Title: Does rehearsal benefit visual memory? The role of semantic associations in the maintenance of intact and phase-scrambled scenes.

Abbreviated title: Rehearsal and Visual Memory

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Abstract

Rehearsal during working memory (WM) maintenance facilitates subsequent retrieval, particularly for verbal material. Less is known about how rehearsal modulates WM delay activity during maintenance of novel visual information. In the present study, 44 participants completed a Sternberg Task with either intact novel scenes or phase-scrambled versions, which had similar color and spatial frequency but lacked semantic content. During each condition participants generated a descriptive label for each stimulus and covertly rehearsed or suppressed it (i.e., repeat “the”) during the delay. This was easy in the former but more difficult in the later condition where scenes lacked semantic content. Behavioral performance and EEG delay activity was analyzed as a function of maintenance strategy. Performance during WM for novel scenes revealed that rehearsal improved neither short- or long-term memory. Delay activity revealed greater amplitude in the beta range in right parietal and centromedial regions during rehearsal compared to suppression. When task difficulty increased in the phase-scrambled condition, there was both a significant short- and long-term behavioral advantage as well as greater activity in the upper alpha and beta ranges throughout the delay period. These results show that rehearsal benefits subsequent memory for visual information, but only when the maintained stimuli lack semantic information. We conclude that cognitive strategy modulates the pattern of delay activity during maintenance of novel visual information with effects on subsequent memory.

Introduction

Rehearsal and Working Memory

It is well documented that rehearsal benefits memory for verbal stimuli, such as words and numbers, typically via cumulative rehearsal when confronted with a list of verbal stimuli to remember. Baddeley (1) established the idea that rehearsal benefits memory, suggesting that the repetition of the to-be-remembered item will refresh the memory trace via the articulatory process in the phonological loop. Studies support that blocking rehearsal with articulatory suppression, repeating a word such as “the” over and over again, decreases performance compared with when someone rehearses (2, 3). Visual stimuli may also benefit from rehearsal when the stimulus is recoded into a verbal representation (4-6); however, some studies suggest that the degree of semantic elaboration in the coded verbal representation is more important than rehearsal (7, 8). The benefit of labeling and rehearsal may depend on the working memory task (7, 9, 10).

Most visual stimuli, no matter how simple or complex, have an affiliated word representation (i.e. a picture of an ocean with sand and trees has a label of “beach”) which automatically links the stimulus with stored semantic representations (11) that contains many features (i.e. sand and ocean) and associated knowledge (i.e. beaches are located in warm places and have palm trees). Thus, combining visual information with a semantic verbal representation may result in a deeper level of encoding (12, 13) because the stimulus is encoded in both the visual and verbal domains (14). The novel features of the visual stimuli may also help to guide attention to salient features which facilitates encoding (14, 15). It has been suggested that the benefit of a semantic label

to a visually presented stimulus depends on whether or not semantic associations are automatically accessed without labeling (5, 16). While simple stimuli lacking deeper semantic representations have been studied, few studies have addressed whether complex visual stimuli benefit from recoding. Complex stimuli may not benefit from recoding or rehearsal, especially if features lack concreteness such as nameable colors or line orientation (6).

To study pure visual information, one needs to use a stimulus that does not have an automatic word representation and semantic association. Few studies have used complex visual information that fit into this category, including abstract shapes (17, 18) and patterns (4). A complex visual stimulus that has not been explored to our knowledge is a phase-scrambled scene which is difficult to recode, specifically with one-word representations, and is often described based on basic features (i.e. colors or line orientation). The difficult-to-describe nature of this stimulus makes it suitable for studying visual memory because it is not likely to automatically be recoded nor trigger a deeper semantic representation (4, 8). Therefore, it is well suited to assess benefits of maintenance strategies (i.e. articulatory rehearsal) for storing and remembering complex visual information.

Delay Activity and Working Memory

To understand mechanisms that support maintenance of encoded information and successful retrieval, it is critical to examine neural activity during the delay period (19). Delay activity can include a period of increased and sustained activation throughout the delay period (19, 20). This traditional view of delay activity suggests that it is supported by persistent neuronal firing, which maintains information online until a

response is made (21). Maintenance strategies can differentially engage brain regions (22). Attentional refreshing involves directing attention inward to selectively keep information active and engages attentional mechanisms (23), while rehearsal engages language areas (24), especially for verbal stimuli (25). If maintenance strategies are not controlled, delay period activity is difficult to interpret and may explain recent challenges to the established patterns (19, 26). Similar to the behavioral rehearsal literature, delay period activity has been examined during maintenance of verbal and simple visual stimuli, but few studies have measured delay activity during maintenance of complex visual stimuli. Controlling for these components is critical to identifying brain regions that support memory for visual information and how activity in these regions changes when words and semantic meaning are associated with visual information to support memory.

In the present study two experiments were completed to understand how articulatory rehearsal influences short- and long-term memory for complex visual stimuli and the underlying neural activity. It was hypothesized that controlling for the maintenance strategy by comparing rehearsal to articulatory suppression would result in differences in behavioral performance and delay period activity. Regardless of the type of complex visual stimulus, it was predicted that rehearsal would provide a behavioral advantage over suppression both in tests of working memory and immediate long-term memory. Delay activity during rehearsal would be sustained throughout the delay period and correlated with performance.

Materials and Methods

Participants

The study was approved by the Institutional Review Board of the City University of New York Human Research Protection Program. A total of 54 participants provided informed consent and completed the study. Participants were compensated with either 15 dollars or one extra course credit per hour of participation. The behavioral task with EEG recordings took approximately 2 hours to complete.

Experiment 1

One participant was excluded from Experiment 1 of the study for failure to follow instructions resulting in a final sample in Experiment 1 of 29 participants (age = 25.4 (8.1) years, 14 females). For EEG analysis a total of 6 participants were excluded: 5 participants for noisy or unusable EEG recordings and 1 participant for failing to follow instructions resulting in a final sample for Experiment 1 consisting of 24 participants (age = 25.8 (8.6) years, range 18-56, 11 females).

Experiment 2

Experiment 2 was a replication of Experiment 1 with phase-scrambled stimuli to increase task difficulty by removing semantic content. Four participants were excluded because of computer malfunction preventing recording of behavioral responses resulting in a final sample of 20 participants (age = 24.8 (9.5) years, range 18-56, 12 females).

