fMRI pattern analysis of working memory representations in auditory and visual cortex

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Introduction

Working memory performance can be predicted from the activity patterns in the visual cortex for orientation (Harrison and Tong, 2009; Serences et al., 2009), color (Serences et al., 2009) , contrast (Xing et al., 2013), and motion (Riggall and Postle, 2012; Emrich et al., 2013; Christophel and Haynes, 2014). In areas V1 and V2 encoding is retinotopic, but not in higher visual areas (Ester et al., 2009; Pratte and Tong, 2014). Categorization of more complex images, such as faces, scenes and flowers, can also be decoded during memory maintenance (Chen et al., 2012; Linden et al., 2012; Sreenivasan et al., 2014). Pattern classification accuracy decreases as a function of memory load and precision (Emrich et al., 2013).

We tested 1) whether memory load interferes the activity patterns reflecting working memory representations in the visual and auditory cortices, and 2) whether the memory interference is modality specific.

Methods

Participants

-Healthy volunteers (N=17, 11 female, mean age 24 years), who signed a written informed consent before the experiment. The experimental protocol was approved by the Ethical Committee of the Hospital District of Helsinki and Uusimaa.

Stimuli

-Sinewave gratings: duration 700 ms, four different orientations (-40, -20, 20 and 40 deg from vertical) and spatial frequencies (0.5-2.0 c/deg)

-Stream of sinewave tones: duration 700 ms (14x40 ms tone + 10 ms silence), random variation of pitch, four different average pitches (800, 1000, 1200 and 1400 Hz) and frequency ranges (150, 175, 200 and 225 Hz)

fMRI

-BOLD signal changes were measured with a 3T fMRI scanner (TR 2300 ms, slice thickness 3.0 mm)

Representational Similarity Analysis

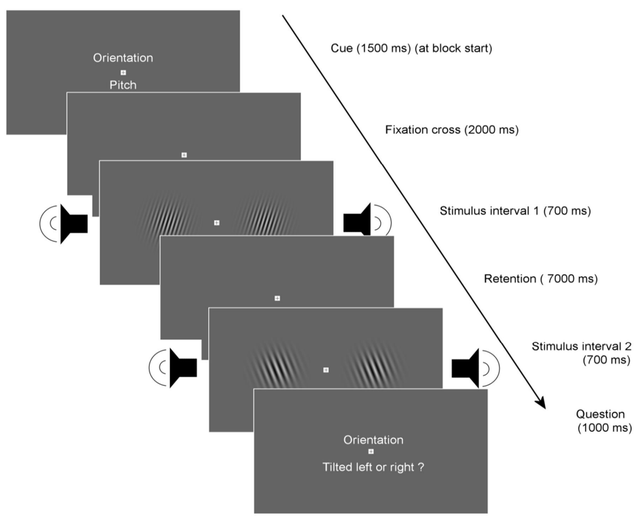
-Representational Dissimilarity Matrices (Kriegeskorte et al., 2008) were calculated separately from all trials, correct trials and incorrect trials

-Measured RDMs were compared to model RDMs based on feature value (e.g., orientation -60, -20, +20, +60), number of features to be remembered (one vs. two features), and modality of features (intra- vs. cross-modal)

Experimental setup

Five delayed (7 s memory interval) two-interval forced-choice discrimination tasks (Salmela et al., 2014) memorize :

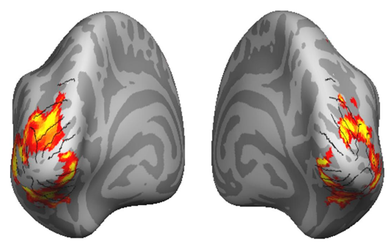
1) one visual feature (orientation)
2) two visual features (orientation and spatial frequency)
3) one auditory feature (average pitch)
4) two auditory features (average pitch and variation of pitch)
5) two features in different modalities (orientation and average pitch)



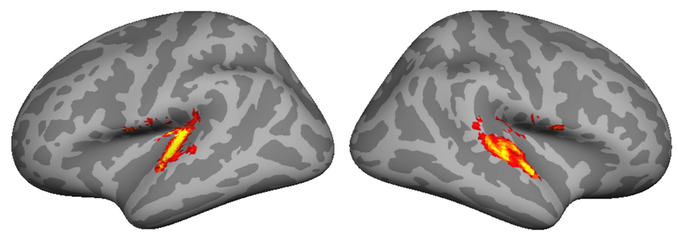
Functional localizers

Visual and auditory cortices were localized with functional localizers. Visual localizer was contrast-reversing checkerboard, and auditory localizer was a random stream of sinewave tones. On average 370 voxels in visual cortex and 140 voxels in auditory cortex were selected for further analyses.

