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Title: Auditory cortex supports verbal working memory capacity

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Abstract

Working memory (WM) is a fundamental construct of human cognition that predicts important faculties such as language abilities and scholastic achievement. 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

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Introduction

Working memory (WM) refers to mental processes that temporarily preserve information to be readily accessible and deployed to our perceptual-cognitive system. WM operations consist of both memory retrieval and active manipulations of those representations. Consequently, it is well documented that human WM is a limited capacity system (Cowan, 1998; Cowan, 2001), capable of buffering ~7±2 items in temporary memory store at any one time (Miller, 1956). Critically, WM capacity varies across different stimuli (Baddeley et al., 1975) and is modulated both by modality-general and modality-specific processes (Fougnie and Marois, 2011). For example, a meta-analysis of n-back tasks shows a general involvement of a frontoparietal network, but additional activation patterns differ between stimuli and presentation modalities (Mencarelli et al., 2019). Given its ubiquity to perceptual-cognitive processing, defining the neural mechanisms of WM is important and it is critical to not only understand the brain basis of this core cognitive function but also its role in normal and disordered human faculties such as speech and language (Füllgrabe and Rosen, 2016; King and Just, 1991; Nation et al., 1999).

WM has generally been regarded as a higher-order cognitive process. As such, it is perhaps unsurprising that a wealth of neuroscientific studies have sought and identified neural correlates of WM in canonical memory and central executive brain regions including parietal lobe, (pre)frontal areas, and hippocampus (Bashivan et al., 2014a; Habeck et al., 2005; Karlsgodt et al., 2005; Kumar et al., 2016; Sreenivasan et al., 2014; Thompson-Schill et al., 2002). For example, patients with lesions to inferior parietal cortex show disproportionality higher deficits in verbal WM span (Baldo and Dronkers, 2006). These regions are thought to lie at the apex of the perceptual-cognitive processing hierarchy (Bagur et al., 2018; de Lafuente and Romo, 2006; Rahnev et al., 2016; Siegel et al., 2015) that underlies complex behaviors like WM (but see Ranganath and Blumenfeld, 2005). Cross-species studies corroborate human work by implicating higher cognitive and association areas outside the sensory cortices (Constantinidis and Procyk, 2004). Moreover, different stages of WM (encoding, maintenance, and retrieval) recruit different neural circuitry over time (Bashivan et al., 2014b; Bashivan et al., 2015; Habeck et al., 2005; Karlsgodt et al., 2005; Metzak et al., 2011). In the context of visual WM, for instance, we have recently shown the directional flow of information between sensory and frontal brain areas reverses when encoding vs. maintaining items in working memory (*encoding*: occipital sensory → frontal; *maintenance*: frontal → occipital sensory), revealing feedforward and feedback modes in the same underlying brain network (Bashivan et al., 2014b; Bashivan et al., 2017). A similar reversal in information flow was more recently reported by

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Linde-Domingo et al. (2019). 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 can account for differences in WM capacity.

The neural circuitry of WM is well-studied in the visual domain (Bashivan et al., 2014a; Luck and Vogel, 2013) but presumably differs across modalities (Lefebvre et al., 2013; Xiao et al., 2019). The role of sensory cortex in WM is supported by increasing evidence for specific involvement of visual cortex in visual WM paradigms (Constantinidis and Procyk, 2004). However, it remains unclear if such findings generalize to audition. In fact, few studies have examined the neurophysiological correlates of *auditory* WM. A persistent and dominant view, adopted from the visual sciences, is that regions beyond auditory cortex (AC) drive WM in human and non-human primates (Gaab et al., 2003b; Grady et al., 2008; Huang et al., 2016; Kumar et al., 2016; Lefebvre et al., 2013; Mencarelli et al., 2019). In this framework, AC is responsible mainly for precise encoding of stimulus representations rather than the active maintenance of information in a memory buffer. The retrieval and subsequent manipulation of mental objects is then orchestrated via controlled coupling between sensory cortex and frontal and/or hippocampal areas (Boran et al., 2019; Petrides and Pandya, 2006). 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 that a substantial portion of auditory WM might be supported by more automatic, lower-level processing *within* the auditory system and without the need for (or at least with minimal reliance on) higher-level brain structures (Demany et al., 2010; Linke and Cusack, 2015; Linke et al., 2011). Evidence across species suggests activity in superior temporal gyrus (STG) (Acheson et al., 2011; Colombo et al., 1990; Grimault et al., 2014) might predict listeners' WM capacity. However, the involvement of STG/STS in verbal WM, particularly posterior regions (e.g., Acheson et al., 2011; Buchsbaum and D'Esposito, 2008), might be expected given the role of such "dorsal stream" areas in phonological production, articulatory planning, and auditory-motor transformation (Hickok and Poeppel, 2004; Hickok and Poeppel, 2007; Wilson et al., 2009). On the contrary, growing evidence implicates sensory AC itself (Grady et al., 2008; Lu et al., 1992a; Lu et al., 1992b) in WM processing. Indeed, in non-human mammals, AC neurons are characterized by sustained activity that is sensitive to WM demands (Sakurai, 1994). These findings suggest that auditory WM, a function traditionally viewed through a "cognitive lens," might be driven not by higher-order neocortex, *per se,* but by earlier memory representations in auditory sensory areas (e.g., Kumar et al., 2016).

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To address these questions, we recorded neuroelectric brain activity as listeners performed an auditory version of the well-known Sternberg serial memory task (Sternberg, 1966). We varied WM demand (and thus cognitive load) by manipulating the number of auditory tokens (letter sounds) held in memory. Using source analysis of the auditory event-related potentials (ERPs), we examined the underlying brain regions that are modulated by memory load and, more critically, whether neural activity prior to memory retrieval could predict listeners' subsequent behavioral WM performance. Our findings reveal early stages of auditory cortical processing in left hemisphere reflect a direct neural correlate of the auditory WM trace and robustly predict individual differences in behavioral capacity limits.

Methods

Participants

The sample included *n*=15 young adults (24-33 years of age, $\mu \pm \sigma$: 28±3 yrs; 8 female) recruited from the University of Memphis student body. All had normal hearing (octave thresholds < 25 dB HL), reported no history of neuropsychiatric illness, and were strongly right-handed (Edinburgh laterality index > 95%) (Oldfield, 1971). One participant's data was excluded due to excessive noisy EEG resulting in a final sample size of *n* =14. Each was paid for their time and gave written informed consent in compliance with a protocol approved by the IRB at the University of Memphis.