Experimental Design and Statistical Analyses

Task

Participants completed a modified version of a Sternberg WM Task (27). The task consisted of two WM tasks (**Figure 1**) and a delayed recognition task. During the WM task, participants completed a low load (2 images) WM task consisting of an encoding phase, delay period, probe choice response, and a phase-scrambled image that indicated the end of the trial. During presentation of the images, participants were instructed to generate a verbal label (i.e. descriptive label like “beach”), and during the delay period they were instructed to rehearse covertly (i.e. using their inner voice) the label throughout the entire delay period (rehearsal) or were prevented from actively rehearsing (suppression). Participants completed both the rehearsal and suppression conditions in a randomized order. The delayed recognition task was administered ten minutes later.

For suppression, participants were discouraged from generating a verbal label and instructed to repeat the word "the" throughout the delay period (28, 29). Suppression was used to block verbal rehearsal by engaging the articulatory process of the phonological loop with an unrelated word. This suppression task uses repetition of a non-task related word such as “the” over and over again (28-30). This classic suppression task was chosen over an alternative task such as random number generation or a math problem because these alternative tasks engage attentional processes. The goal of suppression is to block rehearsal without a demand on attention, which has been demonstrated to have a longer term effect on memory tasks (30, 31).

Stimuli

In Experiment 1, stimuli consisted of high-resolution, color outdoor scenes, which did not contain any faces or words. Scenes were randomly selected from the SUN database (32) and were resized to 800 by 600 pixels.

Experiment 2 employed the same design as Experiment 1 with Fourier phase-scrambled (Matlab, v2016) versions of the scenes used in Experiment 1 (**Supplemental Figure 1**). Importantly, the scenes contained the same colors and spatial frequencies as the scenes used in Experiment 1 but lacked semantic content. It was more challenging to generate labels because phase-scrambling removes all semantic content.

Behavioral Analysis

Behavioral data were processed in Python 3.0, and plots were created using Seaborn 0.9.0. Statistical analysis was conducted in Jasp v0.9.0.1 using paired-samples t-tests to compare behavioral accuracy between conditions (rehearsal vs. suppression) on the WM and recognition tasks.

EEG Acquisition, Processing and Analysis

Continuous 64-channel EEG was collected at 1000 Hz using an active electrode system (actiCHamp, Brain Products). A 10-20 montage was used with a left mastoid reference (TP9). Raw EEG data were processed in BESA Research v6.1. Data were visually inspected, eye blinks were corrected with a pattern-matching algorithm (33, 34), and muscle artifacts were removed. Participants were included if they had more than 50 trials that survived the artifact scan (*see Supplemental Methods*).

Time-frequency analyses (TFA; absolute amplitude and temporal spectral analysis) were conducted on artifact-corrected delay periods (0 to 6000 ms) in BESA Research (*see Supplemental Methods*). TFA was bandpass-filtered between 4 and 30 Hz and generated in 100 ms/0.5 Hz steps. A brain source montage was applied to TFA to distinguish between broad, potentially overlapping sources (i.e. frontal, central, parietal, etc.). The brain region montage consists of 15 discrete regions and source-level analysis calculates weighted combinations of the recorded scalp electrodes in order to reduce the amount of overlap (35, 36).

Scalp-level TFA and source-level TFA were compared using paired-samples t-tests with corrections for multiple comparisons using non-parametric cluster permutation testing (N = 1,000 permutations) (37) in BESA Statistics v2.0 (*see Supplemental Methods*). Correlations were run between TFA and performance with corrections for multiple comparisons.

Results

Experiment 1

Behavioral. Performance on the WM task revealed that there was no significant difference between rehearsal and suppression (.95 vs. .95 proportion correct, $t_{(28)} = .70$, $p = .49$, $d = .13$), suggesting that rehearsal did not provide a short-term behavioral advantage (**Figure 2**). Similarly, there was no long-term behavioral advantage on the delayed recognition task for rehearsal vs. suppression (.80 vs. .78 proportion correct, $t_{(28)} = 1.38$, $p = .18$, $d = .23$).

EEG. Sensor-level changes in absolute amplitudes between the two conditions (n=24 subjects) with corrections for multiple comparisons revealed 100 significant clusters (**Supplemental Table 1**, $p < .05$). Sensor-level analysis revealed two distinct patterns of activity for the rehearsal and suppression conditions (**Figure 3a**). For the rehearsal condition (**Figure 3b** – P8 electrode - orange clusters), amplitude was greater in the theta and beta range for the left frontal, bilateral fronto-temporal, and central regions, and in the beta range for the right parietal region, throughout the delay period. For the suppression condition (**Figure 3c** – F1 electrode - blue clusters), the amplitude was greater in the upper alpha and lower beta range in the mid-frontal regions early in the delay, and in the theta and upper alpha range in the midline and centro-frontal, right parietal, and occipital regions later in the delay.

Change in amplitude over time (temporal spectral analysis) suggests that activity was increased and synchronous early in the delay period in the upper alpha and lower beta range (**Supplemental Figure 2**; 500 msec to 3000 msec) and became desynchronous later in the delay period (4000 msec to 6000 msec). Temporal spectral analysis revealed no significant difference between rehearsal versus suppression (p = .08), nor was rehearsal significantly correlated with working memory (p = .46) or recognition performance (p = .28).

Source-level analysis of the absolute amplitudes found 57 significant clusters across 13 of the 15 brain regions. The main source of activity for the rehearsal condition was central midline (CM_BR; 12 clusters, Time 100 to 6000 msec, Frequency 12-29 Hz), but overall changes were apparent over numerous brain regions. In the suppression condition, three regions were identified as sources of activity including the

right temporal parietal region (TPR_BR; 8 clusters, Time 800 to 5400 msec, Frequency 10.5-17.5 Hz), the left temporal parietal region (TPL_BR; 8 clusters, Time 0 to 5900 msec, Frequency 7-12.5 Hz), and the right anterior temporal region (TAR_BR; 11 clusters, Time 100 to 5800 msec, Frequency 15-30 Hz) regions. The TPL_BR and TPR_BR amplitude differences are more concentrated in the upper alpha and lower beta ranges, whereas the TAR_BR activity was mainly in the beta range.