Visual cortex

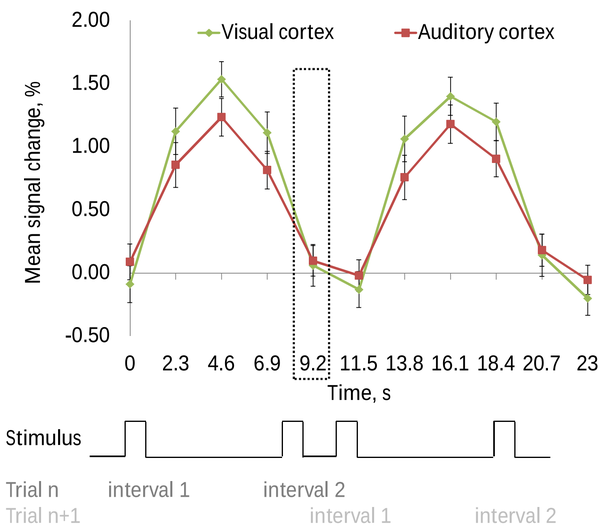


Auditory cortex



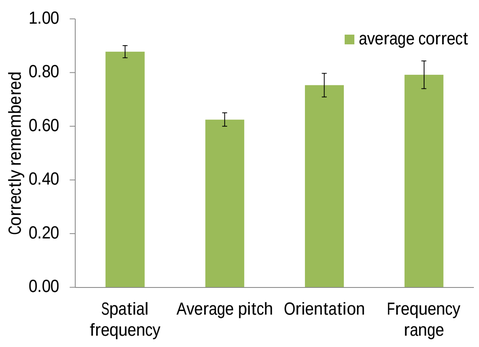
BOLD-signal change

BOLD signal was averaged for each stimulus event for time points 0-12 s. The time point 9.2 s after stimulus onset (dotted box) was selected for further analyses.



Behavioral responses

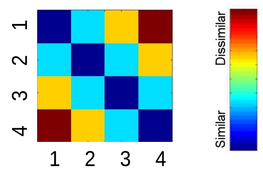
The average of correct responses was 75%.



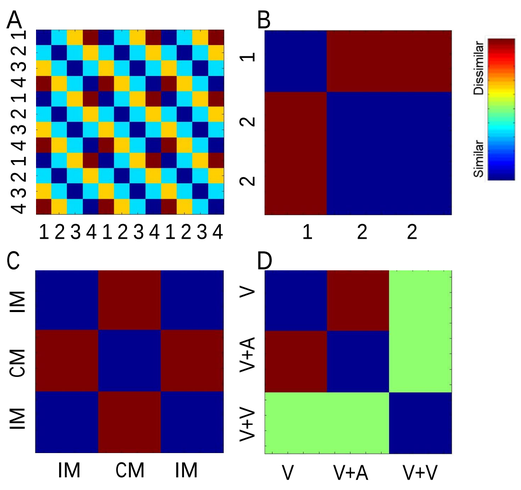
Model RDMs

Expected dissimilarity of activity patterns based on:

