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Abstract

Working memory (WM) is a fundamental construct of human cognition. The neural basis of auditory WM is thought to reflect a distributed brain network consisting of canonical memory and central executive brain regions including frontal lobe, prefrontal areas, and hippocampus. Yet, the role of auditory (sensory) cortex in supporting active memory representations remains controversial. Here, we recorded neuroelectric activity via EEG as listeners actively performed an auditory version of the Sternberg memory task. Memory load was taxed by parametrically manipulating the number of auditory tokens (letter sounds) held in memory. Source analysis of scalp potentials showed that sustained neural activity maintained in auditory cortex (AC) prior to memory retrieval closely scaled with behavioral performance. Brain-behavior correlations revealed lateralized modulations in left (but not right) AC predicted individual differences in auditory WM capacity. Our findings confirm a prominent role of auditory cortex, traditionally viewed as a sensory-perceptual processor, in actively maintaining memory traces and dictating individual differences in behavioral WM limits.

Keywords: auditory cortex; EEG; embedded processing; hemispheric specialization; sustained neural activity

Introduction

Working memory (WM) is the mental process that temporarily preserves and manipulates information for later deployment to our perceptual-cognitive systems. WM operations consist of both memory retrieval and active manipulations of sensory-cognitive representations. Human WM is, however, a limited capacity system (Cowan 2001), capable of buffering ~7±2 items in memory store at any one time (Miller 1956). Given its ubiquity to perceptual-cognitive processing, defining the neural mechanisms of WM is important to understand the brain basis of this core cognitive function.

Neuroimaging studies have identified correlates of WM in canonical memory and central executive brain regions including parietal lobe, (pre)frontal areas, and hippocampus (Bashivan et al. 2014b; Karlsgodt et al. 2005; Kumar et al. 2016). Cross-species studies corroborate human work by implicating higher cognitive association areas outside sensory cortices (Constantinidis et al. 2004). Moreover, different stages of WM (encoding, maintenance, and retrieval) recruit different neural circuitry (Bashivan et al. 2014a; Karlsgodt et al. 2005). In the context of visual WM, we have recently shown the directional flow of information between sensory and frontal brain areas reverses when encoding vs. maintaining items in WM (*encoding*: occipital sensory→frontal; *maintenance*: frontal→occipital sensory), revealing feedforward and feedback modes in the same underlying brain network (Bashivan et al. 2014a). While lower-(sensory) and higher-level (cognitive) brain regions interact during the time course of WM processing, an outstanding question to address is the degree to which sensory cortex itself accounts for differences in WM capacity.

A persistent and dominant view is that regions beyond auditory cortex (AC) drive WM in human and non-human primates (Grady et al. 2008; Huang et al. 2016; Kumar et al. 2016; Lefebvre et al. 2013). Thus, while AC is responsible for precise stimulus encoding, it may not itself participate in the active maintenance of information in a memory buffer. Retrieval and subsequent manipulation of mental objects would be orchestrated via controlled coupling between sensory cortex and frontal and/or hippocampal areas (Boran et al. 2019). Critically, such models assume that regions beyond Heschl's gyrus maintain information, although perhaps in a different representational form (Yue et al. 2019).

On the contrary, emerging evidence suggests a substantial portion of auditory WM might indeed be supported by more automatic, lower-level processing *within* the auditory system without the need for (or minimal reliance on) higher-level brain structures (Linke et al. 2011). Evidence across species suggests activity in superior temporal gyrus (STG) (Acheson et al.

3

97   2011; Grimault et al. 2014) predicts listeners' WM capacity. However, involvement of STG/STS

98   in verbal WM, particularly posterior regions (e.g., Acheson et al. 2011), might be expected given

99   the role of these "dorsal stream" areas in phonological production, articulatory planning, and

100   auditory-motor transformation (Hickok et al. 2007). Growing evidence implicates sensory AC

101   itself in WM processing (Grady et al. 2008). In non-human mammals, AC neurons show

102   sustained activity that is sensitive to WM demands (Sakurai 1994). Such findings suggest that

103   auditory WM, a function traditionally viewed through a "cognitive lens," might be driven not by