Experiment 2

Behavioral. When task difficulty increased, there was both a significant short-term advantage of rehearsal (**Figure 4**) compared to suppression (.85 vs. .78 proportion correct, $t_{(19)} = 7.93$, $p < .001$, $d = 1.77$) as well as a long-term advantage during rehearsal compared to suppression (.71 vs. .62 proportion correct, $t_{(19)} = 4.58$, $p < .001$, $d = 1.02$).

EEG. It was predicted that rehearsal and suppression would produce similar EEG delay period activity as in Experiment 1 since participants would be engaging in the same maintenance strategy, which should engage similar brain regions.

Sensor-level analysis of the absolute amplitude between the two conditions (n = 20 subjects) with corrections for multiple comparisons revealed 15 significant clusters (**Supplemental Table 2**, $p < .05$). Greater amplitude was observed in the upper alpha and beta ranges across a majority of the sensors for the rehearsal condition as compared with the suppression condition, specifically in the bilateral temporal, occipital and parietal regions, and left frontal region (**Figure 5a**). The pattern of delay activity appeared to be continuous throughout the entire delay, specifically in right parietal and

occipital regions (**Figure 5b** – P08 – orange cluster). There was also a brief early period (Time 0 to 1800 msec) in which greater amplitude was observed in the suppression condition in the theta, alpha, and beta range.

Sensor-level temporal spectral analysis suggested transient changes, similar to the delay activity pattern observed in Experiment 1. Activity was increased and synchronous in the early delay period and became desynchronous later in the delay. Comparison between the rehearsal and suppression conditions using temporal spectral analysis revealed three clusters of significantly different activity (**Supplemental Table 3**). Activity during rehearsal was also significantly correlated with WM performance (**Figure 5c**; Cluster 1: blue-negative correlation, cluster value = -38801.2, p = .005, Cluster 2: orange-positive correlation, Cluster value = 20445.5, p = .065), but not performance on the recognition task (p = .62).

Source-level analysis of absolute amplitudes revealed 67 significant clusters across 11 of the 15 brain regions (**Supplemental Figure 3a**). Of the significant clusters, a focus of activity in the rehearsal condition was observed in the left anterior temporal region (TAL_BR; Supplemental **Figure 3b**, 10 clusters, Time 0 to 6000 msec, Frequency 4-30 Hz), left parietal (PL_BR; 10 clusters, Time 0 to 6000 msec, Frequency 6-30 Hz), and midline occiptio-polar (OpM_BR; 6 clusters, Time 100 to 4600 msec, Frequency 9.5-30 Hz) regions. For the suppression condition, an early focal point of activity (Time 0 to 14000 msec) in the alpha range (Frequency 7-13.5 Hz) was found in the right and left parietal, parietal midline, and occipito-polar midline regions; a later focal point in the theta range (4-8 Hz) was found in the same brain regions as well as in the right frontal region (Time 3800 to 6000 msec).

A direct comparison between results of Experiment 1 and Experiment 2 is included in the *Supplemental Results*.

Discussion

In Experiment 1, generating a meaningful label for novel scenes and rehearsing them during the maintenance phase of a Sternberg WM task provided neither a short- or long-term behavioral advantage. Comparison of sensor-level delay activity revealed a distinct pattern of greater activity in the beta range in the right parietal and centromedial regions for the rehearsal compared to suppression. Sensor-level activity was not correlated with either short- or long-term memory. Source analysis revealed no clear focus of activity for either condition.

When task difficulty increased in Experiment 2 using phase-scrambled scenes and participants generated a meaningful label followed by rehearsal, there was both a significant short-term as well as a long-term advantage. Sensor-level EEG activity during rehearsal showed greater activity in the upper alpha and beta ranges, specifically in the bilateral temporal, occipital and parietal regions and a left frontal region. Sensor-level activity for rehearsal was also correlated with short-term memory. Source-level analysis revealed a focus of activity during the rehearsal condition in the left anterior temporal and left parietal regions.

The results of Experiment 1 suggest that “holding onto” the visual information by rehearsal was not as important as generating the label. Hence, recoding the label may have been sufficient for successful probe choice. Specifically, if one is shown a beach and a subsequent probe is a park, even if you could not recall specific details of the encoding beach scene, one could easily determine a category mismatch between park

and beach. Successful performance in the suppression condition could also be explained by an alternate maintenance strategy. When rehearsal is prevented, participants may have relied on attentional refreshing to keep the visual information in WM until the probe response was required. Interestingly, when phase-scrambled scenes were used in Experiment 2, performance in the rehearsal condition suggests that recoding and rehearsal were critical in supporting the behavioral advantage over suppression. Performance on the suppression condition, on the other hand, was likely supported by attentional refreshing, as automatic labeling was less likely to occur and the key difference in performance was maintenance via rehearsal.

Role of Rehearsal in Visual Memory

The role of rehearsal in supporting visual memory remains unclear, especially with regards to whether or not rehearsal benefits complex visual stimuli. Experiments 1 and 2 sought to understand how controlling for rehearsal strategy (rehearsal vs. suppression) influenced memory for complex visual stimuli.

Experiment 1 used intact, novel outdoor scenes that contained semantic information and were easy to generate a descriptive label for (e.g., a beach). In the rehearsal condition, label generation provided a dual means of encoding (4, 14, 15), one in the visual and one in the verbal domains, and was intended to benefit memory. However, there was no difference in performance on the short- or long-term memory task with intact scenes, which suggests that complex scenes do not benefit from this type of maintenance strategy. It has been suggested that complex scenes automatically trigger stored semantic associations (13); as a result, the association provides

automatic deeper encoding (12). It has also been established that humans can remember thousands of images after only seeing the images for a brief time (38-40). This ability is termed the picture superiority effect (41) and may account for the fact that performance for images was near ceiling regardless of maintenance strategy. The results of Experiment 1 suggest that the recoding of the images into a verbal label and the automatic semantic associations are more important than rehearsal (8, 13, 15). Consequently, the addition of rehearsing with a generated label offered no more benefit than accessing those stored associations.

Experiment 2 was conducted to increase task difficulty by using phase-scrambled images that lacked semantic content; as a result, automatic recoding fails to occur. Performance in Experiment 2 suggests that the benefit of rehearsal depends on the ability to associate semantic meaning; therefore, when participants generated a semantic label and rehearsed throughout the delay period, they engaged in deeper encoding and elaborative rehearsal (4, 12, 13, 42, 43) improving short-term memory for these stimuli as well as long-term memory. These findings are consistent with the idea that generating a label and rehearsing is only beneficial to visual stimuli when semantic information is not automatically accessed (15) because it may direct the subjects' attention to salient features (5) to support memory. During suppression participants engaged in more shallow encoding and maintenance, they did not recode or engage in rehearsal, as a result, performance was lower.

