Dynamics underlying auditory working memory

Pradeep Dheerendra[1,2], Sukhbinder Kumar[1,2], Yoshihito Shigihara[1,3], Timothy D Griffiths[1,2]

1 - Wellcome Centre for Human Neuroimaging, University College London, UK 2 - Biosciences Institute, Newcastle University, UK 3 – Hokuto Hospital, Hokkaido, Japan

pradeep.dheerendra@gmail.com **Website: www.auditorycognition.org**

Introduction

- Auditory working memory (WM) pertains to the process of keeping representations of auditory objects in mind for short durations when the sounds are not in the environment. It is different from phonological WM as the sounds cannot be assigned a semantic label.
- A previous fMRI AWM study [1] in humans with a maintenance delay of 16s showed enhanced BOLD activity in a network consisting of auditory cortex (AC), hippocampus, and inferior frontal gyrus (IFG) but the underlying neuronal dynamics was not known.
- Recent Human ECoG study [2] with a maintenance delay of 3s showed theta enhancement in the hippocampus, and alpha suppression in the auditory cortex.

Aim

❖ We sought to reveal the spectral and temporal dynamics underlying the neuronal activity during maintenance of pitch of a single tone in humans using MEG. What is the role of alpha, theta, and beta oscillations? Is the evoked activity transient or persistent?

Experiment I

- Delayed match to sample paradigm was employed: pitch of a test tone was matched against the maintained tone. Button press conveyed same or different response

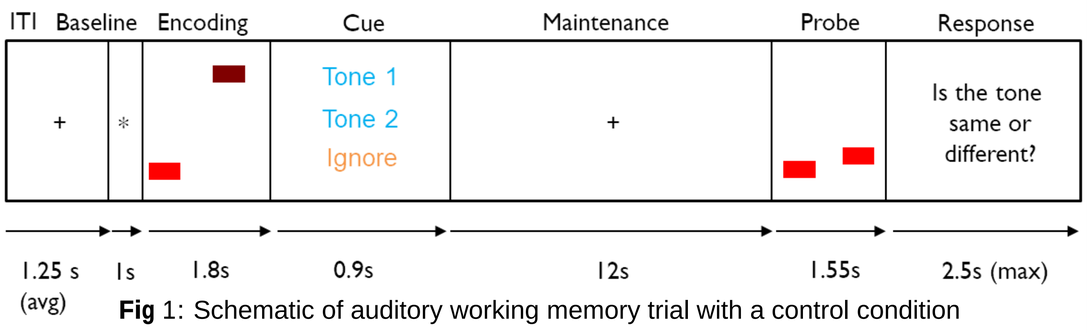

Fig 1: Schematic of auditory working memory trial with a control condition

- Whole head 275-channel MEG data was recorded from 17 subjects using CTF scanner
- MEG data pre-processing: Low pass at 120 Hz. Down-sampled to 300 Hz. SPM's eye-blink artefact rejection applied. Manual artefact rejection (using z-score) performed: 5 subjects rejected. Baseline corrected to pre-stimulus [0 1s] interval.

Results I

- Behaviour: Avg. accuracy in AWM task was 79% while in control task was 91%.
- RMS field strength across all central channels was calculated for both conditions in each subject. The difference between conditions, subjected to bootstrap resampling (1000 iterations, balanced), were considered significant if proportion of bootstrap that fell above or below zero was >99.5% for 15 or more consecutive samples.
- Enhanced evoked activity persistent throughout maintenance as compared to silent pre-stimulus baseline. But enhanced only at start of retention as compared to control condition.

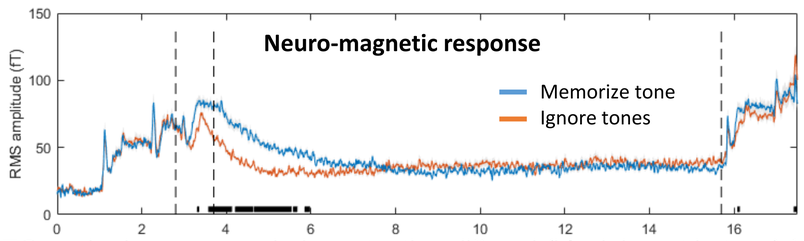

Fig 2: MEG evoked responses during retention differed (black bar at bottom) from control

