

1

2 **Causal evidence for mnemonic metacognition in human precuneus**

3

4 Running title: Mnemonic metacognition in precuneus

5

6 **Qun Ye^{1, *}, Futing Zou^{1, *}, Hakwan Lau^{4, 5, 6}, Yi Hu¹, and Sze Chai Kwok^{1, 2, 3}**

7

8 ¹ Shanghai Key Laboratory of Brain Functional Genomics, Key Laboratory of Brain Functional
9 Genomics (Ministry of Education), School of Psychology and Cognitive Science, East China Normal
10 University, Shanghai 200062, China

11 ² Shanghai Key Laboratory of Magnetic Resonance, East China Normal University, Shanghai 200062,
12 China

13 ³ NYU-ECNU Institute of Brain and Cognitive Science at NYU Shanghai, Shanghai 200062, China

14 ⁴ Department of Psychology, University of California-Los Angeles, Los Angeles, California, 90095,
15 United States

16 ⁵ Brain Research Institute, University of California-Los Angeles, Los Angeles, California, 90095,
17 United States

18 ⁶ Department of Psychology, University of Hong Kong, Hong Kong

19 * Q.Y. and F.Z contributed equally to this work as joint first authors.

20

21 Corresponding Author: Sze Chai Kwok (sze-chai.kwok@st-hughs.oxon.org)

22

23 Acknowledgements: This work was supported by the Ministry of Education of PRC Humanities
24 and Social Sciences Research grant 16YJC190006, STCSM Shanghai Pujiang Program
25 16PJ1402800, STCSM Natural Science Foundation of Shanghai 16ZR1410200, NYU
26 Shanghai and the NYU-ECNU Institute of Brain and Cognitive Science at NYU Shanghai
27 (S.C.K.). We thank Yudian Cai for his help in programming the perceptual task and Xinming
28 Xu for suggesting resolution comparison for the perceptual task. Conflict of Interest: The
29 authors declare no competing financial interests.

30

Mnemonic metacognition in precuneus

31 **ABSTRACT:** Metacognition is the capacity to introspectively monitor and control
32 one's own cognitive processes. Previous anatomical and functional neuroimaging
33 findings implicated the important role of precuneus in metacognition processing,
34 especially during mnemonic tasks. However, the issue of whether this medial parietal
35 cortex is a domain-specific region that supports mnemonic metacognition remains
36 controversial. Here, we focally disrupted this parietal area with repetitive transcranial
37 magnetic stimulation in healthy participants of both sexes, seeking to ascertain its
38 functional necessity for metacognition for memory versus perceptual decisions.
39 Perturbing the precuneal activity impaired the metacognitive efficiency selectively in
40 the memory judgment of temporal-order, but not in perceptual discrimination.
41 Moreover, the correlation in individuals' metacognitive efficiency between the domains
42 disappeared when the precuneus was perturbed. Together with the previous finding that
43 lesion to the anterior prefrontal cortex impairs perceptual but not mnemonic
44 metacognition, we double dissociated the macro-anatomical underpinnings for the two
45 kinds of metacognitive capacity in an interconnected network of brain regions.

46

47

Mnemonic metacognition in precuneus

48 **SIGNIFICANCE STATEMENT:** Theories on the neural basis of metacognition have
49 thus far largely centered on the role of prefrontal cortex. Here we refined the theoretical
50 framework through characterizing a unique precuneal involvement in mnemonic
51 metacognition with a noninvasive but inferentially powerful method: transcranial
52 magnetic stimulation. By quantifying meta-cognitive efficiency across two distinct
53 domains (memory vs. perception) that are matched for stimulus characteristics, we
54 reveal an instrumental – and highly selective – role of the precuneus in mnemonic
55 metacognition. These causal evidence corroborate ample clinical reports that parietal
56 lobe lesions often produce inaccurate self-reports of confidence in memory recollection
57 and establish that the precuneus as a nexus for the introspective ability to evaluate the
58 success of memory judgment in humans.

59

60

Mnemonic metacognition in precuneus

61 INTRODUCTION

62

63 Metacognition is the ability to introspectively monitor and control one's own
64 cognitive processes, which is important to guide adaptive behavior, social interaction
65 and mental health (Flavell, 1979; Frith, 2012; Nelson, 1990; Teasdale et al., 2002).
66 Metacognitive capacity has been mostly assessed by self-reporting of level of
67 confidence in one's own decisions that correlate with objective performance. The initial
68 task is often called "type 1 task" and the ensuing confidence judgment task is called
69 "type 2 task" (Galvin, Podd, Drga, & Whitmore, 2003). A widely used approach to
70 estimate the metacognitive efficiency without having it confounded by the primary task
71 performance and response bias is to calculate the comparison between the type 1
72 sensitivity (d') and the type 2 sensitivity (meta- d'). This approach can quantify meta-
73 ability under the signal detection theory (SDT) framework (Maniscalco & Lau, 2012)
74 or by a recently developed hierarchical Bayesian estimation method (Fleming, 2017).

75 Despite a large amount of recent research showing the neural architecture of
76 metacognition in various cognitive domains, like visual perception and memory (Baird,
77 Smallwood, Gorgolewski, & Margulies, 2013; Fleming, Ryu, Golfinos, & Blackmon,
78 2014; Fleming, Weil, Nagy, Dolan, & Rees, 2010; McCurdy et al., 2013; Rahnev, Nee,
79 Riddle, Larson, & D'Esposito, 2016; Yokoyama et al., 2010), the underlying
80 mechanisms of metacognition are incompletely understood. A central question is
81 whether the human metacognition depends on some domain-general neural structures,
82 or is it supported by domain-specific components? While it has been reported that

Mnemonic metacognition in precuneus

83 metacognitive behavioral indices are correlated across the memory versus perception
84 domains (Faivre, Filevich, Solovey, Kuhn, & Blanke, 2016; McCurdy et al., 2013), their
85 functional neural correlates might be largely independent (Baird et al., 2013).

86 In contrast to the established role of the anterior prefrontal cortex in perceptual
87 metacognition (Fleming et al., 2014), compelling evidence converge to reveal an
88 important role of the precuneus in memory metacognition (Fleck, Daselaar, Dobbins,
89 & Cabeza, 2006; Fleming et al., 2010; McCurdy et al., 2013). Functionally, it has been
90 shown that the task-related activity in the precuneus was greater during memory task
91 compared to during perceptual decision (Morales et al., 2018). Anatomically, the
92 structural variation in the precuneal region was correlated more robustly with memory
93 metacognitive efficiency than with visual perceptual metacognitive efficiency,
94 ascribing a critical role of the precuneus in meta-memory (McCurdy et al., 2013).