Stimuli and task

EEGs were recorded during a modified version of the Sternberg memory task (Sternberg, 1966). This paradigm is advantageous because it allowed us to parametrically assess neural responses to different memory loads and temporally separates *encoding*, *maintenance*, and *recall* stages of the neuronal WM process (Bashivan et al., 2014a). Participants were seated inside an electro-acoustically shielded booth and were instructed to avoid body movement. On each trial, listeners heard a random series of alphanumeric characters selected from a subset of 15 English letters (**Fig. 1a**). Sounds were normalized in duration (300 ms) and RMS amplitude (76 dB SPL), and were presented over ER-3A insert headphones (Etymotic Research). A 700 ms silent gap separated successive tokens. For each trial, the length (size) of the "Memory set" varied from 2, 4, 6, or 8 characters (random draw), followed by a 3000 ms delay ("Retention") in which participants retained the stimulus set in memory. Following the retention period, a single "Probe" character was displayed and participants indicated if it was among the prior memory set via button press. Feedback was provided 300 ms after their response via a colored light on the

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computer screen. A 3.4 sec inter-stimulus interval then followed. On half the trials, the probe occurred in the set; on the other half it did not. Subjects received 20 practice trials for task familiarization and then completed a total of 60 experimental trials per set size in the experiment proper. The task was coded in MATLAB using the Psychophysics Toolbox (Brainard, 1997).

Behavioral data analysis

We logged both mean accuracy (% correct) and median reaction times (RTs) for probe recall. Additionally, we computed each listeners' WM capacity (per set size) using the *K* index, defined as $K = S(H-F)$, where S is the number of items in the memory array, H is the hit rate, and F is the false alarm rate (Cowan, 2001; Pashler, 1988).

EEG recordings

EEG procedures followed our previous report on the neural correlates of visual WM (Bashivan et al., 2013; Bashivan et al., 2014a; Bashivan et al., 2014b; Bashivan et al., 2015). EEG was recorded from 64 sintered Ag/AgCl electrodes at standard 10-10 scalp locations (Oostenveld and Praamstra, 2001). Continuous data were digitized at 500 Hz (SynAmps RT amplifiers; Compumedics Neuroscan) with an online passband of DC-250 Hz. Electrodes placed on the outer canthi of the eyes and the superior and inferior orbit monitored ocular movements. Electrode impedances were < 5 kΩ. Electrodes were referenced to an additional electrode ~1 cm posterior to Cz during acquisition and were subsequently common average referenced (CAR) for analysis.

Preprocessing was conducted in BESA® Research (v7) software (BESA GmbH) and the FieldTrip toolbox (Oostenveld et al., 2011). Ocular artifacts (saccades and blinks) were first corrected in continuous EEGs using topographic principal component analysis (PCA) (Picton et al., 2000). Cleaned EEGs were filtered (0.01-20 Hz; 20th order elliptical), epoched between -6000 and +4000 ms (where t=0 is probe onset), and ensemble averaged across trials to derive ERPs for each stimulus per participant. This window encapsulated transient ERPs to the last several memory tokens in the encoding period, sustained activity within the maintenance period of interest, and the subsequent retrieval/response-related ERPs following the probe (see **Fig. 2a**). Importantly, we assessed relative changes in the ERPs between set sizes, rendering the exact choice of baseline within our long (10 sec) epoch window somewhat arbitrary. Consequently, we chose to baseline correct traces between -4400 and -3700—zeroing EEGs just prior to the final memory set token—to highlight neural activity during the maintenance period relative to the immediately preceding encoding period (see Fig. 2a).

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ERP sensor and source analysis

From channel-level waveforms, we measured load-dependent changes in the ERPs by comparing scalp topographies across set sizes in EEGLAB (Delorme and Makeig, 2004) (**Fig. 2b**). We then conducted topographic *t*-tests on the maps contrasting low (4/2) vs. high (8/6) set sizes to identify electrodes showing WM-related changes in neural activity at the scalp surface. This contrast revealed highly significant ($P<0.01$) load-dependent modulations at central electrodes (C1/2, Cz, CP1/2, CPz) (**Fig. 2c**). We then measured the mean ERP amplitude in the entire maintenance window (-3000-0 ms) within this significant electrode cluster (**Fig. 2a,** *inset*).

We used Classical Low Resolution Electromagnetic Tomography Analysis Recursively Applied (CLARA) [BESA® (v7)] (Iordanov et al., 2014) to estimate the neuronal current density underlying WM effects observed in the ERPs (e.g., Alain et al., 2017; Bidelman, 2018). CLARA models the inverse solution as a large collection of elementary dipoles distributed over nodes on a mesh of the cortical volume. The algorithm estimates the total variance of the scalp data and applies a smoothness constraint to ensure current changes minimally between adjacent brain regions (Michel et al., 2004; Picton et al., 1999). CLARA renders more focal source images by iteratively reducing the source space during repeated estimations. On each iteration (x2), a spatially smoothed LORETA solution (Pascual-Marqui et al., 2002) was recomputed and voxels below a 1% max amplitude threshold were removed. This provided a spatial weighting term for each voxel on the subsequent step. Two iterations were used with a voxel size of 7 mm in Talairach space and regularization (parameter accounting for noise) set at 0.01% singular value decomposition. Group-level statistical (*t*-stat) maps were then computed on full brain volumes using the 'ft_sourcestatistics' function in FieldTrip (Oostenveld et al., 2011) and threshold at $P<0.05$. Source activation contrasts were interpolated and visualized on the MNI adult brain template (Fonov et al., 2009). From individual functional images, we extracted CLARA source amplitudes at the midpoint of the maintenance period (i.e., latency of -1500 ms) within the spatial centroids of significant clusters within bilateral superior temporal gyrus (i.e., AC) (see **Fig. 3a**).

Statistical analysis

We analyzed dependent variables using mixed-model ANOVAs in R (R Core team, 2018; *lmer4* package) with a fixed effect of set size and random effect of subject. Multiple comparisons were

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adjusted using Tukey-Kramer corrections. To assess relations between region-specific neural activity and behavior, we regressed the change in AC source activation (i.e., set size 8 – set size 2) with individuals' maximum WM capacity for the highest load condition ($K_{load\ 8}$) (e.g., Grimault et al., 2014). Left and right hemispheres were analyzed separately. This allowed us to evaluate whether load-dependent changes in left and/or right auditory cortical responses *within AC* predicted listeners' WM capacity. Robust regression (bisquare weighting) was performed using the 'fitlm' function in MATLAB® 2019b (The MathWorks, Inc.).