Delay Activity and Rehearsal

Experiments 1 and 2 sought to understand how delay activity would change as a function of maintenance strategy (rehearsal vs. suppression). When intact scenes served as stimuli in Experiment 1, we observed greater activity in the left temporal and bilateral central regions during rehearsal, which suggests the engagement of the phonological loop (25, 44). Suppression of rehearsal resulted in the engagement of more frontal regions suggesting reliance on attentional mechanisms (45) as well as greater mental effort (46). Source analysis revealed diffuse activity for both rehearsal and suppression conditions, which suggests no underlying focus of delay activity.

In Experiment 2, activity was greater in the upper alpha and beta ranges for the rehearsal condition throughout the delay period, specifically in the bilateral temporal, occipital and parietal regions and left frontal region, as compared with suppression. The brain regions analysis also revealed a focal source for the rehearsal condition in the left anterior temporal and parietal regions. Greater activation in the left temporal and frontal regions suggests the engagement of the phonological loop (36, 44, 47) and has also been implicated in the maintenance of non-spatial visual memory (47). Engagement of occipito-temporal and parietal regions are associated with both visual working memory and attentional selection (17, 48). Parietal lobe involvement in maintenance has been linked to attentional selection (15, 47) specifically with regards to novelty (48) and may also play a role in the integration of features in complex objects (17).

Delay activity during a working memory task is often associated with the engagement of either the prefrontal cortex or the posterior parietal regions but has been reported in studies that often fail to control for maintenance strategy. While the left temporal regions reflect the active use of the phonological loop during rehearsal (2, 25)

activity in the parietal region has been suggested as the store for visual information during maintenance. It serves as the buffer in which information lives until it is needed for retrieval, analogous to the verbal information store (25). The episodic buffer is believed to serve as the interface between the information in the visual and verbal stores with stored semantic knowledge (49). During this association, the episodic buffer temporarily holds onto the activated, stored knowledge, to support the interaction between the verbal label, the visual stimulus and the semantic associations. It has also been proposed that the visual cache, which holds non-spatial visual information, may overlap with the functions of the episodic buffer proposed in the multicomponent model (11). Specifically, the lateral posterior parietal cortex could represent the area in the brain in which the generated verbal label is associated with the visually stored picture, consistent with the output buffer hypothesis (49, 50).

Activation in posterior parietal cortex likely does not exclusively reflect attentional processes (50). If the recoding and semantic associations require increased attention, as in the case of a more effortful association between a stimulus and stored semantic knowledge, the central executive is likely to play an important role as reflected by increased activation of frontal networks. If attentional resources are not required, as in the case of an automatic association, the central executive is less likely to play a role (8). The results of these experiments confirm that controlling for maintenance strategy differentially recruits the prefrontal and parietal regions and implicate the left temporal region when rehearsal is used.

The differences in observed delay activity in Experiment 2 may be attributed to differences in the task demands (19), particularly in the frontal regions during rehearsal.

The increased delay activity in frontal regions could represent the process of actively recoding difficult-to-label images in a more attention-demanding rehearsal period (11). Although, the phase-scrambled scenes contain the same visual features as regular scenes (i.e., color and spatial frequency), they lack the automatic semantic associations. The easy-to-label images used in Experiment 1, on the other hand, had an automatic semantic association and a verbal label (11, 13). Thus, the generation of a label in Experiment 2 was more effortful (i.e., reliance on features (6)) both during the recoding process and rehearsal and did not automatically produce a verbal label. The exploratory analysis comparing the rehearsal conditions of Experiments 1 and 2 showed that overall pattern of activity was not significantly different. This analysis involved different groups of subjects in each condition. Future experiments should compare delay activity with different task demands using the same subjects in each group.

Transient vs. Sustained Delay Activity

Elucidating how different pattern of delay activity contribute to WM is a current research focus (19). While it has long been established that sustained activity observed during maintenance represents both maintenance of encoded information and focusing of attention inward, recent research has suggested that delay activity is more complex (19, 26, 51). For example, only information in the focus of attention may be reflected in delay activity, while items outside the focus of attention may actually be represented by activity silent mechanisms (51, 52).

Examination of the change in amplitude over time in both Experiments 1 and 2 suggests that when controlling for maintenance strategy, the pattern of delay activity is

actually more transient. There is an early period of increased, synchronous activity (until approximately 3000 ms) as has been previously reported in the literature (53-56). The observed activity patterns were in the alpha and beta ranges, frequency ranges that are critical for maintenance of visual information. Alpha enhancement likely reflects inhibition of information that could interfere with maintenance, while beta activity is related to controlling the information that is being actively maintained (57). The early delay activity was followed by a period of desynchronous activity for the remainder of the delay which may suggest preparation for the upcoming response (58). This pattern of activity is consistent with recent reports that maintenance is not necessarily supported by persistent delay activity in prefrontal regions (19, 26); instead, delay activity may reflect more complex processes in cortex and subcortical regions. Alternatively, previous reports of sustained delay activity could reflect a maintenance period in which participants did not utilize a particular strategy, rather, they focused their attention inward until they were required to produce a response (23). Thus, delay activity is modulated by the strategy that is employed to maintain information (19).

Limitations

Participants engaged in covert rehearsal and suppression to reduce the amount of noise introduced into the EEG signals. Task compliance was therefore based on participant confirmation during the recognition task (i.e., they reported their generated labels). It is possible that participants did not engage in suppression; consequently, the failure to produce the intended behavioral outcome in Experiment 1 could be explained by this. While the intended behavioral outcome was found in Experiment 2, it is again

possible that participants did not engage in suppression. Future experiments that rely on covert maintenance mechanisms should include a response-based behavioral confirmation such as an immediate reporting of generated labels or the number of times the suppression word is repeated. Future studies should also examine the type of label generated to see if the depth of label (i.e., deeper descriptive label like “sunset” vs. shallower label like “white and blank lines”) or the verbalizability of the stimulus (8) impacts subsequent memory.