95 The extant evidence for the function of precuneus in metacognition has been
96 correlational. Here we used a disruptive technique that can non-invasively establish the
97 causal role of the precuneus in metacognition across the memory and perceptual
98 domains. We applied transcranial magnetic stimulation (TMS) over either on the
99 precuneus or a control site before the type 1 tasks to perturb the neural activity so as to
100 ascertain whether the precuneus might be causally involved in metacognition in either
101 or both domains. In both tasks, on each trial the participants were required to make a
102 two-alternative forced choice judgment between a pair of still frames, followed by a
103 confidence rating of their choice decision for that trial; the only difference between the
104 two tasks was the task-demands. In the memory task, the participants were asked to

Mnemonic metacognition in precuneus

105 identify the image that was presented earlier in a video gameplay that they had encoded
106 24 hours earlier; in the visual perceptual task, the same group of participants were
107 required to discriminate the difference in resolution between the two images. We kept
108 the individual sets of pair-images identical in both tasks per participant. To anticipate,
109 we expected a Task \times TMS interaction, which shall arise from a more pronounced
110 deficit in the meta-memory efficiency following TMS to the precuneus than in the meta-
111 perceptual efficiency.

112

113

Mnemonic metacognition in precuneus

114 MATERIALS AND METHODS

115

116 *Participants*

117 18 adults (7 female, age 19-24 years) from the student community of the East China
118 Normal University participated in this study. Each of them participated in both tasks,
119 giving us a within-subjects comparison. All participants had normal or corrected-to-
120 normal vision, no reported history of neurological disease, no other contraindications
121 for MRI or TMS, and all gave written informed consent. They were compensated
122 financially for their participation. No subject withdrew due to complications from the
123 TMS procedures, and no negative treatment responses were observed. The study was
124 approved by University Committee on Human Research Protection of East China
125 Normal University (UCHRP-ECNU).

126

127 *Overview of study*

128 The memory task and perceptual task were separated into two experimental
129 sessions. Immediately before performing the main task, the participants received 20
130 min of repetitive TMS that targeted at one of the two cortical sites (Within-subjects:
131 TMS-vertex vs. TMS-precuneus) in a counter-balanced manner (Experimental session
132 1 and session 2 in Figure 1A). The session order, the numbers of trials, the dimension,
133 position and sequence of stimulus presented, the response time allowed for the type 1
134 task judgment and the inter-trial intervals (ITIs) were all identical in both tasks. High-
135 resolution structural scans were acquired for each participant to guide the TMS
136 procedure.

Mnemonic metacognition in precuneus

137

138 *Experimental Design and Statistical Analysis*

139 Tasks and procedure

140 Each participant completed 480 trials in total in each of the two tasks (2 sessions ×
141 4 blocks × 60 trials per block).

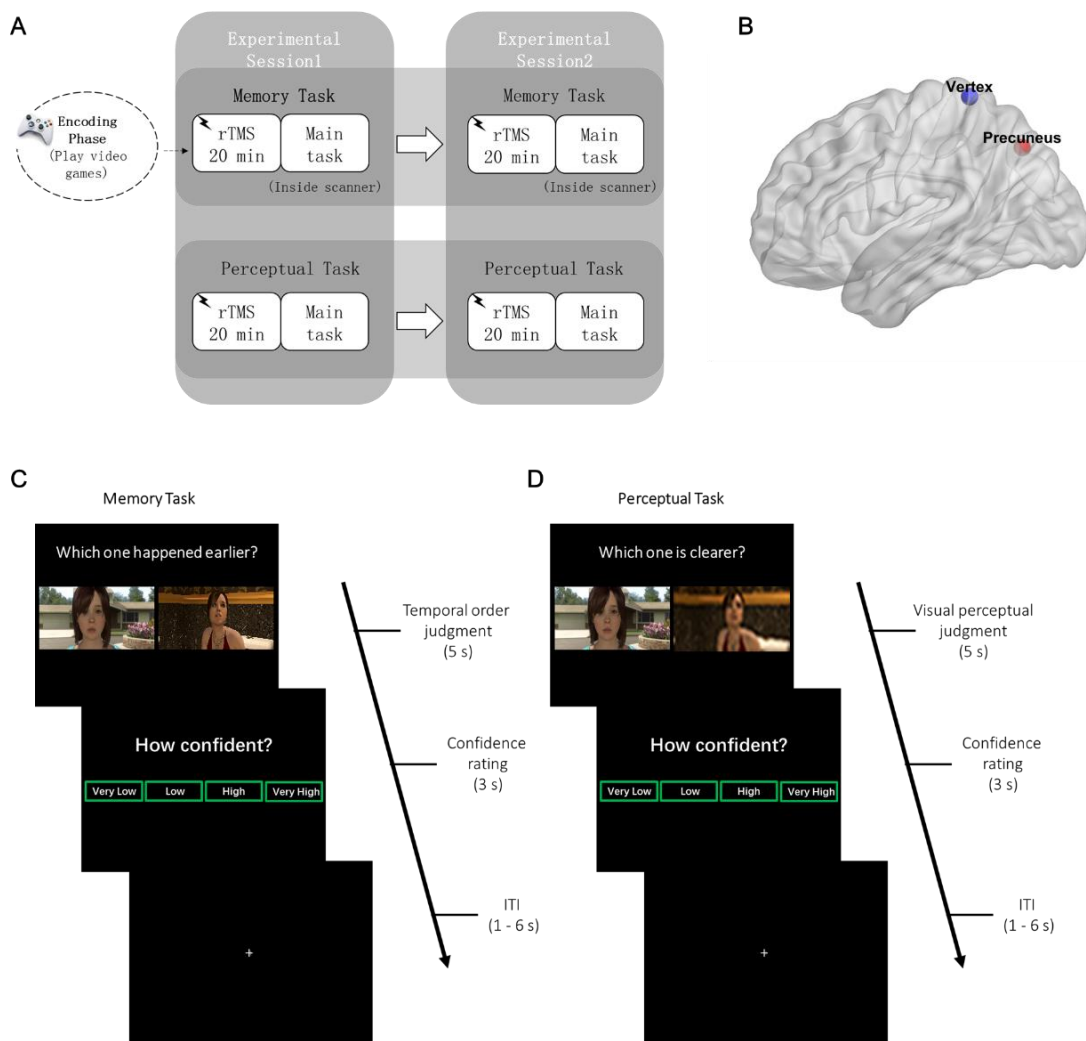
142 The memory task required participants to choose the image that happened earlier
143 (temporal order judgment, TOJ) in the video game they had played one day before. The
144 retrieval task was administrated inside an MRI scanner, where visual stimuli were
145 presented using E-prime software (Psychology Software Tools, Inc., Pittsburgh, PA),
146 as back-projected via a mirror system to the participant. Each trial was presented for 5
147 s during which participants performed the TOJ. They were then allowed 3 s to report
148 their confidence level following the memory judgment. Participants performed the TOJ
149 task using their index and middle fingers of one of their hands via an MRI compatible
150 five-button response keyboard (Sinorad, Shenzhen, China). The participants reported
151 their confidence level (“Very Low”, “Low”, “High”, or “Very High”) regarding their
152 own judgment of the correctness of TOJ with four fingers of the other hand. The
153 left/right hand response contingency was counterbalanced across participants. The
154 participants were encouraged to report their confidence level in a relative way and make
155 use of the whole confidence scale. Following these judgments, a fixation cross with a
156 variable duration (1 – 6 s) was presented (Figure 1C).