Results

Behavioral data

Accuracy for recall expectedly declined [$F_{3,39}$=23.60, p<0.0001] and RTs slowed [$F_{3,39}$=11.31, P<0.0001] for increasing memory load with larger set sizes (**Fig. 1b,c**). Similarly, K, an unbiased measure of WM capacity, increased with set size [$F_{3,39}$=48.95, P<0.0001]. Follow-up contrasts revealed a dramatic increase in performance between 2 and 4 items (t_{39}=-5.62, P<0.0001) with a leveling off in capacity limit from 6 to 8 items (t_{39}=-2.89, P=0.0303) (**Fig. 1d**). For 8 stimulus items, K capacity was 4.72 ± 1.07, indicating ~4-5 items (on average) could be adequately maintained in auditory WM (Vogel and Machizawa, 2004). These data confirm the well-established limit to WM capacity (cf. 7±2; Miller, 1956) observed in both the visual and auditory modalities (Bashivan et al., 2014a; Cowan, 2001; Grimault et al., 2014; Lefebvre et al., 2013; Vogel and Machizawa, 2004).

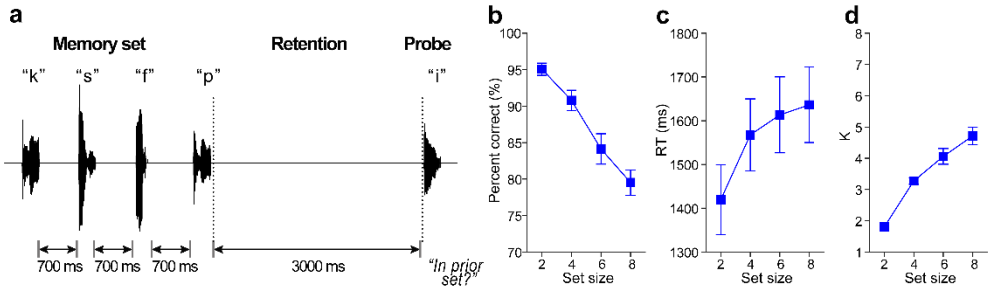

Fig. 1: Auditory WM stimulus paradigm and behavioral data. (**a**) On each trial, listeners heard between 2 and 8 random characters ("Memory set") presented auditorily. Following a 3 sec retention period to maintain items in WM, they indicated whether a "Probe" occurred in the prior memory set. Shown here is a "no match" trial. (**b-c**) Behavioral accuracy (i.e., correct probe recall) decreases and response times increase with additional memory load from 2 to 8 items. (**d**) Working memory capacity (K = S[H-F]; Cowan, 2001; Pashler, 1988) increases for small set sizes but saturates >4 items, above listeners' WM capacity limits. errorbars =± 1 s.e.m.

Electrophysiological data

Scalp ERPs are shown as a function of memory set size in **Figure 2a**. The time course of the responses tagged distinct phases of the task. Separate "wavelet peaks," reflecting the sensory

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response to the last tokens of the stimulus array, were visible at the end of the encoding period. Following the cessation of the stimulus set, ERPs showed sustained activity across the scalp during maintenance as listeners retained items in WM (**Fig. 2b**), followed by a subsequent wavelet reflecting the auditory sensory response to the probe during retrieval.

Our subsequent analyses focused on the *maintenance* period since neural activity within this segment is evoked absent any concomitant stimuli, and thus, reflects *endogenous* brain processing related to memory retention. We found strong, load-dependent changes in neural activity during maintenance [$F_{3,39}$=5.73, P=0.0024]. This effect was characterized by larger ERPs for lower (2/4) vs. higher (6/8) memory loads [sets size 2/4 vs. 6/8: t_{39}=4.14, P=0.0002] (**Fig. 2a, *inset***), which resembled a fatigue of neural activity in more demanding conditions. Load-dependent modulations in maintenance ERP activity were restricted to central electrode sites (**Fig. 2c**), consistent with auditory neural generators in the supratemporal plane (Picton et al., 1999). Moreover, transient activity at the end of the encoding period (i.e., ERP positivity,-3530 ms) before maintenance did not vary with set size [$F_{3,39}$=2.28, P=0.094]. This confirms that the ERP modulations during the maintenance delay were not due to differences in stimulus encoding but rather, activity related to endogenous WM processing.

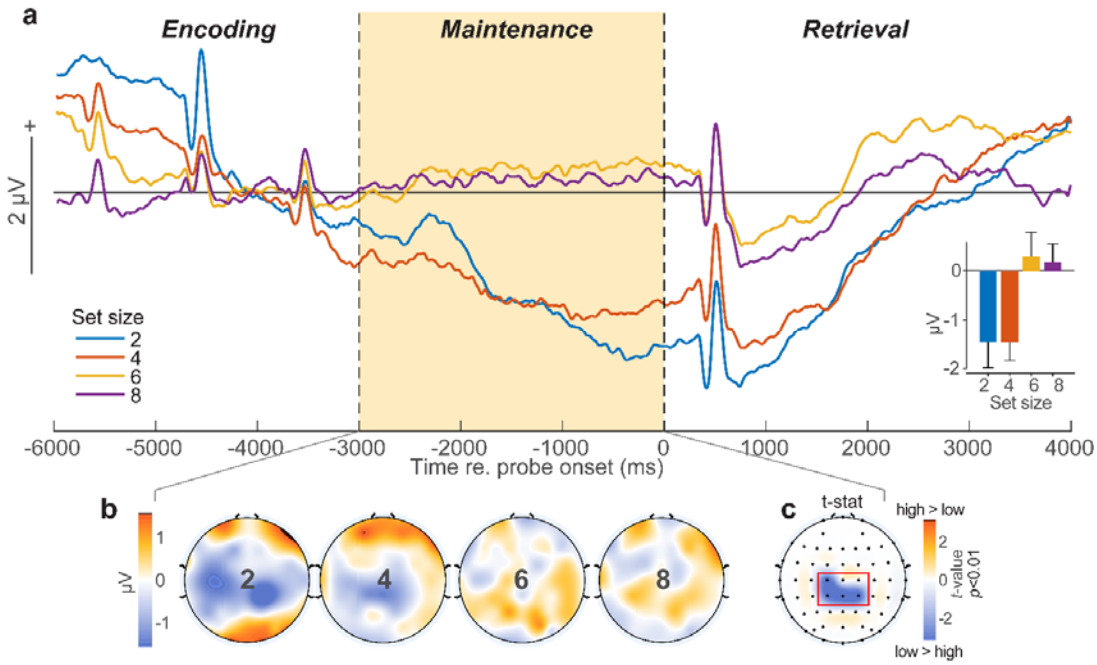

Fig. 2: Scalp ERPs reveal WM load-dependent modulations in sustained neural activity during memory maintenance. (a) ERP time courses at central scalp locations (mean of electrodes C1/2, Cz, CP1/2, CPz; baseline = [-4400 to -3700 ms]). Transient wavelets during "encoding" reflect auditory responses to final stimulus tokens in the memory set. Sustained activity is modulated in the 3 sec maintenance interval during memory retention (highlighted segment) and is stronger for low (2/4) vs. high (6/8) load (inset). **(b)** Topographies show the distribution of activity across the scalp during maintenance [mean: -3000 - 0 ms] and load-dependent decreases at higher set sizes. **(c)** Statistical maps (paired t-test, P<0.01, uncorrected) contrasting low (2/4) vs. high (6/8) memory load. Lower memory

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loads elicit stronger voltage deflections than higher loads at central electrode sites (boxed channels). errorbars =± 1 s.e.m.