104   higher-order neocortex, *per se,* but nascent memory representations in auditory areas (e.g.,

105   Kumar et al. 2016).

106   To investigate the role of AC in auditory WM, we recorded EEG as listeners performed

107   an serial auditory WM task. We varied WM demand (i.e., cognitive load) by manipulating the

108   number of tokens (letter sounds) held in memory. Using source analysis, we examined the

109   underlying brain regions modulated by memory load and, more critically, whether neural activity

110   prior to memory retrieval could predict listeners' subsequent behavioral performance. Our

111   findings reveal early stages of auditory cortical processing in left hemisphere reflect a direct

112   correlate of the auditory WM trace and robustly predict individual differences in behavioral

113   capacity limits.

Methods

Participants

116   The sample included n=15 young adults (28±3 yrs; 8 female) recruited from the University of

117   Memphis. All had normal hearing (thresholds < 25 dB HL), reported no history of

118   neuropsychiatric illness, and were right-handed (Edinburgh laterality index > 95%). One

119   participant's data was excluded due to excessive noisy EEG. Each gave written informed

120   consent in compliance with a protocol approved by the University of Memphis IRB.

Stimuli and task

122   EEGs were recorded during a version of the Sternberg memory task that parametrically varied

123   memory load while temporally separates *encoding*, *maintenance*, and *recall* stages of WM

124   processing (for details, see Bashivan et al. 2014b). On each trial, listeners heard a random

125   series of alphanumeric characters from a subset of 15 English letters (**Fig. 1a**). Tokens were

126   300 ms (SOA = 1000 ms) presented at 76 dB SPL over ER-3A headphones (Etymotic

127   Research). For each trial, we varied the length (size) of the "Memory set" 2, 4, 6, or 8 characters

128   (random draw). A 3000 ms delay ("Retention") followed the offset of the final stimulus in which

129   listeners retained the set in memory. Following retention, a single "Probe" character was played

130   and participants indicated if it was among the prior memory set. Feedback was provided after

131   300 ms. The next trial commenced after 3.4 sec. On half the trials, the probe occurred in the set;

132   on the other half it did not. Participants received 20 practice trials for familiarization and

133   completed a total of 60 experimental trials per set size. The task was coded in MATLAB using

134   the Psychophysics Toolbox (Brainard 1997). We logged both accuracy (% correct) and median

135   reaction times (RTs) for probe recall. We computed listeners' WM capacity (per set size) using

136   the $K = S(H\text{-}F)$, where S is the number of items in the memory array, H is the hit rate, and F is

137   the false alarm rate (Bashivan et al. 2014b; Cowan 2001).

EEG recordings

139   EEGs were recorded from 64 channels at standard 10-10 locations. Continuous data were

140   digitized at 500 Hz with a DC-250 Hz passband (SynAmps RT amplifiers; Compumedics

141   Neuroscan). Electrodes on the outer canthi and the superior and inferior orbit monitored ocular

142   movements. Impedances were < 5 kΩ. Response were common average referenced.

143   Preprocessing was conducted in BESA® Research (v7) (BESA GmbH) and FieldTrip

144   (Oostenveld et al. 2011). Blinks were nullified using principal component analysis (PCA).

145   Cleaned EEGs were filtered (0.01-20 Hz; 20th order elliptical), epoched -6000 to +4000 ms

146   (where t=0 is probe onset), and averaged per set size and listener. This window encapsulated

147   transient ERPs to the last memory tokens in the encoding period, sustained activity within the

148   maintenance period of interest, and subsequent retrieval/response-related ERPs following the

149   probe (see **Fig. 2**). We baselined traces between -4400 and -3700—zeroing EEGs just prior to

150   the final memory set token—to highlight neural activity during maintenance relative to the

151   immediately preceding encoding period.

ERP sensor and source analysis

153   From channel-level waveforms, we measured ERP amplitudes within a cluster of central

154   electrodes (C1/2, Cz, CP1/2, CPz) where load-dependent changes were prominent in initial

155   visualizations of scalp topographies (data not shown). We then measured the mean ERP

156   amplitude in the entire maintenance window (-3000-0 ms) within this electrode cluster (**Fig. 2,**

157   *inset*).

