162/jocn_a_01300), PubMed: 29916791
- Thut, G., & Pascual-Leone, A. (2010). A review of combined TMS-EEG studies to characterize lasting effects of repetitive TMS and assess their usefulness in cognitive and clinical neuroscience. *Brain Topography*, 22, 219–232. <https://doi.org/10.1007/s10548-009-0115-4>, PubMed: 19862614
- Tibon, R., Fuhrmann, D., Levy, D. A., Simons, J. S., & Henson, R. N. (2019). Multimodal integration and vividness in the angular gyrus during episodic encoding and retrieval. *Journal of Neuroscience*, 39, 4365–4374. <https://doi.org/10.1523/JNEUROSCI.2102-18.2018>, PubMed: 30902869
- Tulving, E. (1972). Episodic and semantic memory. In *Organization of memory* (pp. xiii–423). New York: Academic Press.
- Tulving, E. (1985). Memory and consciousness. *Canadian Psychology/Psychologie Canadienne*, 26, 1–12. <https://doi.org/10.1037/h0080017>
- Vilberg, K. L., & Rugg, M. D. (2008). Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia*, 46, 1787–1799. <https://doi.org/10.1016/j.neuropsychologia.2008.01.004>, PubMed: 18343462
- Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, 9, 445–453. <https://doi.org/10.1016/j.tics.2005.07.001>, PubMed: 16054861
- Wang, J. X., Rogers, L. M., Gross, E. Z., Ryals, A. J., Dokucu, M. E., Brandstatt, K. L., et al. (2014). Targeted enhancement of cortical-hippocampal brain networks and associative memory. *Science*, 345, 1054–1057. <https://doi.org/10.1126/science.1252900>, PubMed: 25170153
- Whitfield-Gabrieli, S., & Nieto-Castanon, A. (2012). Conn: A functional connectivity toolbox for correlated and anticorrelated brain networks. *Brain Connectivity*, 2, 125–141. <https://doi.org/10.1089/brain.2012.0073>, PubMed: 22642651
- Wynn, S. C., Hendriks, M. P. H., Daselaar, S. M., Kessels, R. P. C., & Schutter, D. J. L. G. (2018). The posterior parietal cortex and subjectively perceived confidence during memory retrieval. *Learning & Memory*, 25, 382–389. <https://doi.org/10.1101/lm.048033>, PubMed: 30012883
- Yazar, Y., Bergström, Z. M., & Simons, J. S. (2014). Continuous theta burst stimulation of angular gyrus reduces subjective recollection. *PLoS One*, 9, e110414. <https://doi.org/10.1371/journal.pone.0110414>, PubMed: 25333985
- Ye, Q., Zou, F., Dayan, M., Lau, H., Hu, Y., & Kwok, S. C. (2019). Individual susceptibility to TMS affirms the precuneal role in meta-memory upon recollection. *Brain Structure and Function*, 224, 2407–2419. <https://doi.org/10.1007/s00429-019-01909-6>, PubMed: 31254060
- Ye, Q., Zou, F., Lau, H., Hu, Y., & Kwok, S. C. (2018). Causal evidence for mnemonic metacognition in human precuneus. *Journal of Neuroscience*, 38, 6379–6387. <https://doi.org/10.1523/JNEUROSCI.0660-18.2018>, PubMed: 29921714