157 The same sets of paired-images were used in the perceptual task, in which the
158 participants were required to choose either the clearer (or blurrier, counter-balanced

Mnemonic metacognition in precuneus

159 across participants) image among a pair of images on each trial. The participants made
160 an image-resolution comparison judgment and then a confidence rating of their type 1
161 task decision (Figure 1D) with a 17-inch CRT monitor in a dimly illuminated room.
162 There was a practice block before each session for the participant to get familiar with
163 the task demands.

164



165

166 **Figure 1. Study design.** (A) Experimental overview. In experimental sessions 1 and 2
167 of both tasks, participants received 20 min of rTMS to either one of two cortical sites
168 before performing the main task. The stimulation sites (within-subjects design: TMS-

Mnemonic metacognition in precuneus

169 precuneus vs. TMS-vertex) and choices of video game chapters were counterbalanced
170 within subjects across task. **(B)** Location of precuneus (target site) is depicted in red
171 and vertex (control site) in blue. The target site for precuneus stimulation (MNI x y z =
172 6, -70, 44) was based on (Kwok, Shallice, & Macaluso, 2012). **(C)** In memory task, the
173 participants performed a temporal order judgment task, by choosing the image that
174 happened earlier in the video game. **(D)** In perceptual task, participants identified which
175 frame out of the two was clearer (or blurrier). After the type 1 tasks, participants rated
176 their confidence level on a 4-point scale.

177

178 Quantification of metacognitive efficiency

179 Memory and perceptual performance were quantified using the percentage of
180 correct judgments and the d' of type 1 signal detection theory (Green and Swets, 1966;
181 Macmillan and Creelman, 2004). We evaluated the metacognitive ability of both tasks
182 by meta- d' . Meta- d' quantifies metacognitive sensitivity (the ability to discriminate
183 between correct and incorrect judgments) in a signal detection theory (SDT) framework.
184 Meta- d' was widely used as a measure of metacognitive capacity because it is expressed
185 in the same scale as d' , so the type 2 sensitivity (meta- d') could be compared with the
186 type 1 sensitivity (d') directly (Fleming & Lau, 2014; Maniscalco & Lau, 2012). If meta-
187 d' equals to d' , it means that the metacognitive sensitivity is ideal. Here, we calculated
188 the M-diff (meta- d' minus d') for estimating the metacognitive efficiency (the level of
189 metacognition given a particular level of performance or signal processing capacity).
190 The toolbox on MATLAB for the SDT-based meta- d' estimation was available at

Mnemonic metacognition in precuneus

191 <http://www.columbia.edu/~bsm2105/type2sdt/>. Moreover, we computed the
192 metacognitive efficiency using a hierarchical Bayesian estimation method
193 (<https://github.com/smfleming/HMeta-d>), which can avoid edge-correction confounds
194 and enhance statistical power (Fleming & Daw, 2017). The 4-point confidence ratings
195 were collapsed into two categories (high and low) for all analysis.

196 Additionally, to ensure our results were not due to any idiosyncratic violation of
197 the assumptions of SDT, we calculated the phi coefficient index, which represents each
198 subject's correlation between their discrimination accuracy and confidence ratings
199 (Kornell, Son, & Terrace, 2007). The phi coefficient was calculated according to the
200 following formula using the number of trials classified in each case [n(case)]:

$$201 \quad \text{phi coefficient } (\Phi) = \frac{n(\text{Correct High}) \times n(\text{Incorrect Low}) - n(\text{Correct Low}) \times n(\text{Incorrect High})}{\sqrt{n(\text{Correct}) \times n(\text{Incorrect}) \times n(\text{High}) \times n(\text{Low})}}$$

202 Data were processed with in-house software on MATLAB and statistical inference
203 was made using Rstudio.

204

205

206 *Stimuli*

207 The stimuli were extracted from an action-adventure video game (Beyond: Two
208 Souls), which was created by the French game developer Quantic Dream and played in
209 the PlayStation 4 video game console developed by Sony Computer Entertainment. The
210 Participants played 14 chapters in total across two sessions: 7 in experimental session
211 1 and then another 7 in session 2. These subject-specific video were recorded and were
212 used for extraction of still images for the tasks.

Mnemonic metacognition in precuneus

213 For the memory task, we selected static images from the subject-specific recorded
214 videos which the participants had played the day before. Each second in the video
215 consisted of 29.97 static images (frames). In each game-playing session, 240 pairs of
216 images were extracted from the seven chapters and were paired up for the task based
217 on the following criteria: (1) the two images had to be extracted from either the same
218 chapters or adjacent chapters (Within- vs. Across-chapter condition); (2) the temporal
219 distance (TD) between the two images were matched between Within- and Across-
220 chapter condition; (3) in order to maximize the range of TD, we first selected the second
221 longest chapter of the video and determined the longest TD according to a power
222 function (power = 1.5), at the same time ensuring the shortest TD to be longer than 30
223 frames. We generated 60 progressive levels of TD among these pairs.

224 For the perceptual task, the same sets of subject-specific stimuli from the memory
225 task were used. On each trial, the resolution of one of the images was reduced using
226 Python Imaging Library through resizing the image to change the pixel dimension. For
227 instance, setting an image to three-tenths of the original size changed the pixel
228 dimension to three-tenths, then the image was resized to its primary size so that the
229 pixels per inch (PPI) decreased proportionately. The higher the PPI, the smaller the
230 difference between the image resolution of the resized one and the original was, which
231 also meant this pair would be harder to discriminate than another pair with a lower PPI
232 value. Based on participants performance in the memory task, we pre-determined five
233 difficulty levels for the perceptual task ($n = 1\sim 5$, 1 is the hardest). The image resolution
234 was adjusted online using an n-down/1-up adaptive staircase procedure, aiming to

Mnemonic metacognition in precuneus

235 equate individual performance with his or her performance in the memory task.