Conclusions

The results of these experiments provide evidence that rehearsal of visual stimuli impacts short-term memory and modulates the pattern of delay period activity. Moreover, the benefit on short-term memory also results in better long-term memory for visual stimuli, but only when semantic connections are not automatically associated with the visual stimuli.

References

1. Baddeley A, Logie R, Bressi S, Sala SD, Spinnler H. Dementia and working memory. The Quarterly Journal of Experimental Psychology. 1986;38(4):603-18.

2. Baddeley A, Lewis V, Vallar G. Exploring the articulatory loop. The Quarterly journal of experimental psychology. 1984;36(2):233-52.

3. Baddeley A. Working memory: theories, models, and controversies. Annual review of psychology. 2012;63:1-29.

4. Brown LA, Forbes D, McConnell J. Short Article: Limiting the use of Verbal Coding in the Visual Patterns Test. Quarterly Journal of Experimental Psychology. 2006;59(7):1169-76.

5. Souza AS, Skóra Z. The interplay of language and visual perception in working memory. Cognition. 2017;166:277-97.

6. Verhaeghen P, Palfai T, Johnson MP. Verbal labeling as an assimilation mnemonic for abstract visual stimuli: The sample case of recognition memory for Chinese characters. Memory & cognition. 2006;34(4):795-803.

7. Souza AS, Oberauer K. Does articulatory rehearsal help immediate serial recall? Cognitive psychology. 2018;107:1-21.

8. Brown LA, Wesley RW. Visual working memory is enhanced by mixed strategy use and semantic coding. Journal of Cognitive Psychology. 2013;25(3):328-38.

9. Dent K, Smyth MM. Verbal coding and the storage of form-position associations in visual–spatial short-term memory. Acta Psychologica. 2005;120(2):113-40.

10. Sense F, Morey CC, Prince M, Heathcote A, Morey RD. Opportunity for verbalization does not improve visual change detection performance: A state-trace analysis. Behavior research methods. 2017;49(3):853-62.

11. Logie RH. The functional organization and capacity limits of working memory. Current directions in Psychological science. 2011;20(4):240-5.

12. Craik FI, Lockhart RS. Levels of processing: A framework for memory research. Journal of verbal learning and verbal behavior. 1972;11(6):671-84.

13. Ensor TM, Surprenant AM, Neath I. Increasing word distinctiveness eliminates the picture superiority effect in recognition: Evidence for the physical-distinctiveness account. Memory & cognition. 2019;47(1):182-93.

14. Paivio A. Mental imagery in associative learning and memory. Psychological review. 1969;76(3):241.

15. Nelson DL, Reed VS. On the nature of pictorial encoding: A levels-of-processing analysis. Journal of Experimental Psychology: Human Learning and Memory. 1976;2(1):49.

16. Santangelo V. Forced to remember: when memory is biased by salient information. Behavioural brain research. 2015;283:1-10.

17. Mayer JS, Bittner RA, Nikolić D, Bledowski C, Goebel R, Linden DE. Common neural substrates for visual working memory and attention. Neuroimage. 2007;36(2):441-53.

18. Song J-H, Jiang Y. Visual working memory for simple and complex features: An fMRI study. Neuroimage. 2006;30(3):963-72.

19. Sreenivasan KK, D'Esposito M. The what, where and how of delay activity. Nature Reviews Neuroscience. 2019:1.

20. Sreenivasan KK, Curtis CE, D'Esposito M. Revisiting the role of persistent neural activity during working memory. Trends in cognitive sciences. 2014;18(2):82-9.

21. Constantinidis C, Funahashi S, Lee D, Murray JD, Qi X-L, Wang M, et al. Persistent spiking activity underlies working memory. Journal of Neuroscience. 2018;38(32):7020-8.

22. Weiss S, Mueller HM. "Too many betas do not spoil the broth": the role of beta brain oscillations in language processing. Frontiers in Psychology. 2012;3.

23. Cowan N, Elliott EM, Saults JS, Morey CC, Mattox S, Hismjatullina A, et al. On the capacity of attention: Its estimation and its role in working memory and cognitive aptitudes. Cognitive psychology. 2005;51(1):42-100.

24. Henson R, Burgess N, Frith CD. Recoding, storage, rehearsal and grouping in verbal short-term memory: an fMRI study. Neuropsychologia. 2000;38(4):426-40.

25. Baddeley A. Working memory: looking back and looking forward. Nature reviews neuroscience. 2003;4(10):829-39.

26. Miller EK, Lundqvist M, Bastos AM. Working Memory 2.0. Neuron. 2018;100(2):463-75.

27. Sternberg S. High-speed scanning in human memory. Science. 1966;153(3736):652-4.

28. Baddeley AD, Thomson N, Buchanan M. Word length and the structure of short-term memory. Journal of verbal learning and verbal behavior. 1975;14(6):575-89.

29. Landry P, Bartling C. The Phonological Loop and Articulatory Suppression. American Journal of Psychological Research. 2011;7(1):79-86.

30. Ricker TJ, Cowan N, Morey CC. Visual working memory is disrupted by covert verbal retrieval. Psychonomic Bulletin & Review. 2010;17(4):516-21.

31. Norris D, Hall J, Butterfield S, Page MP. The effect of processing load on loss of information from short-term memory. Memory. 2019;27(2):192-7.

32. Xiao J, Hays J, Ehinger KA, Oliva A, Torralba A, editors. Sun database: Large-scale scene recognition from abbey to zoo. Computer vision and pattern recognition (CVPR), 2010 IEEE conference on; 2010: IEEE.

33. Picton TW, van Roon P, Armilio ML, Berg P, Ille N, Scherg M. The correction of ocular artifacts: a topographic perspective. Clinical Neurophysiology. 2000;111(1):53-65.

34. Ille N, Berg P, Scherg M. Artifact correction of the ongoing EEG using spatial filters based on artifact and brain signal topographies. Journal of clinical neurophysiology. 2002;19(2):113-24.

35. Hoechstetter K, Bornfleth H, Weckesser D, Ille N, Berg P, Scherg M. BESA source coherence: a new method to study cortical oscillatory coupling. Brain topography. 2004;16(4):233-8.

36. Scherg M. Functional imaging and localization of electromagnetic brain activity. Brain topography. 1992;5(2):103-11.

37. Maris E, Oostenveld R. Nonparametric statistical testing of EEG-and MEG-data. Journal of neuroscience methods. 2007;164(1):177-90.