Source analysis of the ERPs uncovered neural activations distinguishing WM load in foci located in AC, with coverage in primary and posterior auditory cortices (BA 41/42 and BA 22) (**Fig. 3a**). AC amplitudes varied with hemisphere [$F_{1,91}$=4.76, P=0.0317] and set size [$F_{3,91}$=4.78, P=0.0038] with no interaction [$F_{3,91}$=0.65, P=0.58]. Responses were stronger in LH compared to RH across the board. Post hoc contrasts further showed left AC differentiated lower (2/4) vs. higher (6/8) load conditions whereas right AC was invariant across set sizes (**Fig. 3b,c**).

Having established that sustained activity in left AC was sensitive to auditory WM load, we next asked whether source activity was related to listeners' behavioral WM capacity. Brain-behavioral regressions revealed that listeners' maximum WM capacity (i.e., $K_{load\ 8}$) was predicted by load-dependent changes in source responses for left [R^2= 0.36, P=0.0401] but not right AC [R^2= 0.45, P=0.37] (**Fig. 3d,e**).

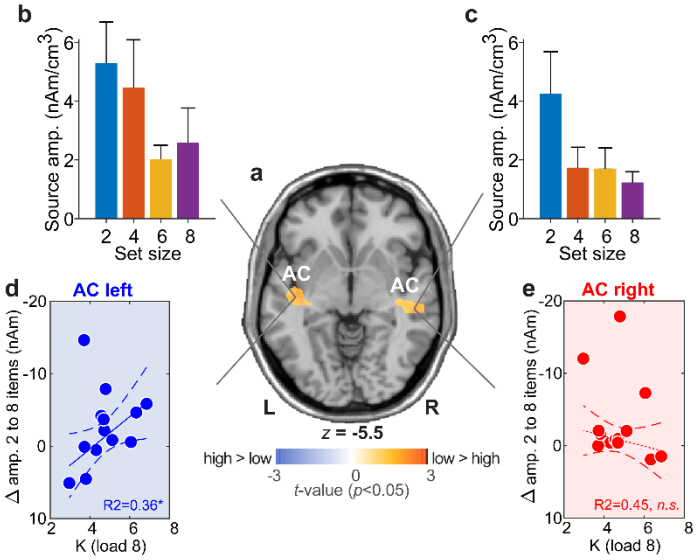

Fig. 3: Sustained neural activity maintained in AC predicts behavioral auditory WM capacity. (a) T-stat map contrasting low (2/4) vs. high (6/8) CLARA source activation maps (P<0.05 masked, uncorrected). Functional data are overlaid on the MNI brain template brain template (Fonov et al., 2009). WM load is distinguished principally in bilateral auditory AC [MNI coordinates (*x,y,z;* in mm): *ACleft*=(-42.5, -18.5, -5.5); *ACright*=(50.5, -26.5, -5.5)] **(b-c)** AC amplitudes vary with set size but load-related changes in left (but not right) AC mirror the pattern observed in scalp EEG (cf. Fig. 2a) (**d-e**) Maximum behavioral WM capacity (*Kload* $_8$) is predicted by AC activity in left hemisphere; individuals with larger change in source amplitudes from set size 2 to 8 have larger WM capacity. No brain-behavior relation was observed in right hemisphere. Dashed lines=95% CI; solid lines, significant correlation; dotted lines, n.s. correlation. *P<0.05. errorbars =± 1 s.e.m.; AC, auditory cortex.

Discussion

By recording EEG during active WM tasks, we show that early stages of auditory cortical processing in AC reflect a direct neural correlate of the auditory WM trace. This neural index of

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WM performance is dominant in left hemisphere where the degree of modulation in AC predicts individuals' behavioral WM capacity (i.e., larger ERP changes associated with larger memory store).

We found that source localized neural activity showed load-related modulations at both the sensor and source level with larger sustained responses observed for lower- (easier) compared to higher-load (harder) set size conditions. Previous fMRI work linking sustained delay period activity to WM performance has been somewhat equivocal. Some reports show enhancements (Gaab et al., 2003a; Grimault et al., 2009; Kumar et al., 2016) and others suppression (Linke et al., 2011; Zatorre et al., 1994) of auditory cortical responses with memory load. ERP studies are similarly ambiguous with studies showing a decrease (Golob and Starr, 2000; Pratt et al., 1989) or increase (Alain et al., 2009; Grimault et al., 2014; Huang et al., 2016; Lefebvre et al., 2013; Vogel and Machizawa, 2004) in late (> 400 ms) slow wave potentials with load level. On the contrary, direct unit recordings from animals suggest AC neurons can actually show *both* suppression and enhancement effects according to the mnemonic context of sounds (Scott et al., 2014). Additionally, AC units also code for constructs typically considered "higher level" functions including memory load (Sakurai, 1994), associative learning (Weinberger, 1993), and long-term memory (Weinberger, 2004).

Discrepancies on the nature of sustained activity in WM are unclear. Sustained firing patterns might be not be related to WM *per se*, but rather, other concurrent mental processes necessary to execute the task. DC potentials are thought to reflect higher states of arousal, alertness, and or attention (for review see Kovac et al., 2018). Interestingly, suppression of such responses during the delay period is reduced in individuals who rely more heavily on a covert rehearsal strategy (Linke et al., 2011). Thus, stronger AC responses we find for lower set sizes may reflect more covert rehearsal by our participants in order to refresh short-term memory representations from being overwritten and therefore protect memory items from decay. This interpretation is consistent with our brain-behavior correlations, which showed listeners with stronger reduction (cf. suppression) of sustained AC activity had higher K capacity limits (e.g., Fig. 3d). Moreover, although sustained auditory ERPs are recordable absent a task, they are enhanced by goal-directed attention (Picton et al., 1978), presumably through engagement of attention-sensitive belt regions of AC (Woods et al., 2010). Therefore, the larger neural responses we observe for lower set sizes could reflect a stronger deployment of attention in those easier, less taxing conditions. Nevertheless, intracranial recordings in macaques demonstrate both suppression and enhancement effects in different subpopulations of neurons within rostral STG (Scott et al., 2014). Yet, only excitatory responses mirror declining behavioral

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performance (Scott et al., 2014), which parallels our EEG data. Collectively, our results best align with the notion that "dynamic enhancement seems more closely tied to the sensory trace, whereas dynamic suppression may represent a more general attention effect that may be necessary, but not sufficient to support short-term memory (Scott et al., 2014; p. 2771)."