236

237 *Anatomical MRI images*

238 A 3-Tesla Siemens Trio magnetic resonance imaging scanner (Siemens Medical
239 Solutions, Erlangen, Germany) was used to acquire the high-resolution T1-weighted
240 images for each participant (192 sagittal slices, TR = 2530 ms, TE = 2.34 ms, TI = 1100
241 ms, flip angle = 7°, FOV = 256 × 256 mm, 0.9 mm thickness, voxel size = 1 × 1 × 1
242 mm) to stereotaxically guide the transcranial stimulation.

243

244 *Repetitive transcranial magnetic stimulation (rTMS): procedure, protocol and sites.*

245 TMS is a form of noninvasive cortical stimulation method that can modulate
246 cognitive functions. Previous studies have demonstrated that repetitive stimulation with
247 TMS over the precuneus (Kraft et al., 2015) or lateral parietal cortices (Nilakantan,
248 Bridge, Gagnon, VanHaerents, & Voss, 2017; Wang et al., 2014) produce robust effects
249 on memory related ability, showing the efficacy of rTMS targeted at relatively deep
250 regions. The present study adopted the identical stimulation magnitude and protocols
251 used in our previous study (Ye, Hu, Ku, Appiah, & Kwok, 2018).

252 The rTMS was applied using a Magstim Rapid² magnetic stimulator connected to
253 a 70mm double air film coil (Magstim Company). The structural T1-weighted magnetic
254 resonance images were obtained for each subject and used in theBrainsight2.0, a
255 computerized frameless stereotaxic system (Rogue Research), to localize the target
256 brain regions. Target stimulation regions for rTMS were selected in the system by

Mnemonic metacognition in precuneus

257 transformation of the Montreal Neurological Institute (MNI) stereotaxic coordinates to
258 participant's normalized brain. The sites stimulated were located in the precuneus at the
259 MNI coordinate $x=6$, $y=-70$, $z=44$ (Kwok et al., 2012), and in a control area on the
260 vertex, which was identified at the point of the same distance to the left and the right
261 pre-auricular, and of the same distance to the nasion and the inion (Figure 1B). For
262 combining each subject's head with the MRI images, location information of each
263 subject's head was obtained individually by touching four fiducial points, which are the
264 tip of the nose, the nasion, and the inter-tragal notch of each ear using an infrared pointer.
265 The real-time locations of reflective markers which were attached to the coil and the
266 subject were monitored by an infrared camera using a Polaris Optical Tracking System
267 (Northern Digital, Waterloo, Canada).

268 In each session, TMS was delivered to either the precuneus or vertex before the
269 main task. TMS was applied at 1 Hz frequency for a continuous duration of 20 min
270 (1,200 pulses in total) at 110% of active motor threshold (MT), which was defined as
271 the lowest TMS intensity delivered over the motor cortex necessary to elicit visible
272 twitches of the right index finger in at least 5 out of 10 consecutive pulses (Rossini et
273 al., 2015). The MT was measured both at the beginning of experiment session 1 in the
274 memory and perceptual tasks. The order of stimulation sites was counterbalanced
275 within subjects across tasks. During stimulation, participants wore earplugs to attenuate
276 the sound of the stimulating coil discharge. The coil was held to the scalp of the
277 participant with a custom coil holder and the subject's head was propped a comfortable
278 position. Coil orientation was parallel to the midline with the handle pointing downward.

Mnemonic metacognition in precuneus

279 Immediately after the 20 min of rTMS, subjects performed four blocks of memory task
280 in the MRI scanner (mean delay from rTMS to beginning of test: TMS-precuneus =
281 15.29 min, TMS-vertex= 20.76 min), or performed a visual perceptual task in a
282 psychophysics room (mean delay from rTMS to beginning of test: TMS-precuneus =
283 6.7 min, TMS-vertex= 6.3 min). For safety reason and to avoid carry-over effects of
284 rTMS across sessions, experimental sessions 1 and 2 were conducted on two separate
285 days for both tasks (memory: mean interval = 8 days; perceptual: mean interval= 3.9
286 days).
287
288

Mnemonic metacognition in precuneus

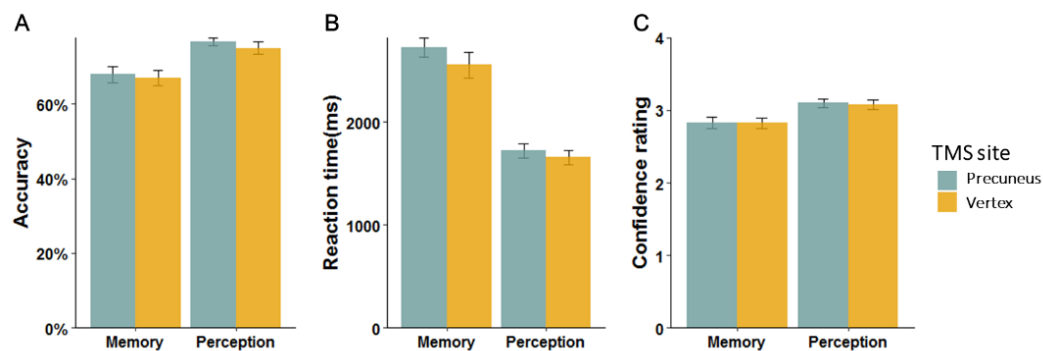
289 RESULTS

290

291 Overall, the participants missed 2.9% of TOJ trials and 2.2% confidence rating in
292 the memory task, whereas the participants missed 0.7% trials in the perceptual type 1
293 task. Trials missing either one of the measures were excluded from the analysis.

294 We first examined whether the type 1 task performance in accuracy (% correct,
295 Figure 1A), reaction time (RT, Figure 1B), and confidence rating (Figure 1C) might be
296 affected by TMS. As expected, the task performance was not different between the two
297 TMS conditions in neither memory (accuracy, $t(17) = 0.349$, $p = 0.640$; RT, $t(17) =$
298 1.997 , $p = 0.090$; confidence rating, $t(17) = 0.069$, $p = 0.780$) nor perceptual part
299 (accuracy, $t(17) = 1.091$, $p = 0.480$; RT, $t(17) = 0.842$, $p = 0.490$; confidence rating, t
300 $(17) = 0.461$, $p = 0.560$).

301



302

303 **Figure 2. Basic task performance.** Type 1 task performance was not affected by TMS
304 in either of the tasks: (A) Accuracy (B) Reaction time (C) Mean level of confidence
305 ratings. Error bars denote the standard error of the mean (SEM).