38. Brady TF, Konkle T, Alvarez GA, Oliva A. Visual long-term memory has a massive storage capacity for object details. Proceedings of the National Academy of Sciences. 2008;105(38):14325-9.

39. Standing L, Conezio J, Haber RN. Perception and memory for pictures: Single-trial learning of 2500 visual stimuli. Psychonomic Science. 1970;19(2):73-4.

40. Standing L. Learning 10000 pictures. The Quarterly journal of experimental psychology. 1973;25(2):207-22.

41. Stenberg G. Conceptual and perceptual factors in the picture superiority effect. European Journal of Cognitive Psychology. 2006;18(6):813-47.

42. Cermak GW. Short-term recognition memory for complex free-form figures. Psychonomic Science. 1971;25(4):209-11.

43. Phaf RH, Wolters G. Attentional shifts in maintenance rehearsal. The American journal of psychology. 1993:353-82.

44. Hwang G, Jacobs J, Geller A, Danker J, Sekuler R, Kahana MJ. EEG correlates of verbal and nonverbal working memory. Behavioral and Brain Functions. 2005;1(1):20.

45. Camos V, Mora G, Oberauer K. Adaptive choice between articulatory rehearsal and attentional refreshing in verbal working memory. Memory & Cognition. 2011;39(2):231-44.

46. Kopp F, Schröger E, Lipka S. Synchronized brain activity during rehearsal and short-term memory disruption by irrelevant speech is affected by recall mode. International Journal of Psychophysiology. 2006;61(2):188-203.

47. Munk MH, Linden DE, Muckli L, Lanfermann H, Zanella FE, Singer W, et al. Distributed cortical systems in visual short-term memory revealed by event-related functional magnetic resonance imaging. Cerebral Cortex. 2002;12(8):866-76.

48. Mayer JS, Kim J, Park S. Enhancing visual working memory encoding: The role of target novelty. Visual cognition. 2011;19(7):863-85.

49. Baddeley A. The episodic buffer: a new component of working memory? Trends in cognitive sciences. 2000;4(11):417-23.

50. Hutchinson JB, Uncapher MR, Wagner AD. Posterior parietal cortex and episodic retrieval: convergent and divergent effects of attention and memory. Learning & Memory. 2009;16(6):343-56.

51. Rose NS, LaRocque JJ, Riggall AC, Gosseries O, Starrett MJ, Meyering EE, et al. Reactivation of latent working memories with transcranial magnetic stimulation. Science. 2016;354(6316):1136-9.

52. Stokes MG. 'Activity-silent'working memory in prefrontal cortex: a dynamic coding framework. Trends in Cognitive Sciences. 2015;19(7):394-405.

53. Berger B, Omer S, Minarik T, Sterr A, Sauseng P. Interacting Memory Systems—Does EEG Alpha Activity Respond to Semantic Long-Term Memory Access in a Working Memory Task? Biology. 2014;4(1):1-16.

54. Jensen O, Gelfand J, Kounios J, Lisman JE. Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. Cerebral cortex. 2002;12(8):877-82.

55. Tuladhar AM, Huurne Nt, Schoffelen JM, Maris E, Oostenveld R, Jensen O. Parieto-occipital sources account for the increase in alpha activity with working memory load. Human brain mapping. 2007;28(8):785-92.

56. Khader PH, Jost K, Ranganath C, Rösler F. Theta and alpha oscillations during working-memory maintenance predict successful long-term memory encoding. Neuroscience letters. 2010;468(3):339-43.

57. de Vries IE, Slagter HA, Olivers CN. Oscillatory Control over Representational States in Working Memory. Trends in Cognitive Sciences. 2019.

58. Ellmore TM, Ng K, Reichert CP. Early and late components of EEG delay activity correlate differently with scene working memory performance. PloS one. 2017;12(10):e0186072.

Figure 1. Example Working Memory Trial in Experiment 1 (Intact Scenes). The task consisted of a low cognitive load (2 images). Participants were presented with a fixation cross (1 sec) that indicates the start of the trial, followed by 2 images in succession (2 sec each), a blank screen during the delay period (6 sec), a probe choice (2 sec), which is either one of the earlier presented images or a new image, and a phase-scrambled image (1 sec) that indicates the end of the trial. An example of a rehearsal trial in which participants generate the label for each image and rehearse during the delay period (a). An example of a suppression trial in which participants suppress during the delay period (b).

Figure 2. Working Memory and Recognition Performance in Experiment 1 (Intact Scenes) Suggests Rehearsal Does Not Benefit Memory. Boxplots of performance accuracy, each dot represents a single participant (n = 29). a) Comparison of performance, as measured by proportion correct, shows that rehearsal (light green boxplot) provided no benefit for short-term memory as compared with suppression (dark green boxplot) on the working memory task (p = .49). b) Comparison of performance on the recognition task, for images from the rehearsal condition (light green boxplot) versus images from the suppression condition (dark green box plot), suggested that there was no long-term benefit of rehearsal (p = .18).

Figure 3. Comparison of Absolute Amplitude Delay Period Activity in Experiment 1 Reveals Different Activity Patterns Between Rehearsal and Suppression. Select absolute amplitude plots in the left frontal and right parietal regions of the 6-sec delay period revealed 106 clusters of significant differences in activity (p < .05). The y-axis shows frequency (Hz); x-axis shows the time in sec. a) Head plot of the overall pattern of absolute amplitude difference during the delay period for all sensors. Orange clusters represent rehearsal delay activity great than suppression and blue clusters represent suppression delay activity great than rehearsal. These cluster details are described in *Supplemental Table 1*. b) Selected electrode shown from the right parietal region (P8 electrode) displays orange clusters which represents the bins in frequency-time that are greater in amplitude for the rehearsal condition as compared with the suppression condition. Electrode selected based on results from previous research in our lab highlighting the right parieto-occipital region (58). c) Selected electrode from the left frontal region (F1 electrode) shows blue clusters which represents the bins in frequency-time that are greater in amplitude for the suppression condition as compared with the rehearsal condition.