The physiological basis—and thus functional interpretation—of sustained EEG is difficult to ascertain from scalp responses. Seminal studies in primates and fMRI in humans have demonstrated that neurons maintain a representation of the stimulus via sustained activity in prefrontal cortex which outlasts the eliciting event (Courtney et al., 1997; Fuster and Alexander, 1971). Sustained maintenance activation has now been observed across multiple brain regions in tasks involving various sensory modalities (Bashivan et al., 2014a; Masse et al., 2020; Salazar et al., 2012; but see Yue et al., 2019). In agreement with prior neuroimaging studies on WM (Grimault et al., 2014; Huang et al., 2016; Vogel and Machizawa, 2004), we similarly find that sustained EEG activity during WM maintenance is modulated by stimulus load. Our results corroborate fMRI findings (Kumar et al., 2016) by confirming, electrophysiologically, that successful auditory WM depends on elevated activity within AC and adjacent auditory cortex. These structures are typically associated with sensory-perceptual processing rather than higher cognition (Boran et al., 2019; Petrides and Pandya, 2006; Yue et al., 2019). As such, our data support an "embedded" rather than "buffer" account of WM, whereby auditory cortex acts to both encode perceptually relevant sound features but also functions as memory buffer which maintains information over short periods (cf. Yue et al., 2019). Nevertheless, our data cannot rule out the possibility that information could be held in WM via other signaling modes not readily captured via EEG, including persistent spiking activity (Huang et al., 2016) and/or "activity silent" synaptic mechanisms (Masse et al., 2020; Rose et al., 2016).

A question that naturally arises from our data is the degree to which sustained AC reflects a form of the contingent negative variation (CNV) response (for discussion, see Lefebvre et al., 2013). CNVs are readily recorded in reaction time/expectancy tasks between the presentation of a cueing stimulus (cf. memory set) and imperative stimulus (cf. test probe) (Walter et al., 1964). However, we argue against this possibility based on several observations. First, as shown in previous MEG WM studies (Lefebvre et al., 2013), sustained neuromagnetic activity is differentiable from CNV. Second, the stronger negative deflections we find during maintenance are unlikely CNV since our probe is always an imperative stimulus and consequently, induces similar expectancy. Third, the CNV is closely related to perceptual timing in tasks that demand a motor response or have motivational value (Kononowicz and Penney, 2016). Yet, we find that neither left (r = 0.10, P = 0.47) nor right (r = -0.05, P = 0.71) AC source

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responses correlate with behavioral RTs. Lastly, CNV and other related motor-readiness potentials are localized to premotor areas (Hultin et al., 1996; Leuthold and Jentzsch, 2001) whereas our load-dependent modulations originated from sources within AC. Instead, the most parsimonious interpretation of our data is that AC responses reflect a direct neural correlate of the auditory sensory memory trace, where changes in the strength of neural representation decays following stimulus cessation.

We also found a stark hemispheric asymmetry in how AC predicts WM capacity. “High modulators” of left hemisphere AC activity showed superior auditory WM performance. In contrast, right hemisphere did not predict behavior. These effects are similar to previous neuroimaging studies that have shown stronger engagement of primary AC for more successful perceivers (in speech categorization tasks; Bidelman and Walker, 2019; Mankel et al., 2020). Pertinent to the present findings, fMRI studies show left AC activation positively correlates with behavioral performance in WM tasks (Brechmann et al., 2007; Kumar et al., 2016). Thus, while bilateral AC is critical to WM (current study; Grimault et al., 2014; Huang et al., 2016; Kumar et al., 2016), modulations primarily in left hemisphere best correlate with behavior. The leftward laterality of this brain-behavior association is perhaps expected given the well-known dominance of left cerebral hemisphere to auditory-linguistic processing (Hickok and Poeppel, 2007), particularly under challenging task demands that recruit WM (e.g., perceiving degraded speech; Alain et al., 2018; Bidelman and Howell, 2016; Bidelman et al., 2019). Indeed, both children and adults show strong brain asymmetry in WM organization, with greater rightward bias for spatial WM and leftward bias for verbal WM (Thomason et al., 2009). Similarly, temporal lobe lesions in right but not left hemisphere produce deficits in WM for tonal (i.e., non-speech) stimuli (Zatorre and Samson, 1991). Collectively, these studies demonstrate a hemispheric bias in the neural resources marshaled for WM processing that depends on the linguistic context of the stimuli. Given our WM task required covert verbal labeling, the stronger activation and association we find between left AC and behavior is consistent with the left hemisphere dominance of the auditory-linguistic loop.

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Figure legends

Fig. 1: Auditory WM stimulus paradigm and behavioral data. (**a**) On each trial, listeners heard between 2 and 8 random characters ("Memory set") presented auditorily. Following a 3 sec retention period to maintain items in WM, they indicated whether a "Probe" occurred in the prior memory set. Shown here is a "no match" trial. (**b-c**) Behavioral accuracy (i.e., correct probe recall) decreases and response times increase with additional memory load from 2 to 8 items. (**d**) Working memory capacity (K = S[H-F]; Cowan, 2001; Pashler, 1988) increases for small set sizes but saturates >4 items, above listeners' WM capacity limits. errorbars =± 1 s.e.m.

Fig. 2: Scalp ERPs reveal WM load-dependent modulations in sustained neural activity during memory maintenance. (a) ERP time courses at central scalp locations (mean of electrodes C1/2, Cz, CP1/2, CPz; baseline = [-4400 to -3700 ms]). Transient wavelets during "encoding" reflect auditory responses to final stimulus tokens in the memory set. Sustained activity is modulated in the 3 sec maintenance interval during memory retention (highlighted segment) and is stronger for low (2/4) vs. high (6/8) load (inset). **(b)** Topographies show the distribution of activity across the scalp during maintenance [mean: -3000 - 0 ms] and load-dependent decreases at higher set sizes. **(c)** Statistical maps (paired t-test, P<0.01, uncorrected) contrasting low (2/4) vs. high (6/8) memory load. Lower memory loads elicit stronger voltage deflections than higher loads at central electrode sites (boxed channels). errorbars =± 1 s.e.m.

Fig. 3: Sustained neural activity maintained in AC predicts behavioral auditory WM capacity. (a) T-stat map contrasting low (2/4) vs. high (6/8) CLARA source activation maps (P<0.05 masked, uncorrected). Functional data are overlaid on the MNI brain template brain template (Fonov et al., 2009). WM load is distinguished principally in bilateral auditory AC [MNI coordinates ($x,y,z;$ in mm): AC_{left}=(-42.5, -18.5, -5.5); AC_{right}=(50.5, -26.5, -5.5)] **(b-c)** AC amplitudes vary with set size but load-related changes in left (but not right) AC mirror the pattern observed in scalp EEG (cf. Fig. 2a) (**d-e**) Maximum behavioral WM capacity ($K_{load\ 8}$) is predicted by AC activity in left hemisphere; individuals with larger change in source amplitudes from set size 2 to 8 have larger WM capacity. No brain-behavior relation was observed in right hemisphere. Dashed lines=95% CI; solid lines, significant correlation; dotted lines, n.s. correlation. *P<0.05. errorbars =± 1 s.e.m.; AC, auditory cortex.