1. Feature value

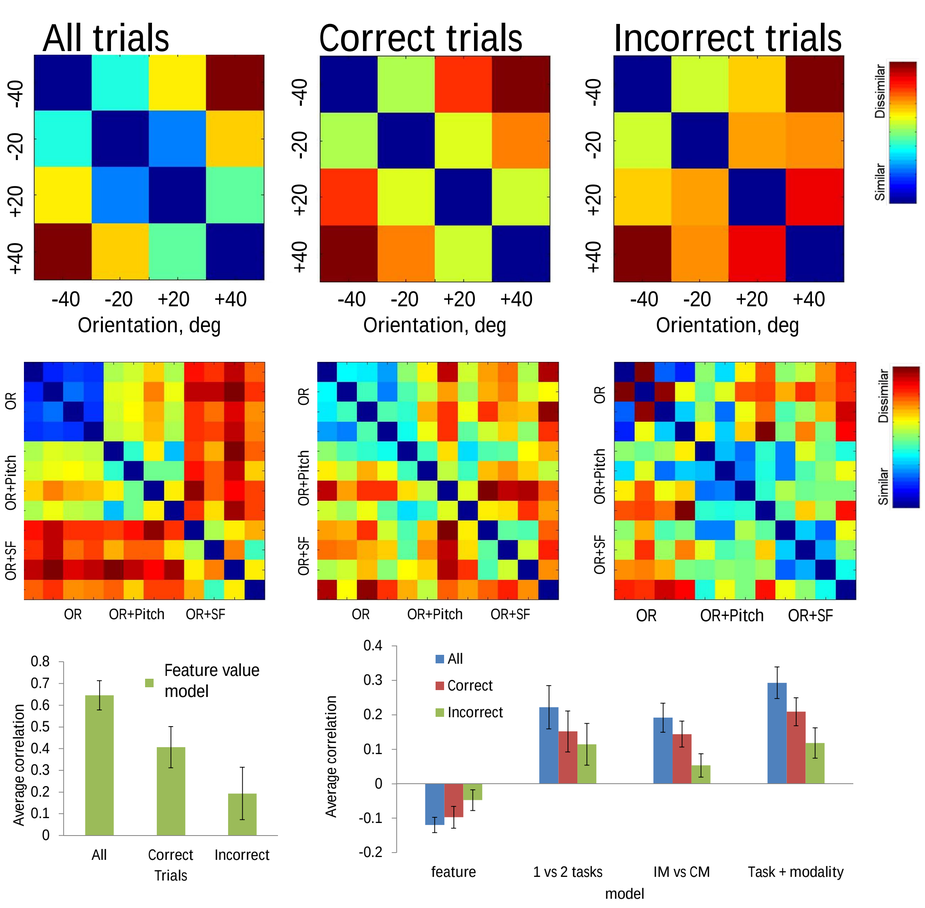


2. A) Feature value, B) number and C) modality of features to remembered, and D) both number and modality of features

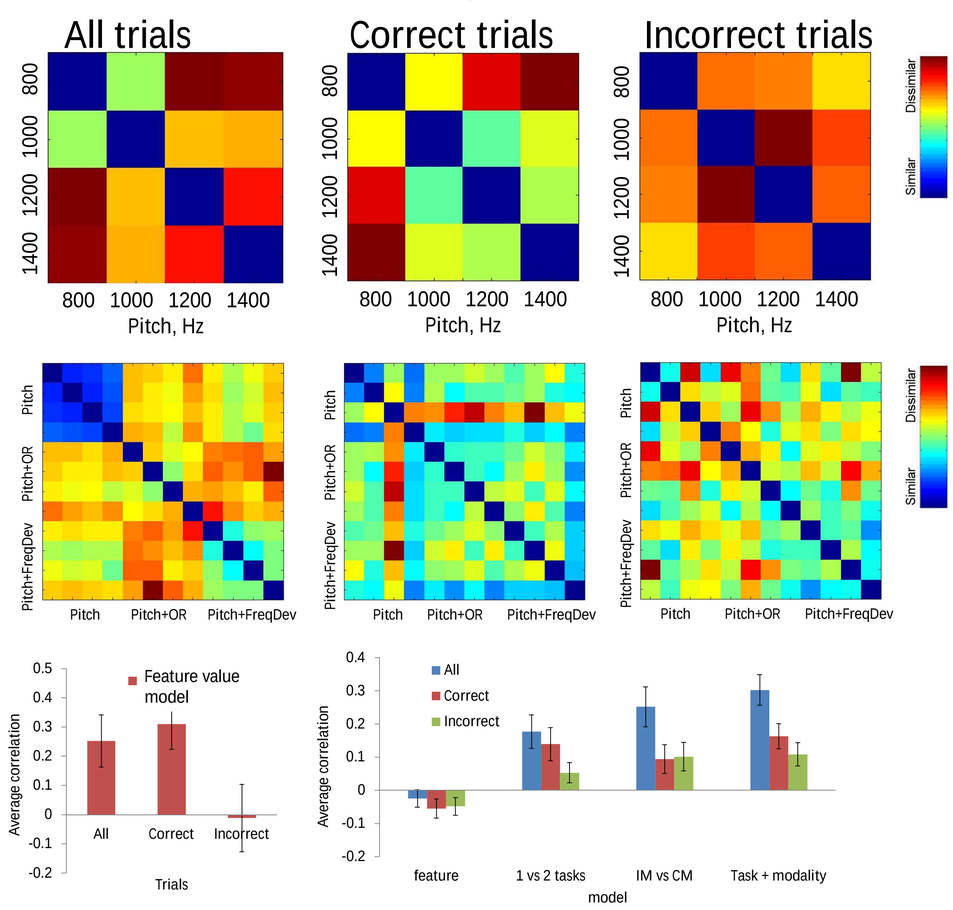


IM = Intra-Modal; CM = Cross-Modal; V = Visual; A = Auditory

Measured RDMs: Visual cortex



Measured RDMs: Auditory cortex



Results

Orientation related activity patterns in visual cortex

Similar orientations elicited more similar patterns than dissimilar orientations ($p<.05$, permutation test).

Pitch related activity patterns in auditory cortex

Tones with similar pitches elicited more similar patterns than tones with dissimilar pitches ($p<.05$, permutation test).

More prominent patterns during correctly remembered trials than incorrect trials

Higher correlations between expected and measured patterns in correct than in incorrect trials.

In incorrect trials average correlation dropped to zero (auditory cortex) or close to zero (visual cortex).

Global task-related effects abolish feature-related patterns

The experimental manipulations (one vs. two features; intra- vs. cross-modal features) had a strong effect on the similarity structure of the activity patterns.

The task-related effects slightly stronger for correct than incorrect trials.

Dissimilar patterns for one vs. two feature conditions, irrespective of the modality of the features.

Strongest correlation between the measured matrices and the model matrix describing the experimental manipulations.

Conclusions

We found feature specific activity patterns during working memory maintenance, both in visual and auditory cortices.

Feature-specific patterns were suppressed by the strong effect of multi-tasking or memory load.

The results support the role of sensory cortices in working memory maintenance, but highlight the role of global task-related effects in these areas.

Similar patterns during intra-modal and cross-modal conditions might suggest domain-general working memory resources.

Acknowledgements

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References