Figure 4. Working Memory and Recognition Performance in Experiment 2 (Scrambled Scenes) Suggests that Rehearsal Benefits Both Short- and Long-Term Memory. Boxplots of performance accuracy, each dot represents a single participant (n = 20). a) Examination of performance on the working memory task shows that rehearsal (light blue boxplot) provided a short-term advantage as compared with suppression (dark blue boxplot) on the working memory task (p < .001). b) Comparison of performance on the recognition task also revealed a long-term advantage for images from the rehearsal condition (light blue boxplot) versus images from the suppression condition (dark blue box plot), (p < .001).

Figure 5. Delay Period Activity Time Frequency Analysis in Experiment 2 (Scrambled Scenes) Reveals Greater Activity for Rehearsal and Correlations with Performance. The y-axis is frequency (Hz); x-axis is the time in sec. a) Head plot of the overall pattern of absolute amplitude difference during the delay period for all sensors. These cluster details are described in *Supplemental Table 2*. Orange clusters represent rehearsal delay activity great than suppression and blue clusters represent suppression delay activity great than rehearsal. b) Absolute amplitude plot for the PO8 electrode during the 6-sec delay period. PO8 was selected from all electrodes in the head map because it has the broadest clusters present of the other electrodes. The orange represents the clusters in frequency-time that are greater in amplitude for the rehearsal condition as compared with the suppression condition (15 significant clusters across all electrodes, $p < 0.05$). These cluster details are described in *Supplemental Table 3*. c) Time Frequency Analysis correlation plot for the PO8 electrode during the 6-sec delay period in a whole window analysis. The first cluster represents a positive correlation between activity during the delay period and performance on the working memory task from the rehearsal condition (orange, Cluster value = 20445.5, $p = .065$) and the second cluster represents a negative correlation with performance (blue, cluster value = -38801.2, $p = .005$).

a) Rehearsal

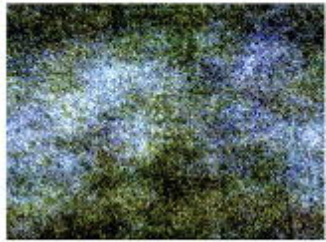
Trial Start

Generate a label:
Mountain

Generate a label:
Lake

Repeat the generated labels:
" Mountain ... Lake ... Mountain ... Lake"

Did I see this image before?
Press **green button** [yes] or
Press **red button** [no]



Trial End

b) Suppression

Trial Start

Look at the image &
do not generate a label

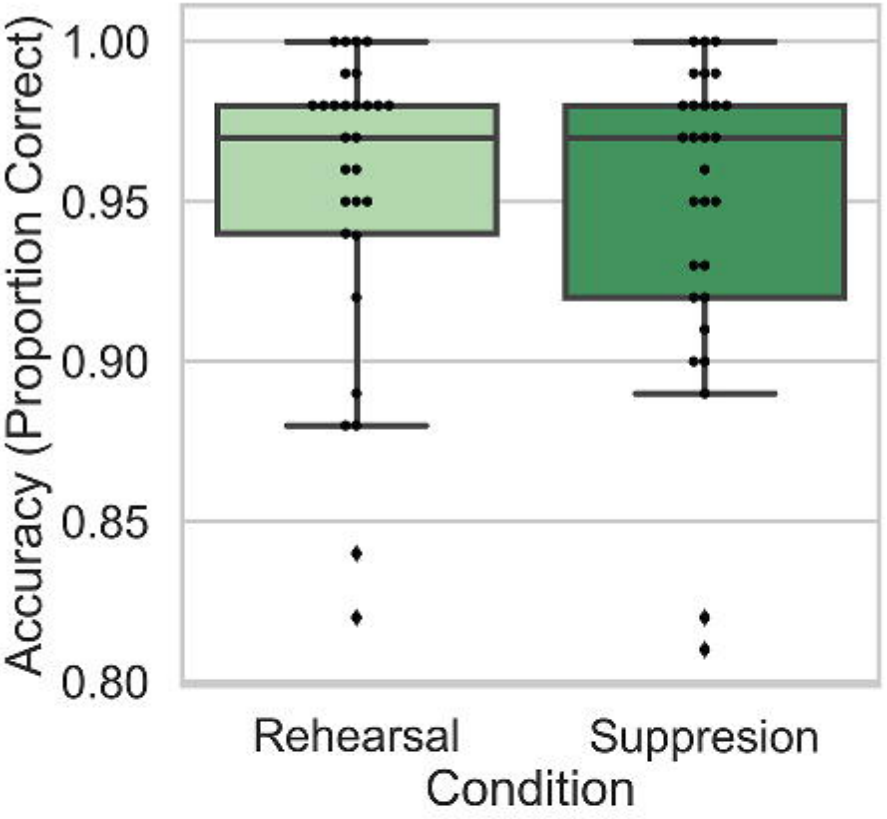
Look at the image &
do not generate a label

Repeat the word "the":
"the ... the ... the .. the"

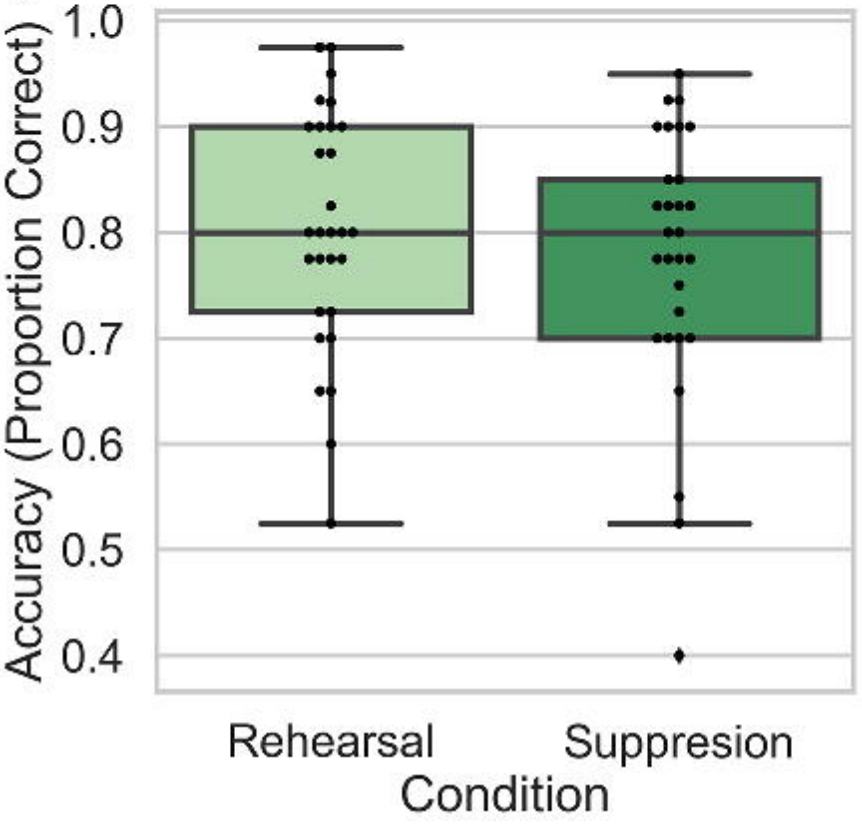
Did I see this image before?
Press **green button** [yes] or
Press **red button** [no]