158   We used Classical Low Resolution Electromagnetic Tomography Analysis Recursively

159   Applied (CLARA) [BESA® (v7)] to estimate the neuronal current density underlying WM. CLARA

160   renders focal source images by iteratively reducing the source space during repeated

161   estimations. On each iteration (x2), a spatially smoothed LORETA image was recomputed.

162   Voxels below 1% max amplitude were removed. Two iterations were used with a voxel size of 7

163   mm in Talairach space (regularization = 0.01% singular value decomposition). Group-level

164   statistical (*t*-stat) maps were computed on full brain volumes using the 'ft_sourcestatistics'

165   function in FieldTrip (Oostenveld et al. 2011) (*P*<0.05 mask). From individual CLARA images,

166   we extracted source amplitudes at the midpoint of the maintenance period (i.e., latency of -1500

167   ms) within the spatial centroids of significant clusters within bilateral superior temporal gyrus

168   (i.e., AC) (see **Fig. 3a**).

Statistical analysis

170   We used mixed-model ANOVAs in R (R Core team, 2018; *lme4* package) with a fixed effect of

171   set size (subjects = random effect). We used Tukey-Kramer corrections for multiple

172   comparisons. To assess relations between region-specific neural activity and behavior, we

173   regressed the change in AC source activation (i.e., set size 8 – set size 2) with individuals'

174   maximum WM capacity for the highest load condition ($K_{load\ 8}$) (e.g., Grimault et al. 2014). Left

175   and right hemispheres were analyzed separately. Robust regression (bisquare weighting) was

176   performed using the 'fitlm' function in MATLAB® 2019b (The MathWorks, Inc.).

Results

Behavioral data

179   Recall accuracy expectedly declined [$F_{3,39}$=23.60, *p*<0.0001] and RTs slowed [$F_{3,39}$=11.31,

180   *P*<0.0001] for increasing memory load (**Fig. 1b,c**). Similarly, *K*, an unbiased measure of WM

181   capacity, increased with set size [$F_{3,39}$=48.95, *P*<0.0001] but with more dramatic improvements

182   between 2 and 4 items (t_{39}=-5.62, *P*<0.0001) and capacity plateauing between 6 to 8 items (t_{39}=-

183   2.89, *P*=0.0303) (**Fig. 1d**). For 8 stimulus items, *K* capacity was 4.72 ± 1.07, indicating ~4-5

184   items could be adequately maintained in auditory WM (Vogel et al. 2004). This is consistent with

185   known limits to WM capacity (cf. 7±2; Miller 1956) observed in both the visual and auditory

186   modalities (Bashivan et al. 2014b; Cowan 2001; Grimault et al. 2014; Lefebvre et al. 2013;

187   Vogel and Machizawa 2004).

188   [Insert Fig. 1 near here]

EEG data

190   The time course of scalp ERPs (**Fig. 2**) tagged distinct phases of the task including evoked

191   peaks reflecting sensory responses to the final tokens of the stimulus array and probe.

192   Moreover, with our baseline definition, transient activity at the end of the encoding period (i.e.,

193   ERP positivity, -4000 ms) before maintenance was similar between set sizes [$F_{3,39}$=1.64,

194   P=0.19]. Yet, strong load-dependent changes in neural activity were observed during

195   maintenance [$F_{3,39}$=4.98, P=0.0051]. Scalp ERPs were larger for lower (2/4) vs. higher (6/8)

196   memory loads [sets size 2/4 vs. 6/8: t_{39}=3.84, P=0.0004] (**Fig. 2, *inset***), resembling a fatigue of

197   neural activity in more demanding conditions.

198   [Insert Fig. 2 near here]

199   Source ERP analysis uncovered activations distinguishing WM load in foci located in

200   AC, with coverage in primary and posterior auditory cortices (BA 41/42 and BA 22) (**Fig. 3a**). AC

201   amplitudes varied with hemisphere [$F_{1,91}$=4.76, P=0.0317] and set size [$F_{3,91}$=4.78, P=0.0038]

202   with no interaction [$F_{3,91}$=0.65, P=0.58]. Responses were stronger in left compared to right

203   hemisphere and AC differentiated lower (2/4) vs. higher (6/8) load conditions (**Fig. 3b,c**).

