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The Neural Fate of Individual Item Representations in Visual Working Memory

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Summary

Problem/Research Questions

Visual working memory (VWM) allows us to temporarily store relevant information from the visual world despite frequent interruptions such as saccades. Despite the importance of VWM in a variety of cognitive tasks, this process is capacity limited. Behavioral estimates of capacity converge on a storage limit of ~3-4 items (Cowan, 2001). Converging neural evidence from neuroimaging techniques supports these behavioral estimates. For example, in functional magnetic resonance imaging (fMRI) experiments, delay-related activity in regions of posterior parietal cortex increases according to the number of items held within VWM (Todd & Marois, 2004; Xu & Chun, 2006). When capacity is reached the signal asymptotes, indicating that no additional neural resources are available to store any remaining items. Additionally, an event-related potential (ERP) known as the contralateral delay activity (CDA) has been used to measure storage capacity by recording from posterior scalp sites during the delay period during VWM tasks. The CDA amplitude increases as additional items are added, reaching asymptote when individual item limits are reached (Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005).

Importantly, in these previous studies the neural correlates of VWM capacity reflect the aggregate processing of all of the presented stimuli. As such, the neural-correlate signal associated with each individual item is obscured within this cumulative activity. Additionally, the majority of these studies have focused almost exclusively on maintenance processes, creating uncertainty regarding the influence of encoding processes on capacity limitations. This leaves a fundamental but important question regarding basic VWM processes unanswered. Can cumulative neural activity during encoding be used to understand the neural fate of individual items presented in VWM tasks? Here we present evidence that cumulative activity during VWM encoding can be used to identify and quantify the neural-correlate signals associated with individual stimuli. Additionally, we describe novel frequency tagging, steady-state visual evoked potential (SSVEP) techniques used to isolate and examine these neural-correlate signals.

Hypotheses

Given the assumption that a greater amount of neural resources are needed to facilitate subsequent retrieval of previously viewed items presented during a VWM change detection task, our predictions were as follows. First, across experimental trials, we predicted that items successfully retrieved from VWM would be associated with larger frequency tag amplitudes compared to those that were not. Such an outcome would be consistent with a

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hypothesis that differential processing of items during encoding contributes to errors made at the time of retrieval.

Methods

Behavioral task procedure—For each trial, four novel shapes were presented. Each shape flickered black and white at one of four distinct frequencies (3 Hz, 5 Hz, 12 Hz, 20 Hz), for 1000 milliseconds. After a blank delay period (1000 ms) a single, static shape appeared at one of the previous locations. Participants were to respond whether the test item was "old" or "new" (chance = 50%).

Electrophysiological techniques and SSVEP analyses—During the behavioral task the EEG was continuously recorded from an array of standard electrode sites (O1, O2, Oz, P1, P2, C1, C2). First, to ensure that SSVEP's were detectable across all trials in general, we analyzed the activity during the encoding period using the T2circ statistic to assess whether the amplitude and phase of the Fourier component at each frequency of interest could be reliably detected for each participant (Victor & Mast, 1991). Trials were sorted according to the frequency tag of the probed item and accuracy of the response (correct or incorrect). Due to an uneven number of correct and incorrect trials at each frequency, permutation analyses were conducted wherein the same number of correct and incorrect trials contributed to the analysis of the frequency tag amplitudes for each frequency. Specifically, because there were more correct than incorrect trials for each frequency tag, a subset of correct trials, equal to the number of incorrect trials, were randomly sampled (during 100 independent permutations) to compute the average amplitude corresponding to each frequency tag.

Results—For each condition (3 Hz-correct, 3 Hz –incorrect, 5 Hz-correct, 5 Hz –incorrect, 12 Hz-correct, 12 Hz –incorrect, 20 Hz-correct, 20 Hz -incorrect) the amplitude of the corresponding fundamental frequency 'f1' (i.e., 3, 5, 12, 20 Hz) and second harmonic 'f2' (i.e., 5, 10, 24, 40 Hz) was extracted from the amplitude spectrum. For each condition an accuracy index was computed for both the fundamental and second harmonic using the formulas: $AI_{f1} = (f1_{correct} - f1_{incorrect})/ (f1_{correct} + f1_{incorrect})$ and $AI_{f2} = (f2_{correct} - f2_{incorrect})/ (f2_{correct} + f2_{incorrect})$, respectively. Group-level analyses were based on the average of these AI values across the four flicker frequencies. For each electrode site, one-sample t-tests were used to determine whether the mean of accuracy indices comparing items which were successfully retrieved from those that were not were significantly different from zero. The resulting accuracy indices were significant at several electrode sites corresponding to the second harmonic. Thus, cumulative activity during encoding can be examined using frequency tagging, SSVEP techniques to identify and measure the neural-correlate signals associated with individual stimuli. In turn, comparing these neural-correlate signals for items successfully retrieved from VWM and those that were not can be used to understand the fate of individual stimuli presented in VWM paradigms.

Conclusions & Implications—We present a novel approach to identify and measure neural activity associated with individual items during VWM encoding. This work applied frequency tagging, SSVEP techniques. These signals can be compared to subsequent measures of VWM retrieval to understand the fate of individual stimuli. This is an important contribution to existing efforts to examine VWM capacity limitations, which, to date, have only examined the aggregate processing of all of the stimuli presented during VWM task paradigms. Additionally, the current work highlights the importance of examining neural activity during encoding to understand the neural fate of individual stimuli. These techniques will allow researchers to further understand important aspects of VWM processes. This may include examinations of the process by which items are selected or eliminated from VWM, the neural-correlate signals associated with individual item

representations during VWM maintenance, and comparing responses associated with individual stimuli throughout encoding and maintenance processes.

References

Cowan N. The magical number 4 in short-term memory: A reconsideration of mental storage capacity. Behavioral and Brain Sciences. 2001; 24:87–114. [PubMed: 11515286]

Todd JJ, Marois R. Capacity limit of visual short-term memory in human posterior parietal cortex. Nature. 2004; 428:751–754. [PubMed: 15085133]

Victor JD, Mast J. A new statistic for steady-state evoked potentials. Electroencephalography and Clinical Neurophysiology. 1991; 78:378–388. [PubMed: 1711456]

Vogel EK, Machizawa MG. Neural activity predicts individual differences in visual working memory capacity. Nature. 2004; 428:748–751. [PubMed: 15085132]

Vogel EK, McCollough AW, Machizawa MG. Neural measures reveal individual differences in controlling access to visual working memory. Nature. 2005; 438:500–503. [PubMed: 16306992]

Xu Y, Chun MM. Dissociable neural mechanisms supporting visual short-term memory for objects. Nature. 2006; 440:91–95. [PubMed: 16382240]