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References

Acheson, D.J., Hamidi, M., Binder, J.R., Postle, B.R. 2011. A common neural substrate for language production and verbal working memory. J. Cogn. Neurosci. 23, 1358-1367.

Alain, C., McDonald, K.L., Kovacevic, N., McIntosh, A.R. 2009. Spatiotemporal analysis of auditory “what” and “where” working memory. Cereb. Cortex 19, 305-314.

Alain, C., Arsenault, J.S., Garami, L., Bidelman, G.M., Snyder, J.S. 2017. Neural correlates of speech segregation based on formant frequencies of adjacent vowels. Sci. Rep. 7, 1-11.

Alain, C., Du, Y., Bernstein, L.J., Barten, T., Banai, K. 2018. Listening under difficult conditions: An activation likelihood estimation meta-analysis. Hum. Brain Mapp. 39, 2695-2709.

Baddeley, A.D., Thomson, N., Buchanan, M. 1975. Word length and the structure of working memory, Journal of Verbal Learning and Verbal Behavior, Vol. 14. pp. 575-589.

Bagur, S., Averseng, M., Elgueda, D., David, S., Fritz, J., Yin, P., Shamma, S., Boubenec, Y., Ostojic, S. 2018. Go/No-Go task engagement enhances population representation of target stimuli in primary auditory cortex. Nat. Commun. 9, 2529.

Baldo, J.V., Dronkers, N.F. 2006. The role of inferior parietal and inferior frontal cortex in working memory. Neuropsychology 20, 529-38.

Bashivan, P., Bidelman, G.M., Yeasin, M. 2013. Neural correlates of visual working memory load through unsupervised spatial filtering of EEG. Proceedings of Machine Learning and Interpretation in Neuroimaging (MLINI’13), Lake Tahoe, NV, Dec. 9–10, 2013.

Bashivan, P., Bidelman, G.M., Yeasin, M. 2014a. Spectrotemporal dynamics of the EEG during working memory encoding and maintenance predicts individual behavioral capacity. Eur. J. Neurosci. 40, 3774–3784.

Bashivan, P., Bidelman, G.M., Yeasin, M. 2014b. Modulation of brain connectivity by cognitive load in the working memory network, Proceedings on the IEEE Symposium Series on Computational Intelligence (IEEE SSCI), Orlando, FL.

Bashivan, P., Bidelman, G.M., Yeasin, M. 2015. Single trial prediction of normal and excessive cognitive load through EEG feature fusion, Proceedings on the IEEE Signal Processing in Medicine and Biology Symposium (IEEE SPMB), Philadelphia, PA.

Bashivan, P., Yeasin, M., Bidelman, G.M. 2017. Temporal progression in functional connectivity determines individual differences in working memory capacity. Proceedings of the International Joint Conference on Neural Networks (IJCNN 2017), Anchorage, AK, May 14 -19, 2017.

Bidelman, G.M. 2018. Subcortical sources dominate the neuroelectric auditory frequency-following response to speech. Neuroimage 175, 56–69.

Bidelman, G.M., Howell, M. 2016. Functional changes in inter- and intra-hemispheric auditory cortical processing underlying degraded speech perception. Neuroimage 124, 581-590.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.05.237727; this version posted August 5, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Bidelman, G.M., Walker, B.S. 2019. Plasticity in auditory categorization is supported by differential engagement of the auditory-linguistic network. Neuroimage 201, doi: 10.1016/j.neuroimage.2019.116022.

Bidelman, G.M., Mahmud, M.S., Yeasin, M., Shen, D., Arnott, S., Alain, C. 2019. Age-related hearing loss increases full-brain connectivity while reversing directed signaling within the dorsal-ventral pathway for speech. Brain Structure and Function 224, 2661-2676.

Boran, E., Fedele, T., Klaver, P., Hilfiker, P., Stieglitz, L., Grunwald, T., Sarnthein, J. 2019. Persistent hippocampal neural firing and hippocampal-cortical coupling predict verbal working memory load. Science advances 5, eaav3687.

Brainard, D.H. 1997. The psychophysics toolbox. Spat. Vis. 10.

Brechmann, A., Gaschler-Markefski, B., Sohr, M., Yoneda, K., Kaulisch, T., Scheich, H. 2007. Working memory–specific activity in auditory cortex: Potential correlates of sequential processing and maintenance. Cereb. Cortex 17, 2544-2552.

Buchsbaum, B.R., D'Esposito, M. 2008. The search for the phonological store: From loop to convolution. J. Cogn. Neurosci. 20, 762-78.

Colombo, M., D'Amato, M., Rodman, H., Gross, C. 1990. Auditory association cortex lesions impair auditory short-term memory in monkeys. Science 247, 336-338.

Constantinidis, C., Procyk, E. 2004. The primate working memory networks. Cogn Affect Behav Neurosci 4, 444-465.

Courtney, S.M., Ungerleider, L.G., Keil, K., Haxby, J.V. 1997. Transient and sustained activity in a distributed neural system for human working memory. Nature 386, 608-611.

Cowan, N. 1998. Visual and auditory working memory capacity, Trends. Cogn. Sci., Vol. 2. pp. 77-78.

Cowan, N. 2001. The magical number 4 in short-term memory: a reconsideration of mental storage capacity. Behav. Brain Sci. 24, 87-114; discussion 114-85.

de Lafuente, V., Romo, R. 2006. Neural correlate of subjective sensory experience gradually builds up across cortical areas. Proc. Natl. Acad. Sci. USA 103, 14266-71.

Delorme, A., Makeig, S. 2004. EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Meth. 134, 9-21.

Demany, L., Semal, C., Cazalets, J.R., Pressnitzer, D. 2010. Fundamental differences in change detection between vision and audition, Exp. Brain Res., Vol. 203. pp. 261-270.

Fonov, V.S., Evans, A.C., McKinstry, R.C., Almli, C.R., Collins, D.L. 2009. Unbiased nonlinear average age-appropriate brain templates from birth to adulthood. Neuroimage 47, S102.

Fougnie, D., Marois, R. 2011. What limits working memory capacity? Evidence for modality-specific sources to the simltaneous storage of visual and auditory arrays, J Exp Psychol Lean Mem Cog, Vol. 37. pp. 1329-1341.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.05.237727; this version posted August 5, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Füllgrabe, C., Rosen, S. 2016. On the (un)importance of working memory in speech-in-noise processing for listeners with normal hearing thresholds. Front. Psychol. 7.