306

307 We then used a robust metacognitive index (meta-d' – d') to investigate whether

Mnemonic metacognition in precuneus

308 TMS on the precuneus might affect the metacognitive performance on the tasks. We
309 performed a 2 (Task: memory/perception) \times 2 (TMS: precuneus/vertex) repeated
310 measures ANOVA for metacognitive efficiency – quantified as meta- d' - d' – from the
311 SDT-based model and the hierarchical model separately. In the SDT-based model, we
312 found an interaction effect between Task and TMS site ($F(1, 17) = 7.25, p = 0.015$;
313 Figure 3A middle). The interaction was driven by lower metacognitive efficiency
314 following TMS to precuneus relative to TMS to vertex in the memory task ($t(17) = -$
315 $2.155, p = 0.046$), whereas no difference in metacognitive efficiency was found in the
316 perceptual task ($t(17) = 1.378, p = 0.186$). Metacognitive efficiency using the
317 hierarchical model revealed the same pattern of results (Task \times TMS interaction: $F(1,$
318 $17) = 7.312, p = 0.015$; memory: $t(17) = -2.119, p = 0.049$; perception: $t(17) = 1.334,$
319 $p = 0.200$). To better characterize the effect of TMS on metacognitive efficiency, we
320 performed sign tests to verify the extent of changes between TMS to precuneus and
321 vertex. The metacognitive efficiency was reduced by TMS to precuneus in a majority
322 of participants in the memory task (13/18 reduced, $p = 0.035$, sign test; Figure 3A left),
323 but not in the perceptual task (10/18 reduced, $p = 0.290$, sign test; Figure 3A right).

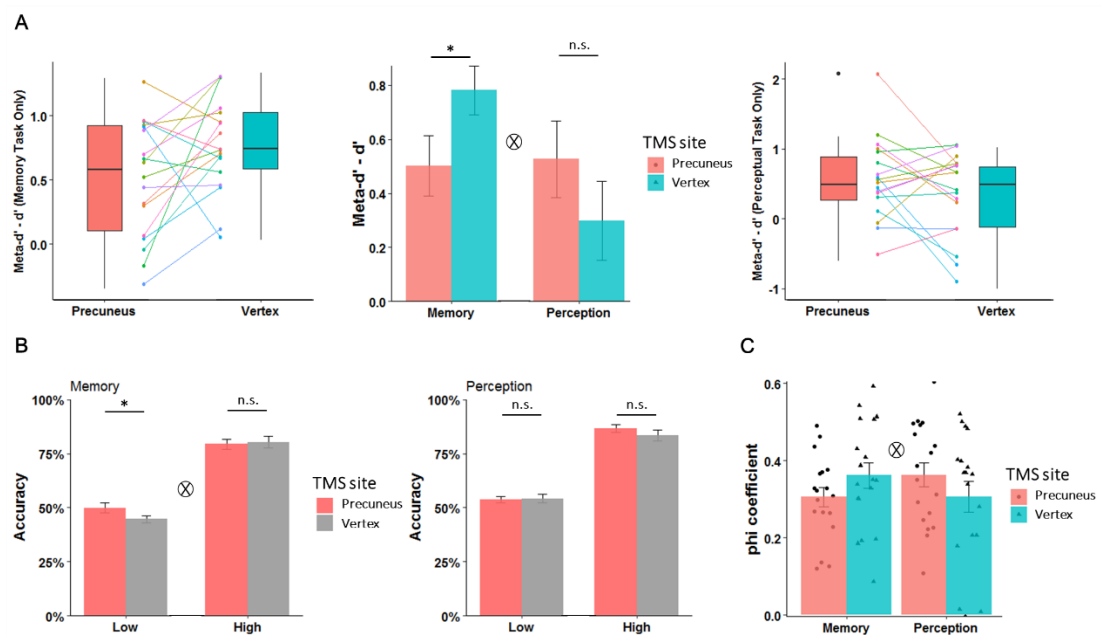
324 These meta-indices are in principle based on how people rate their confidence,
325 which refer to how meaningful a person's confidence rating is in distinguishing between
326 correct and incorrect responses. We accordingly ran a 3-way repeated measures
327 ANOVA (Task: Memory/Perception \times TMS: precuneus/vertex \times Confidence:
328 Low/High) on the type 1 task percentage correct and obtained a significant 3-way
329 interaction ($F(1, 17) = 10.652, p = 0.005$). The TMS effect was disproportionately

Mnemonic metacognition in precuneus

330 stronger in the memory task, as evident in a TMS \times Confidence interaction ($F(1, 17) =$
331 $4.487, p = 0.049$; Figure 3B left), than in the perceptual task ($F(1, 17) = 1.24, p = 0.281$;
332 Figure 3B right). Such effects in the memory task were driven by higher accuracy
333 following TMS-precuneus than TMS-vertex in the low confidence ratings condition (t
334 $(17) = 2.354, p = 0.031$), but not in the high confidence ratings condition ($t(17) = -0.4,$
335 $p = 0.694$).

336 To add credibility to these results, we replicated these findings with the Phi
337 coefficient ($F(1, 17) = 13.81, p = 0.002$; Figure 3C), confirming that our results were
338 not biased by any idiosyncratic violations of the assumptions of SDT. These findings
339 of lower metacognitive efficiency in the memory task following TMS to precuneus
340 compared to vertex confirm our prediction that the precuneus causally mediates
341 memory metacognition, but not perceptual metacognition.

342



343

344 **Figure 3. Differential effects of TMS on metacognitive performance. (A)**

Mnemonic metacognition in precuneus

345 Metacognitive efficiency in SDT-based model (meta- d' - d') under TMS-precuneus was
346 lower than metacognitive efficiency under TMS-vertex in memory task but not in
347 perceptual task. Each colored line depict within-subjects changes across conditions. **(B)**
348 TMS \times Confidence ratings interaction in memory task. The accuracy for low confidence
349 ratings under TMS-precuneus is significantly higher than that under TMS-vertex; no
350 such effect for high confidence ratings. No significant effect of TMS in perceptual task.
351 **(C)** TMS \times Task interaction in phi coefficient. \otimes indicates significant interaction $p <$
352 0.05 , $*p < 0.05$, *n.s.* = not significant. Error bars represent SEM.