204   Lastly, brain-behavioral regressions revealed listeners' maximum WM capacity (i.e., K_{load}

205   $_8$) was predicted by load-dependent changes in source responses for left [R^2= 0.36, P=0.0401]

206   but not right AC [R^2= 0.45, P=0.37] (**Fig. 3d,e**).

207   [Insert Fig. 3 near here]

208

Discussion

210   Using EEG during active WM tasks, we show early stages of auditory cortical processing in AC

211   reflect a robust neural correlate of the auditory WM trace. This neural index of WM performance

212   is dominant in left hemisphere where the degree of modulation in AC predicts individuals'

213   behavioral WM capacity (i.e., larger ERP changes associated with larger memory store).

214   Source localized activity showed load-related modulations at both the sensor and source

215   level with larger sustained responses observed for lower- (easier) compared to higher-load

216   (harder) set size conditions. Previous fMRI work linking sustained delay period activity to WM

217   performance is equivocal. Some reports show enhancements (Kumar et al. 2016) and others

218   suppression (Linke et al. 2011) of cortical responses with memory load. ERP studies are

219   similarly ambiguous finding decreases and increases (Grimault et al. 2014; Huang et al. 2016;

220   Lefebvre et al. 2013; Vogel and Machizawa 2004) in late (> 400 ms) slow wave potentials with

221   load level. Reconciling these findings, direct recordings in animals show *both* suppression and

222   enhancement effects in AC neurons dependent on the mnemonic context of sounds (Scott et al.

223   2014).

224   Sustained firing patterns might be not be related to WM *per se*, but rather, other

225   concurrent mental processes for task execution (although they are unlikely contingent negative

226   variations; see *SI Discussion*). DC potentials likely reflect higher states of arousal, alertness,

227 and or attention (Kovac et al. 2018). Indeed, low-frequency (delta band) EEG responses are

228 closely linked to sustained attention (Kirmizi-Alsan et al. 2006). Interestingly, suppression of

229 sustained responses during the delay period is reduced in individuals that rely on a covert

230 rehearsal strategies (Linke et al. 2011). Thus, stronger AC responses for lower set sizes may

231 reflect more covert rehearsal by our participants to refresh short-term memory representations

232 from being overwritten and protecting memory items from decay. This interpretation is

233 consistent with our brain-behavior correlations, which showed listeners with stronger reduction

234 (cf. suppression) of sustained AC activity had higher K capacity limits (e.g., Fig. 3d). Larger

235 neural responses for lower set sizes could reflect a stronger deployment of attention in easier,

236 less taxing conditions.

237 Seminal studies in primates and fMRI in humans have demonstrated that neurons

238 maintain a representation of the stimulus via sustained activity in prefrontal cortex which

239 outlasts the eliciting event (Courtney et al. 1997). Sustained maintenance activation is observed

240 across multiple brain regions in tasks involving various sensory modalities (Bashivan et al.

241 2014b; Yue et al. 2019). In agreement with prior neuroimaging WM studies (Grimault et al.

242 2014; Huang et al. 2016; Vogel and Machizawa 2004), we similarly found sustained EEG

243 activity during WM maintenance is modulated by stimulus load. Our results corroborate fMRI

244 findings (Kumar et al. 2016) by confirming successful auditory WM depends on elevated activity

245 within AC. These structures are typically associated with sensory-perceptual processing rather

246 than higher cognition (Boran et al. 2019; Yue et al. 2019). Thus, our data support an

247 "embedded" rather than "buffer" account of WM, whereby auditory cortex acts to both encode

248 perceptually relevant sound features but also functions as memory buffer to maintain

249 information over short periods (cf. Yue et al. 2019).

250 We also found a stark hemispheric asymmetry in how AC predicts WM capacity. "High

251 modulators" of left hemisphere AC activity showed superior auditory WM performance. In

252 contrast, right hemisphere did not predict behavior. fMRI studies similarly show left AC

253 activation positively correlates with behavioral performance in WM tasks (Kumar et al. 2016).