Fuster, J.M., Alexander, G.E. 1971. Neuron activity related to short-term memory. Science 173, 652-4.

Gaab, N., Keenan, J.P., Schlaug, G. 2003a. The effects of gender on the neural substrates of pitch memory. J. Cogn. Neurosci. 15, 810-20.

Gaab, N., Gaser, C., Zaehle, T., Jancke, L., Schlaug, G. 2003b. Functional anatomy of pitch memory--an fMRI study with sparse temporal sampling. Neuroimage 19, 1417-26.

Golob, E.J., Starr, A. 2000. Effects of stimulus sequence on event-related potentials and reaction time during target detection in Alzheimer's disease. Clin. Neurophysiol. 111, 1438–49.

Grady, C.L., Yu, H., Alain, C. 2008. Age-related differences in brain activity underlying working memory for spatial and nonspatial auditory information, Cereb. Cortex, Vol. 18. pp. 189-199.

Grimault, S., Lefebvre, C., Vachon, F., Peretz, I., Zatorre, R., Robitaille, N., Jolicoeur, P. 2009. Load-dependent brain activity related to acoustic short-term memory for pitch: magnetoencephalography and fMRI. Ann. N. Y. Acad. Sci. 1169, 273-7.

Grimault, S., Nolden, S., Lefebvre, C., Vachon, F., Hyde, K., Peretz, I., Zatorre, R., Robitaille, N., Jolicoeur, P. 2014. Brain activity is related to individual differences in the number of items stored in auditory short-term memory for pitch: Evidence from magnetoencephalography. Neuroimage 94, 96-106.

Habeck, C., Rakitin, B.C., Moeller, J., Scarmeas, N., Zarahn, E., Brown, T., Stern, Y. 2005. An event-related fMRI study of the neural networks underlying the encoding, maintenance, and retrieval phase in a delayed-match-to-sample task. Cognitive Brain Research 23, 207-220.

Hickok, G., Poeppel, D. 2004. Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. Cognition 92, 67-99.

Hickok, G., Poeppel, D. 2007. The cortical organization of speech processing. Nat. Rev. Neurosci. 8, 393-402.

Huang, Y., Matysiak, A., Heil, P., König, R., Brosch, M. 2016. Persistent neural activity in auditory cortex is related to auditory working memory in humans and nonhuman primates. eLife 5, e15441.

Hultin, L., Rossini, P., Romani, G.L., Högstedt, P., Tecchio, F., Pizzella, V. 1996. Neuromagnetic localization of the late component of the contingent negative variation. Electroencephalogr. Clin. Neurophysiol. 98, 435-448.

Iordanov, T., Hoechstetter, K., Berg, P., Paul-Jordanov, I., Scherg, M. 2014. CLARA: classical LORETA analysis recursively applied, OHBM 2014.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.05.237727; this version posted August 5, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Karlsgodt, K.H., Shirinyan, D., Van Erp, T.G.M., Cohen, M.S., Cannon, T.D. 2005. Hippocampal activations during encoding and retrieval in a verbal working memory paradigm, Neuroimage, Vol. 25. pp. 1224-1231.

King, J., Just, M.A. 1991. Individual differences in syntactic processing: The role of working memory. Journal of Memory and Language 30, 580-602.

Kononowicz, T.W., Penney, T.B. 2016. The contingent negative variation (CNV): Timing isn't everything. Current Opinion in Behavioral Sciences 8, 231-237.

Kovac, S., Speckmann, E.J., Gorji, A. 2018. Uncensored EEG: The role of DC potentials in neurobiology of the brain. Prog. Neurobiol. 165-167, 51-65.

Kumar, S., Joseph, S., Gander, P.E., Barascud, N., Halpern, A.R., Griffiths, T.D. 2016. A brain system for auditory working memory. J. Neurosci. 36, 4492-4505.

Lefebvre, C., Vachon, F., Grimault, S., Thibault, J., Guimond, S., Peretz, I., Zatorre, R.J., Jolicoeur, P. 2013. Distinct electrophysiological indices of maintenance in auditory and visual short-term memory. Neuropsychologia 51, 2939-52.

Leuthold, H., Jentzsch, I. 2001. Neural correlates of advance movement preparation: a dipole source analysis approach. Cognitive Brain Research 12, 207-224.

Linde-Domingo, J., Treder, M.S., Kerrén, C., Wimber, M. 2019. Evidence that neural information flow is reversed between object perception and object reconstruction from memory. Nat. Commun. 10, 179.

Linke, A.C., Cusack, R. 2015. Flexible information coding in human auditory cortex during perception, imagery, and STM of complex sounds, J. Cogn. Neurosci., Vol. 27. pp. 1322-1333.

Linke, A.C., Vicente-Grabovetsky, A., Cusack, R. 2011. Stimulus-specific suppression preserves information in auditory short-term memory. Proc. Natl. Acad. Sci. USA 108, 12961-12966.

Lu, Z.L., Williamson, S.J., Kaufman, L. 1992a. Behavioral lifetime of human auditory sensory memory predicted by physiological measures. Science 258, 1668-70.

Lu, Z.L., Williamson, S.J., Kaufman, L. 1992b. Human auditory primary and association cortex have differing lifetimes for activation traces. Brain Res. 572, 236-41.

Luck, S.J., Vogel, E.K. 2013. Visual working memory capacity: From psychophysics and neurobiology to individual differences. Trends. Cogn. Sci. 17, 391-400.

Mankel, K., Barber, J., Bidelman, G.M. 2020. Auditory categorical processing for speech is modulated by inherent musical listening skills. Neuroreport 31, 162-166.

Masse, N.Y., Rosen, M.C., Freedman, D.J. 2020. Reevaluating the role of persistent neural activity in short-term memory. Trends. Cogn. Sci. 24, 242-258.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.05.237727; this version posted August 5, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Mencarelli, L., Neri, F., Momi, D., Menardi, A., Rossi, S., Rossi, A., Santarnecchi, E. 2019. Stimuli, presentation modality, and load-specific brain activity patterns during n-back task. Hum. Brain Mapp. 40, 3810-3831.

Metzak, P., Feredoes, E., Takane, Y., Wang, L.M., Weinstein, S., Cairo, T., Ngan, E.T.C., Woodward, T.S. 2011. Constrained principal component analysis reveals functionally connected load-dependent networks involved in multiple stages of working memory. Hum. Brain Mapp. 32, 856-871.

Michel, C.M., Murray, M.M., Lantz, G., Gonzalez, S., Spinelli, L., Grave de Peralta, R. 2004. EEG source imaging. Clin. Neurophysiol. 115, 2195-222.