353

354 To further probe whether the TMS effect on memory metacognition would be
355 reflected by within-subjects changes in the between-tasks covariations, we calculated
356 the between-tasks (Memory/Perception) correlations for all individuals' type 1 task
357 sensitivity (d') and metacognitive efficiency respectively. We found that participants'
358 type 1 sensitivity (d') between the perceptual and memory tasks are positively correlated,
359 and that the magnitude of the correlation was not affected by TMS (TMS-vertex: $r =$
360 0.90 , $p < 0.001$; TMS-precuneus: $r = 0.82$, $p < 0.001$; comparison between correlations:
361 $z = -0.86$, $p = 0.390$; Figure 4A). This again indicates that TMS had no effect on the
362 basic task performance, in line with the pattern shown in Figure 2. In contrast, while
363 the metacognitive efficiency for the two tasks were significantly correlated in the TMS-
364 vertex condition ($r = 0.72$, $p < 0.001$; Figure 4B), as of what was reported previously
365 (McCurdy et al., 2013), such correlational pattern was notably eliminated under TMS-
366 precuneus treatment ($r = -0.13$, $p = 0.63$; Figure 4B), and the correlation coefficient was

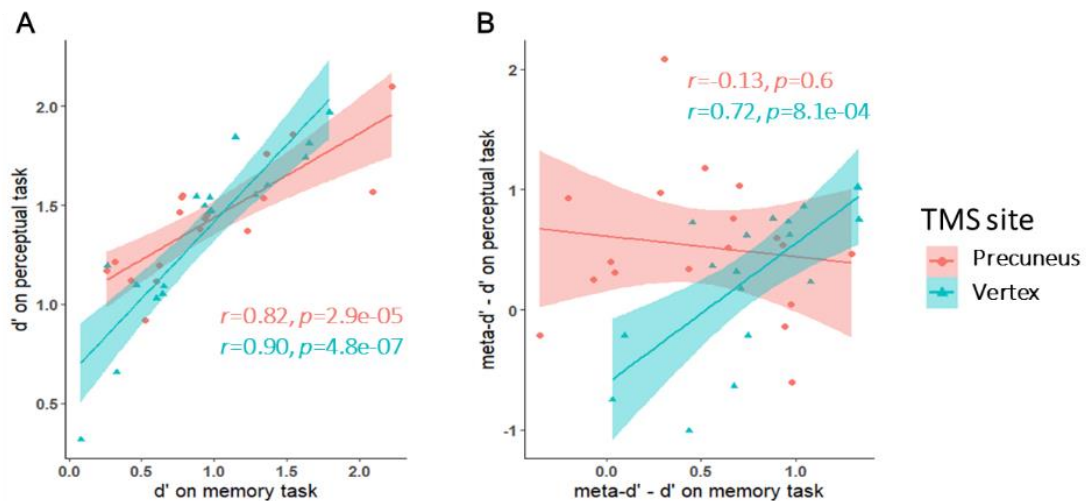
Mnemonic metacognition in precuneus

367 significantly lower than that of the TMS-vertex condition ($z = -3.38$, $p < 0.001$).

368 Taken altogether, these results reveal that TMS to precuneus affects the metacognitive

369 performance specifically for the memory domain.

370



371

372 **Figure 4. Correlation between memory and perceptual task performance and**

373 **metacognitive indices. (A)** TMS had no effect on the participants' type 1 sensitivity

374 (d'). The positive correlation between d' on the perceptual and memory tasks was not

375 affected by TMS. **(B)** In the TMS-vertex condition, the metacognitive efficiencies

376 across the group were significantly correlated between memory and perceptual tasks.

377 However, following TMS-precuneus, such between-tasks metacognitive efficiencies

378 were no longer correlated.

379

380

Mnemonic metacognition in precuneus

381 **DISCUSSION**

382

383 We employed an inferentially powerful technique to investigate the critical role of
384 precuneus in the metacognitive ability in two distinct domains: memory and perception.
385 We demonstrated that magnetic fields stimulation targeted at the precuneus impairs
386 metacognitive efficiency in a long-term memory task without eliciting amnesia. TMS
387 targeted to the precuneus affects the efficacy of confidence ratings specifically in a
388 manner that subjects became less certain with their correct memory decisions. Critically,
389 the TMS's task-specific effect on the memory task, but not in the perceptual counterpart,
390 implies that the neurobiological prerequisite for metacognitive ability is indeed
391 supported by domain-specific components, some of which might be housed in the
392 precuneus.

393 Previous studies showed that the precuneus is implicated in memory metacognition,
394 derived from correlative measures such as anatomical connectivity and related
395 functional activity analyses. For instance, a previous study identified a link between
396 memory metacognitive efficiency and the precuneal gray matter density in healthy
397 individuals (McCurdy et al., 2013), whereas a similar relationship was found between
398 mnemonic metacognitive efficiency and functional connectivity between precuneus
399 and medial aPFC (Baird et al., 2013). A recent study identified respective domain-
400 specific and domain-general functional signals engaged by metacognitive judgments in
401 perceptual and memory tasks using multivariate pattern analysis (Morales et al., 2018).
402 They found that the domain-specific pattern for metacognition was encoded in the

Mnemonic metacognition in precuneus

403 prefrontal cortex whereas the domain-general pattern was distributed in a widespread
404 network in the frontal and posterior midline, including the precuneus. These studies
405 thus suggest that the precuneus might be dually involved in both memory and
406 perceptual metacognition for the close relationship shared between precuneus and
407 perceptual metacognition (McCurdy et al., 2013; Morales et al., 2018). Considering that
408 no prior study has executed controlled, targeted perturbation on this medial parietal
409 region, we thus set out to examine its functional necessity for mnemonic metacognition
410 by disrupting the precuneal function with TMS. Our TMS-induced focal disruption
411 imposed a significant and selective effect on metacognitive ability in memory, but
412 without altering the perceptual metacognitive performance at all. In a complementary
413 manner, lesions to the anterior PFC are found to impair perceptual metacognitive ability
414 while sparing the metacognitive efficiency for memory, indicating a domain-specific
415 deficit in metacognition by anterior PFC lesions (Fleming et al., 2014). These findings
416 conjointly provide causal evidence for a double dissociation in neural areas between
417 memory and perceptual metacognition.

418 Our work carries implications for extending the metacognitive principle to episodic
419 memory beyond the realm of working memory. The present finding is compatible with
420 other human lesion and neuroimaging studies implicating the role of the parietal cortex
421 in memory retrieval. For example, a lesion study showed that a patient with parietal
422 cortex damage reporting that she felt less confident and experienced a lack of richness
423 in the memories she retrieved (Davidson et al., 2008). This is consistent with other
424 reports showing that lesions to the parietal cortex significantly diminish the

Mnemonic metacognition in precuneus

425 retrospective confidence ratings, despite the performance remaining intact in a source
426 recollection task (Simons, Peers, Mazuz, Berryhill, & Olson, 2010). Furthermore, in a
427 functional neuroimaging study designed to tease apart different components of memory
428 retrieval, activation in the precuneus was found to be associated with vividness
429 judgments during episodic memory retrieval (Richter, Cooper, Bays, & Simons, 2016),
430 consistent with the evidence that the precuneus serves to represent personally relevant
431 content accompanied by vivid recollection (Sreekumar, Nielson, Smith, Dennis, &
432 Sederberg, 2017) and detailed abstraction of temporal information required to support
433 recollective TOJ (Ye et al., 2018). Given that vivid reminiscence is a defining feature
434 of successful recollection of episodic events, the involvement of the precuneus during
435 memory retrieval tasks might actually lie in its role in subserving the subjective
436 experience of remembering. This argument aligns with the recent finding that EEG
437 activity in the precuneus is linked with conscious dreaming experience (i.e., subjects
438 remembered the content of dreaming experience after being awakened from a dream)
439 (Siclari et al., 2017), in line with its role in mental imagery during retrieval (Fletcher et
440 al., 1995). These behavioral and neural evidence convergently implicate the medial
441 parietal cortex in the assessment of recollection during retrieval in support of its role in
442 meta-memory. In line with the contribution to recollection of past episodes, our data
443 corroborated the exiting evidence for the participation of precuneus in higher-order
444 conscious processes during episodic memory retrieval.