- Using Greedy Search, source localisation of evoked response showed activity in the right auditory cortex (HG, PT) during the 1st sec of retention and in bilateral AC during entire 12 s of retention. This is similar to auditory cortex activity during encoding phase.
- Using DICS beamforming algorithm, induced activity during the first second of maintenance was source localised in different frequency bands contrasted against the silent pre-stimulus baseline.
- **Theta** (4-8 Hz) was enhanced (cluster corrected) in medial pre-frontal cortex which was phase locked [7] to activity in left temporal pole. Frontal midline theta activity during WM retention is well known [3].
- Theta was suppressed (FWE) in left posterior STG. Gamma (30-60 Hz) was suppressed (FWE) in Ant Cingulate Gyrus.
- **Alpha** (8-12 Hz) was suppressed (cluster corr.) in left Auditory Cortex in line with mnemonic retention: inhibition of relevant sensory cortex [4]
- **Beta** (13-30 Hz) was enhanced (small vol. corr.) in cerebellum. Previous studies [5] has shown cerebellar involvement in verbal WM for covert rehearsal. The cerebellum result from Experiment II was used as spatial prior in small volume correction.
- **Beta** was suppressed (FWE) in left supramarginal gyrus (SMG). This suggests suppression of the phonological loop which is implicated in verbal WM studies [6].

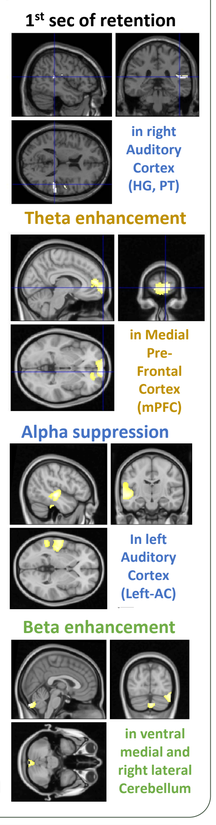

Fig 3: DICS source localisation of induced response during 1st s of retention

Abstract

- We aimed to understand the dynamics underlying auditory working memory for maintaining 'simple' tones. We recorded magnetoencephalography (MEG) in 17 subjects while they maintained one of the 2 presented tones or ignored both in the control condition. After 12s, they compared the pitch of a test tone with the maintained tone.
- Analysis of evoked responses showed persistent activity throughout retention compared to the pre-stimulus baseline but only at the start compared to the control condition. The evoked response during maintenance was source localised against baseline to bilateral auditory cortex. Analysis of the induced responses showed suppressed alpha in the left AC, enhanced theta in the medial prefrontal, and enhanced beta in the cerebellum.
- 19 new subjects were presented with a tone and a Gabor patch and a cue indicating whether to maintain auditory or visual information for 12s. Analysis of the induced responses in auditory condition yielded results similar to those observed in the first experiment. Connectivity analysis showed that the theta activity in the medial pre-frontal cortex was phase-locked to activity in the left hippocampus and left auditory cortex. The beta activity in the cerebellum was phase-locked to left IFG activity and correlated to subject's task accuracy.
- Our data shows a WM network involving pre-frontal cortex, hippocampus, & cerebellum for maintaining sounds.

Experiment II

- Delayed match to sample paradigm was employed in 19 new subjects: pitch of a pure tone was maintained for 12s or width of a Gabor patch in alternate visual task. Button press conveyed same or different response

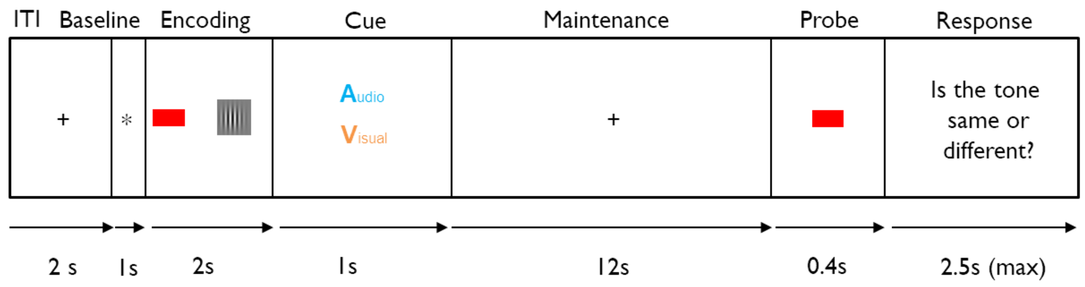

Fig 4: Schematic of auditory working memory trial with a visual WM as control condition

Results II

- Behaviour: Avg. accuracy in AWM task was 83% while in VWM task was 65%. Due to the difference in task difficulty between conditions the visual WM condition is not interpreted or compared with AWM condition.
- RMS field strength across all temporal channels in each subject was averaged across group. Enhanced evoked activity was observed during entire retention w.r.t silent pre-stimulus baseline.