Chen AJ, Britton M, Turner GR, Vytlacil J, Thompson TW, D'Esposito M (2012) Goal-directed attention alters the tuning of object-based representations in extrastriate cortex. Frontiers in human neuroscience 6:187.

Christophel TB, Haynes JD (2014) Decoding complex flow-field patterns in visual working memory. Neuroimage 91:43-51.

Emrich SM, Riggall AC, Larocque JJ, Postle BR (2013) Distributed patterns of activity in sensory cortex reflect the precision of multiple items maintained in visual short-term memory. J Neurosci 33:6516-6523.

Ester EF, Serences JT, Awh E (2009) Spatially global representations in human primary visual cortex during working memory maintenance. J Neurosci 29:15258-15265.

Harrison SA, Tong F (2009) Decoding reveals the contents of visual working memory in early visual areas. Nature 458:632-635.

Kriegeskorte N, Mur M, Bandettini P (2008) Representational similarity analysis - connecting the branches of systems neuroscience. Frontiers in systems neuroscience 2:4.

Linden DE, Oosterhof NN, Klein C, Downing PE (2012) Mapping brain activation and information during category-specific visual working memory. J Neurophysiol 107:628-639.

Pratte MS, Tong F (2014) Spatial specificity of working memory representations in the early visual cortex. J Vis 14:22.

Riggall AC, Postle BR (2012) The relationship between working memory storage and elevated activity as measured with functional magnetic resonance imaging. J Neurosci 32:12990-12998.

Salmela VR, Moisala M, Alho K (2014) Working memory resources are shared across sensory modalities. Attention, perception & psychophysics in press.

Serences JT, Ester EF, Vogel EK, Awh E (2009) Stimulus-specific delay activity in human primary visual cortex. Psychological science 20:207-214.

Sreenivasan KK, Vytlacil J, D'Esposito M (2014) Distributed and dynamic storage of working memory stimulus information in extrastriate cortex. J Cogn Neurosci 26:1141-1153.

Xing Y, Ledgeway T, McGraw PV, Schluppeck D (2013) Decoding working memory of stimulus contrast in early visual cortex. J Neurosci 33:10301-10311.