445 Individual metacognitive efficiency scores were found to be positively correlated
446 across the memory and perceptual domains under the control condition in some studies

Mnemonic metacognition in precuneus

447 (Faivre et al., 2016; McCurdy et al., 2013; Ruby, Giles, & Lau, 2017; Samaha & Postle,
448 2017), but not in others (Baird et al., 2013; Vo et al., 2014; Fitzgerald et al., 2017;
449 Sadeghi et al., 2017; Morales et al., 2018). It is plausible that such discord in correlation
450 between metacognitive scores across domains is partly driven by the different types of
451 judgments required (Ruby et al., 2017). A caveat is that the comparison did not take the
452 stimulus characteristics across different tasks into account. Indeed, most studies of
453 metacognition employed different categories of materials for the respective tasks, like
454 word-list memory task versus dots-contained perceptual task (Baird et al., 2013;
455 Fleming et al., 2014; McCurdy et al., 2013; Sadeghi et al., 2017). Following two recent
456 studies (Ruby et al., 2017; Morales et al., 2018), here we also employed stimuli
457 belonging to the same category – in fact identical sets of subject-specific stimuli
458 material – for the memory and perceptual tasks, which would eliminate any confounds
459 attributable to stimulus or featural characteristics.

460 To conclude, our findings reinforce the notion that precuneal region plays a critical
461 role in mediating metacognition in episodic memory retrieval. To our knowledge, our
462 study is the first one to causally verify the domain-specificity hypothesis of the
463 precuneus in mnemonic metacognition in the human. Together with the contribution of
464 anterior prefrontal cortex to perceptual metacognition, a challenge for future work is to
465 understand how these different kinds of metacognition can be integrated into a unified
466 framework.

Mnemonic metacognition in precuneus

467 REFERENCES

468

469 Baird, B., Smallwood, J., Gorgolewski, K. J., & Margulies, D. S. (2013). Medial and
470 lateral networks in anterior prefrontal cortex support metacognitive ability for
471 memory and perception. *J Neurosci*, *33*(42), 16657-16665.
472 doi:10.1523/JNEUROSCI.0786-13.2013

473 Davidson, P. S., Anaki, D., Ciaramelli, E., Cohn, M., Kim, A. S., Murphy, K. J., . . .
474 Levine, B. (2008). Does lateral parietal cortex support episodic memory?
475 Evidence from focal lesion patients. *Neuropsychologia*, *46*(7), 1743-1755.
476 doi:10.1016/j.neuropsychologia.2008.01.011

477 Faivre, N., Filevich, E., Solovey, G., Kuhn, S., & Blanke, O. (2016). Behavioural,
478 modeling, and electrophysiological evidence for domain-generalty in human
479 metacognition. *bioRxiv*. doi:10.1101/095950

480 Fitzgerald, L. M., Arvaneh, M., & Dockree, P. M. (2017). Domain-specific and domain-
481 general processes underlying metacognitive judgments. *Conscious Cogn*, *49*,
482 264-277. doi:10.1016/j.concog.2017.01.011

483 Flavell, J. H. (1979). Metacognition and cognitive monitoring: A new area of cognitive-
484 developmental inquiry. *American Psychologist*, *34*(10), 906.

485 Fleck, M. S., Daselaar, S. M., Dobbins, I. G., & Cabeza, R. (2006). Role of prefrontal
486 and anterior cingulate regions in decision-making processes shared by memory
487 and nonmemory tasks. *Cereb Cortex*, *16*(11), 1623-1630.
488 doi:10.1093/cercor/bhj097

Mnemonic metacognition in precuneus

- 489 Fleming, S. M. (2017). HMeta-d: hierarchical Bayesian estimation of metacognitive
490 efficiency from confidence ratings. *Neuroscience of Consciousness*, 3(1).
491 doi:10.1093/nc/nix007
- 492 Fleming, S. M., & Daw, N. D. (2017). Self-evaluation of decision-making: A general
493 Bayesian framework for metacognitive computation. *Psychol Rev*, 124(1), 91-
494 114. doi:10.1037/rev0000045
- 495 Fleming, S. M., & Lau, H. C. (2014). How to measure metacognition. *Front Hum*
496 *Neurosci*, 8, 443. doi:10.3389/fnhum.2014.00443
- 497 Fleming, S. M., Ryu, J., Golfinos, J. G., & Blackmon, K. E. (2014). Domain-specific
498 impairment in metacognitive accuracy following anterior prefrontal lesions.
499 *Brain*, 137(Pt 10), 2811-2822. doi:10.1093/brain/awu221
- 500 Fleming, S. M., Weil, R. S., Nagy, Z., Dolan, R. J., & Rees, G. (2010). Relating
501 introspective accuracy to individual differences in brain structure. *Science*,
502 329(5998), 1541-1543. doi:10.1126/science.1191883
- 503 Fletcher, P. C., Frith, C. D., Baker, S. C., Shallice, T., Frackowiak, R. S., & Dolan, R.
504 J. (1995). The mind's eye--precuneus activation in memory-related imagery.
505 *Neuroimage*, 2(3), 195-200. doi:10.1006/nimg.1995.1025
- 506 Frith, C. D. (2012). The role of metacognition in human social interactions. *Philos*
507 *Trans R Soc Lond B Biol Sci*, 367(1599), 2213-2223.
508 doi:10.1098/rstb.2012.0123
- 509 Galvin, S. J., Podd, J. V., Drga, V., & Whitmore, J. (2003). Type 2 tasks in the theory
510 of signal detectability: Discrimination between correct and incorrect decisions.