Miller, G.A. 1956. The magical number seven plus or minus two: some limits on our capacity for processing information. Psychol. Rev. 63, 81-97.

Nation, K., Adams, J.W., Bowyer-Crane, C.A., Snowling, M.J. 1999. Working memory deficits in poor comprehenders reflect underlying language impairments. J. Exp. Child Psychol. 73, 139-158.

Oldfield, R.C. 1971. The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia 9, 97-113.

Oostenveld, R., Praamstra, P. 2001. The five percent electrode system for high-resolution EEG and ERP measurements. Clin. Neurophysiol. 112, 713-719.

Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.M. 2011. Fieldtrip: Open source software for advanced analysis of meg, eeg, and invasive electrophysiological data. Comput. Intell. Neurosci. 2011, 1-9.

Pascual-Marqui, R.D., Esslen, M., Kochi, K., Lehmann, D. 2002. Functional imaging with low-resolution brain electromagnetic tomography (LORETA): a review. Methods Find. Exp. Clin. Pharmacol. 24 Suppl C, 91-5.

Pashler, H. 1988. Familiarity and visual change detection. Percept. Psychophys. 44, 369-378.

Petrides, M., Pandya, D.N. 2006. Efferent association pathways originating in the caudal prefrontal cortex in the macaque monkey. J. Comp. Neurol. 498, 227-51.

Picton, T.W., Woods, D.L., Proulx, G.B. 1978. Human auditory sustained potentials. I. The nature of the response. Electroencephalogr. Clin. Neurophysiol. 45, 186-197.

Picton, T.W., van Roon, P., Armilio, M.L., Berg, P., Ille, N., Scherg, M. 2000. The correction of ocular artifacts: A topographic perspective. Clin. Neurophysiol. 111, 53-65.

Picton, T.W., Alain, C., Woods, D.L., John, M.S., Scherg, M., Valdes-Sosa, P., Bosch-Bayard, J., Trujillo, N.J. 1999. Intracerebral sources of human auditory-evoked potentials. Audiol. Neurootol. 4, 64-79.

Pratt, H., Michalewski, H.J., Barrett, G., Starr, A. 1989. Brain potentials in a memory-scanning task. I. Modality and task effects on potentials to the probes. Electroencephalogr. Clin. Neurophysiol. 72, 407-421.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.05.237727; this version posted August 5, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Rahnev, D., Nee, D.E., Riddle, J., Larson, A.S., D'Esposito, M. 2016. Causal evidence for frontal cortex organization for perceptual decision making. Proc. Natl. Acad. Sci. USA 113, 6059-6064.

Ranganath, C., Blumenfeld, R.S. 2005. Doubts about double dissociations between short- and long-term memory. Trends in Cognitive Science 9, 374-80.

Rose, N.S., LaRocque, J.J., Riggall, A.C., Gosseries, O., Starrett, M.J., Meyering, E.E., Postle, B.R. 2016. Reactivation of latent working memories with transcranial magnetic stimulation. Science 354, 1136-1139.

Sakurai, Y. 1994. Involvement of auditory cortical and hippocampal neurons in auditory working memory and reference memory in the rat. J. Neurosci. 14, 2606-2623.

Salazar, R.F., Dotson, N.M., Bressler, S.L., Gray, C.M. 2012. Content-specific fronto-parietal synchronization during visual working memory. Science 338, 1097-100.

Scott, B.H., Mishkin, M., Yin, P. 2014. Neural correlates of auditory short-term memory in rostral superior temporal cortex. Curr. Biol. 24, 2767-2775.

Siegel, M., Buschman, T.J., Miller, E.K. 2015. Cortical information flow during flexible sensorimotor decisions. Science 348, 1352-1355.

Sreenivasan, K.K., Curtis, C.E., D'Esposito, M. 2014. Revisiting the role of persistent neural activity during working memory, Trends. Cogn. Sci., Vol. 18. Elsevier Ltd. pp. 82-89.

Sternberg, S. 1966. High-speed scanning in human memory. Science 153, 652-654.

Thomason, M.E., Race, E., Burrows, B., Whitfield-Gabrieli, S., Glover, G.H., Gabrieli, J.D.E. 2009. Development of spatial and verbal working memory capacity in the human brain. J. Cogn. Neurosci. 21, 316-332.

Thompson-Schill, S.L., Jonides, J., Marshuetz, C., Smith, E.E., D'Esposito, M., Kan, I.P., Knight, R.T., Swick, D. 2002. Effects of frontal lobe damage on interference effects in working memory, Cognitive, Affective and Behavioral Neuroscience, Vol. 2. pp. 109-120.

Vogel, E.K., Machizawa, M.G. 2004. Neural activity predicts individual differences in visual working memory capacity. Nature 428, 748-51.

Walter, W.G., Cooper, R., Aldridge, V.J., McCallum, W.C., Winter, A.L. 1964. Contingent negative variation: An electric sign of sensorimotor association and expectancy in the human brain. Nature 203, 380-4.

Weinberger, N.M. 1993. Learning-induced changes of auditory receptive fields. Curr. Opin. Neurobiol. 3, 570-7.

Weinberger, N.M. 2004. Specific long-term memory traces in primary auditory cortex. Nature reviews. Neuroscience 5, 279-290.

bioRxiv preprint doi: https://doi.org/10.1101/2020.08.05.237727; this version posted August 5, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Wilson, S.M., Isenberg, A.L., Hickok, G. 2009. Neural correlates of word production stages delineated by parametric modulation of psycholinguistic variables. Hum. Brain Mapp. 30, 3596-608.

Woods, D.L., Herron, T.J., Cate, A.D., Yund, E.W., Stecker, G.C., Rinne, T., Kang, X. 2010. Functional properties of human auditory cortical fields. Front Syst Neurosci 4, 155.

Xiao, Y., Wu, J., Li, J., Tang, W., Ma, F., Sun, C., Yang, Y., Zhan, W., Wang, L., Yan, H., Xu, F., Chen, S. 2019. The neuro patterns prior to error responses in long-lasting working memory task: An event-related potential study, Frontiers in Behavioral Neuroscience, Vol. 13. pp. 1-11.

Yue, Q., Martin, R.C., Hamilton, A.C., Rose, N.S. 2019. Non-perceptual regions in the left inferior parietal lobe support phonological short-term memory: Evidence for a buffer account? Cereb. Cortex 29, 1398-1413.

Zatorre, R.J., Samson, S. 1991. Role of the right temporal neocortex in retention of pitch in auditory short-term memory. Brain 114 (Pt 6), 2403-17.

Zatorre, R.J., Evans, A.C., Meyer, E. 1994. Neural mechanisms underlying melodic perception and memory for pitch. J. Neurosci. 14, 1908-1919.