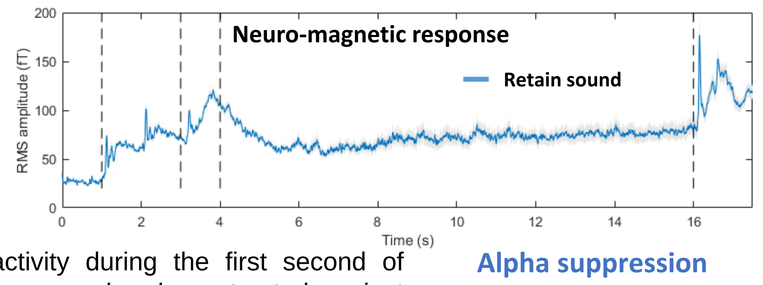

Fig 5: MEG evoked responses for AWM condition

- Using DICS beamforming algorithm, induced activity during the first second of maintenance was source localised in different frequency bands contrasted against the silent pre-stimulus baseline.
- **Alpha** (8-12 Hz) was suppressed (small volume corrected) in left Auditory Cortex during AWM. This is in line with alpha's mnemonic retention role [4]
- **Theta** (4-8 Hz) was enhanced (FWE) in medial prefrontal which was phase locked [7] (cluster corr.) to activity in left posterior hippocampus, left auditory cortex, right IFG, right SMA. Frontal midline theta activity during WM retention is well known [3].
- Theta was suppressed (FWE corrected across entire brain) in left supramarginal gyrus (SMG).
- Lower Gamma (30-60 Hz) was suppressed (cluster corrected) in left SMG.
- **Beta** (13-30 Hz) was enhanced (FWE) in cerebellum which was phase locked [7] (FWE) to activity in left inferior frontal gyrus or Broca's area and this PLV was correlated to subject accuracy (rho= 0.88, p<7e-7). Cerebellum might be involved in covert rehearsal [5] of pure tones.
- **Beta** was suppressed (FWE) in left SMG. Robust self replication of this result. Possible suppression of the phonological loop implied in verbal WM studies [6].

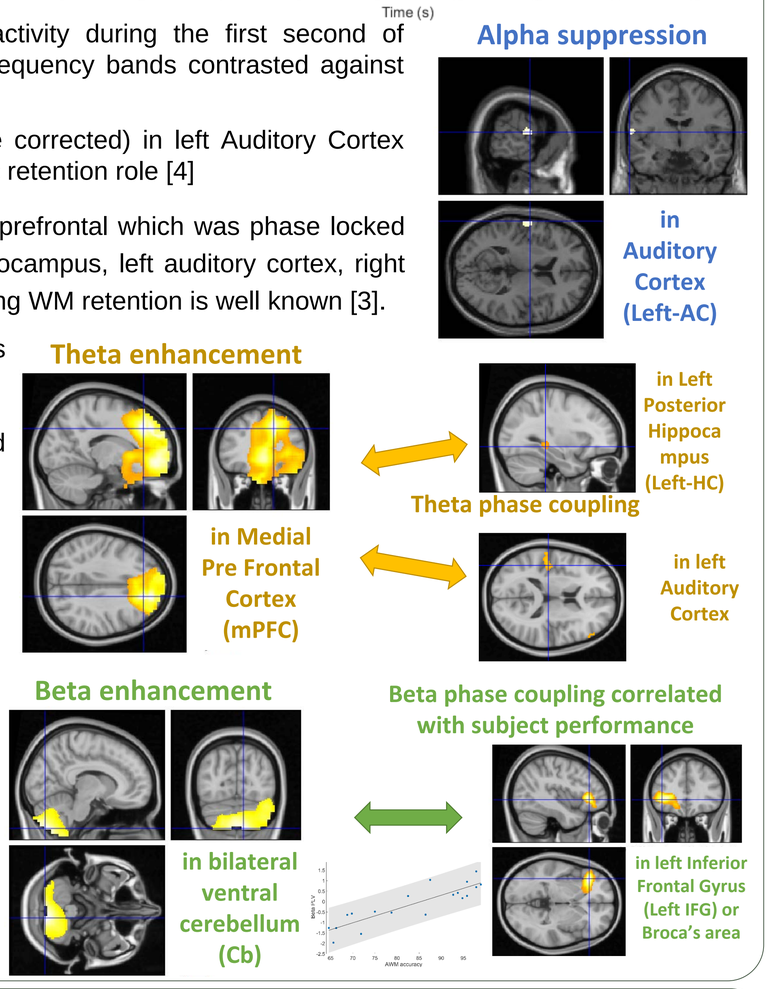

Fig 6: DICS source localisation of MEG induced responses during 1st s of retention in AWM cond.

Model

Conclusions

❖ Auditory Cortex retains representations of sounds for short durations.

❖ We speculate that this is enabled by focus of attention via the prefrontal cortex and covert rehearsal by Broca's area.

References:

[1] Kumar S, et al., (2016) J Neurosci.

[2] Kumar S, et al., (2020) bioRxiv.

[3] Hsieh & C Ranganath, (2014) Neuroimage.

[4] Freek van Ede, (2018) EJN.

[5] Marvel, C.L. and Desmond, J.E., (2010) Neuropsychology review

[6] Deschamps et. al., (2014), Neuropsychologia

[7] Rick Adams, et. al., (2020), Brain