254 Thus, while activity is bilateral during WM (current study; Grimault et al. 2014; Huang et al.

255 2016; Kumar et al. 2016), left hemisphere best correlates with behavioral capacity. Leftward

256 laterality is perhaps expected given the well-known dominance of left cerebral hemisphere to

257 auditory-linguistic processing (Hickok and Poeppel 2007). Indeed, both children and adults

258 show strong brain asymmetry in WM organization, with greater rightward bias for spatial WM

259 and leftward bias for verbal WM (Thomason et al. 2009). Given our WM task required covert

260 verbal labeling, the stronger activation and association we find between left AC and behavior is

261   consistent with the left hemisphere dominance of auditory-linguistic processing (Hickok and

262   Poeppel 2007).

263

264 **Figure legends**

265 **Fig. 1: Auditory WM stimulus paradigm and behavioral data.** (**a**) Listeners heard between 2

266 and 8 characters ("Memory set") presented auditorily. Following a retention period, they

267 indicated whether a "Probe" occurred in the prior memory set. Shown here is a "no match" trial.

268 (**b-c**) Behavioral accuracy for probe recall decreases and response times increase with

269 additional memory load. (**d**) Working memory capacity (K) increases for small set sizes but

270 saturates >4 items, above listeners' WM capacity limits. errorbars =± 1 s.e.m.

271

272 **Fig. 2: Scalp ERPs reveal load-dependent modulations in sustained neural activity during**

273 **WM maintenance. (a)** ERP time courses at central scalp locations (mean of electrodes C1/2,

274 Cz, CP1/2, CPz; baseline = [-4400 to -3700 ms]). Transient peaks during "encoding" reflect

275 auditory responses to final stimulus tokens in the memory set. Sustained activity is modulated in

276 the 3 sec maintenance interval during memory retention (highlighted segment) and is stronger

277 for low (2/4) vs. high (6/8) load (inset). errorbars =± 1 s.e.m.

278

279 **Fig. 3: Sustained neural activity maintained in AC predicts behavioral auditory WM**

280 **capacity. (a)** T-stat map contrasting low (2/4) vs. high (6/8) CLARA source activation maps

281 (*P*<0.05 masked, uncorrected). Functional data are overlaid on the MNI brain template. WM

282 load is distinguished in bilateral auditory AC [MNI coordinates (*x,y,z;* in mm): AC_{left}=(-42.5, -

283 18.5, -5.5); AC_{right}=(50.5, -26.5, -5.5)] **(b-c)** AC amplitudes vary with set size but load-related

284 changes in left (but not right) AC mirror the pattern observed in scalp EEG (cf. Fig. 2a) (**d-e**)

285 Maximum behavioral WM capacity ($K_{load\ 8}$) is predicted by AC activity in left hemisphere;

286 individuals with larger changes in source amplitudes with set size have larger WM capacity. No

287 brain-behavior relation is observed in right hemisphere. Dashed lines=95% CI; solid lines,

288 significant correlation; dotted lines, n.s. correlation. *P*<0.05. errorbars =± 1 s.e.m.; AC, auditory

289 cortex.

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355

356

357

358

a

Memory set   Retention   Probe

"k"   "s"   "f"   "p"   "i"

1000 ms   300 ms   3000 ms   *In prior set?*

Encoding   *Maintenance*   *Retrieval*

2 μV +

Set size
— 2
--- 4
— 6
··· 8

μV

Set size
2 4 6 8

Time re. probe (ms)

b

Source amp. (nAm/cm³) vs Set size (2, 4, 6, 8)

c

Source amp. (nAm/cm³) vs Set size (2, 4, 6, 8)

a

AC   AC

L   R

z = -5.5

high > low   low > high

−3   0   3

t-value (*p*<0.05)

d AC left

Δ amp. 2 to 8 items (nAm) vs K (load 8)

R2=0.36*

e AC right

Δ amp. 2 to 8 items (nAm) vs K (load 8)

R2=0.45, *n.s.*