Mnemonic metacognition in precuneus

- 511 *Psychonomic Bulletin & Review*, 10(4), 843-876. doi:Doi 10.3758/Bf03196546
- 512 Kornell, N., Son, L. K., & Terrace, H. S. (2007). Transfer of metacognitive skills and
513 hint seeking in monkeys. *Psychol Sci*, 18(1), 64-71. doi:10.1111/j.1467-
514 9280.2007.01850.x
- 515 Kraft, A., Dyrholm, M., Kehrer, S., Kaufmann, C., Bruening, J., Kathmann, N., . . .
516 Brandt, S. A. (2015). TMS over the right precuneus reduces the bilateral field
517 advantage in visual short term memory capacity. *Brain Stimul*, 8(2), 216-223.
518 doi:10.1016/j.brs.2014.11.004
- 519 Kwok, S. C., Shallice, T., & Macaluso, E. (2012). Functional anatomy of temporal
520 organisation and domain-specificity of episodic memory retrieval.
521 *Neuropsychologia*, 50(12), 2943-2955.
522 doi:10.1016/j.neuropsychologia.2012.07.025
- 523 Maniscalco, B., & Lau, H. (2012). A signal detection theoretic approach for estimating
524 metacognitive sensitivity from confidence ratings. *Conscious Cogn*, 21(1), 422-
525 430. doi:10.1016/j.concog.2011.09.021
- 526 McCurdy, L. Y., Maniscalco, B., Metcalfe, J., Liu, K. Y., de Lange, F. P., & Lau, H.
527 (2013). Anatomical coupling between distinct metacognitive systems for
528 memory and visual perception. *J Neurosci*, 33(5), 1897-1906.
529 doi:10.1523/JNEUROSCI.1890-12.2013
- 530 Morales, J., Lau, H., & Fleming, S. M. (2018). Domain-specific patterns of activity
531 support metacognition in human prefrontal cortex. *J Neurosci*, 2360-17.
532 doi:10.1523/JNEUROSCI.2360-17.2018

Mnemonic metacognition in precuneus

- 533 Nelson, T. O. (1990). Metamemory: A theoretical framework and new findings
534 *Psychology of learning and motivation* (Vol. 26, pp. 125-173): Elsevier.
- 535 Nilakantan, A. S., Bridge, D. J., Gagnon, E. P., VanHaerents, S. A., & Voss, J. L. (2017).
536 Stimulation of the posterior cortical-hippocampal network enhances precision
537 of memory recollection. *Curr Biol*, 27(3), 465-470.
538 doi:10.1016/j.cub.2016.12.042
- 539 Rahnev, D., Nee, D. E., Riddle, J., Larson, A. S., & D'Esposito, M. (2016). Causal
540 evidence for frontal cortex organization for perceptual decision making. *Proc*
541 *Natl Acad Sci U S A*, 113(21), 6059-6064. doi:10.1073/pnas.1522551113
- 542 Richter, F. R., Cooper, R. A., Bays, P. M., & Simons, J. S. (2016). Distinct neural
543 mechanisms underlie the success, precision, and vividness of episodic memory.
544 *Elife*, 5. doi:10.7554/eLife.18260
- 545 Rossini, P. M., Burke, D., Chen, R., Cohen, L. G., Daskalakis, Z., Di Iorio, R., . . .
546 Ziemann, U. (2015). Non-invasive electrical and magnetic stimulation of the
547 brain, spinal cord, roots and peripheral nerves: Basic principles and procedures
548 for routine clinical and research application. An updated report from an I.F.C.N.
549 Committee. *Clin Neurophysiol*, 126(6), 1071-1107.
550 doi:10.1016/j.clinph.2015.02.001
- 551 Ruby, E., Giles, N., & Lau, H. (2017). Finding domain-general metacognitive
552 mechanisms requires using appropriate tasks. *bioRxiv*. doi:10.1101/211805
- 553 Sadeghi, S., Ekhtiari, H., Bahrami, B., & Ahmadabadi, M. N. (2017). Metacognitive
554 deficiency in a perceptual but not a memory task in methadone maintenance

Mnemonic metacognition in precuneus

- 555 patients. *Sci Rep*, 7(1), 7052. doi:10.1038/s41598-017-06707-w
- 556 Samaha, J., & Postle, B. R. (2017). Correlated individual differences suggest a common
557 mechanism underlying metacognition in visual perception and visual short-term
558 memory. *Proc Biol Sci*, 284(1867). doi:10.1098/rspb.2017.2035
- 559 Siclari, F., Baird, B., Perogamvros, L., Bernardi, G., LaRocque, J. J., Riedner, B., . . .
560 Tononi, G. (2017). The neural correlates of dreaming. *Nat Neurosci*, 20(6), 872-
561 878. doi:10.1038/nn.4545
- 562 Simons, J. S., Peers, P. V., Mazuz, Y. S., Berryhill, M. E., & Olson, I. R. (2010).
563 Dissociation between memory accuracy and memory confidence following
564 bilateral parietal lesions. *Cereb Cortex*, 20(2), 479-485.
565 doi:10.1093/cercor/bhp116
- 566 Sreekumar, V., Nielson, D. M., Smith, T. A., Dennis, S. J., & Sederberg, P. B. (2017).
567 The experience of vivid autobiographical reminiscence is supported by personal
568 semantic representations in the precuneus. *bioRxiv*. doi:10.1101/197665
- 569 Teasdale, J. D., Moore, R. G., Hayhurst, H., Pope, M., Williams, S., & Segal, Z. V.
570 (2002). Metacognitive awareness and prevention of relapse in depression:
571 empirical evidence. *J Consult Clin Psychol*, 70(2), 275-287.
- 572 Vo, V. A., Li, R., Kornell, N., Pouget, A., & Cantlon, J. F. (2014). Young children bet
573 on their numerical skills: metacognition in the numerical domain. *Psychol Sci*,
574 25(9), 1712-1721. doi:10.1177/0956797614538458
- 575 Wang, J. X., Rogers, L. M., Gross, E. Z., Ryals, A. J., Dokucu, M. E., Brandstatt, K.
576 L., . . . Voss, J. L. (2014). Targeted enhancement of cortical-hippocampal brain

Mnemonic metacognition in precuneus

577 networks and associative memory. *Science*, 345(6200), 1054-1057.

578 doi:10.1126/science.1252900

579 Ye, Q., Hu, Y., Ku, Y., Appiah, K., & Kwok, S. C. (2018). Locally distributed

580 abstraction of temporal distance in human parietal cortex. *bioRxiv*.

581 doi:10.1101/249904

582 Yokoyama, O., Miura, N., Watanabe, J., Takemoto, A., Uchida, S., Sugiura, M., . . .

583 Nakamura, K. (2010). Right frontopolar cortex activity correlates with

584 reliability of retrospective rating of confidence in short-term recognition

585 memory performance. *Neurosci Res*, 68(3), 199-206.

586 doi:10.1016/j.neures.2010.07.2041

587