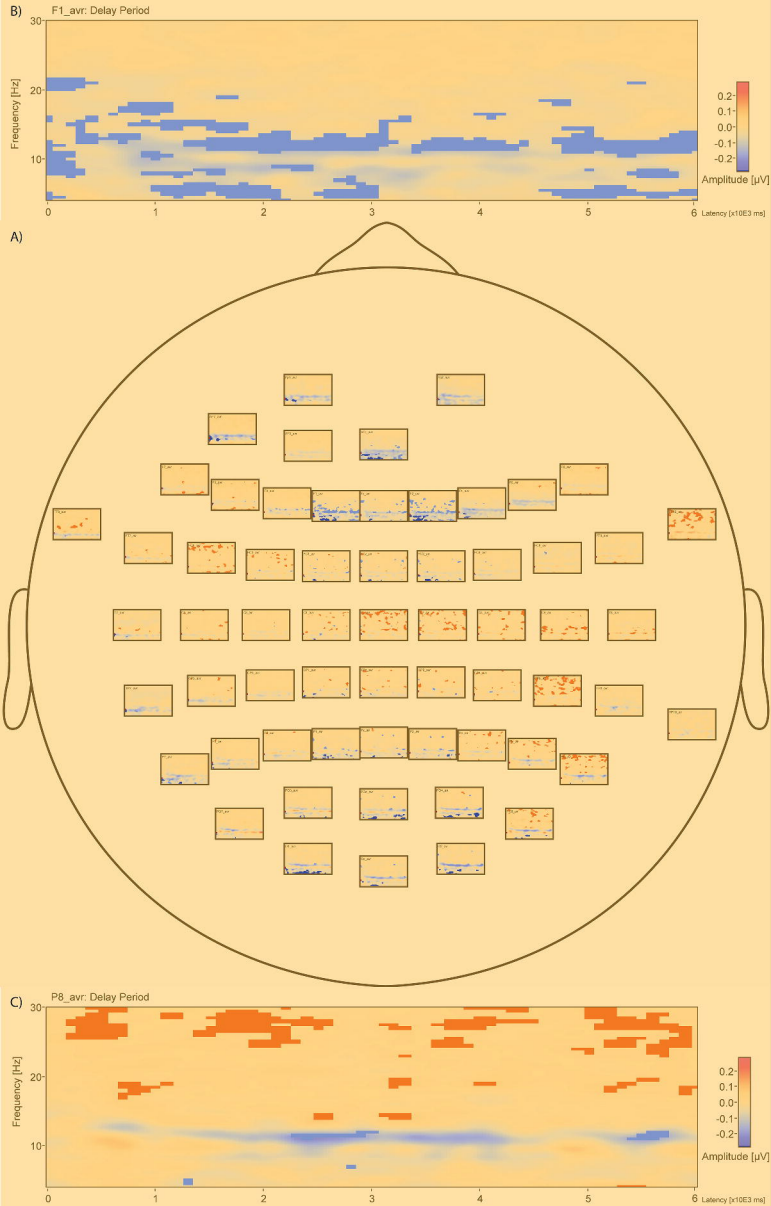
Trial End

a)

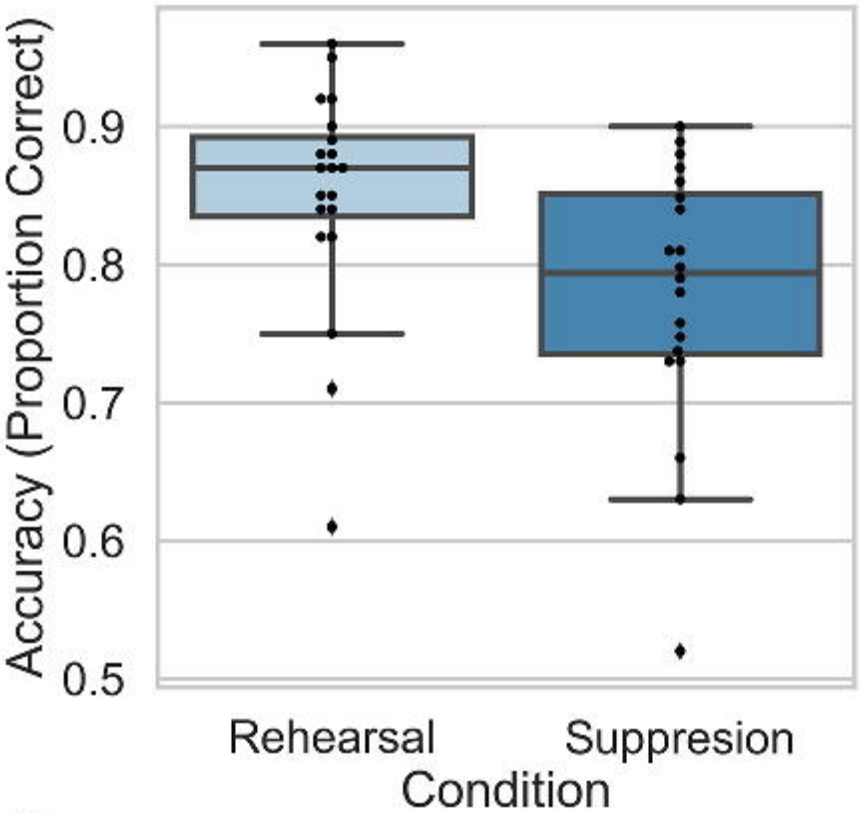

Accuracy (Proportion Correct)
1.00
0.95
0.90
0.85
0.80
Rehearsal
Suppresion
Condition

b)

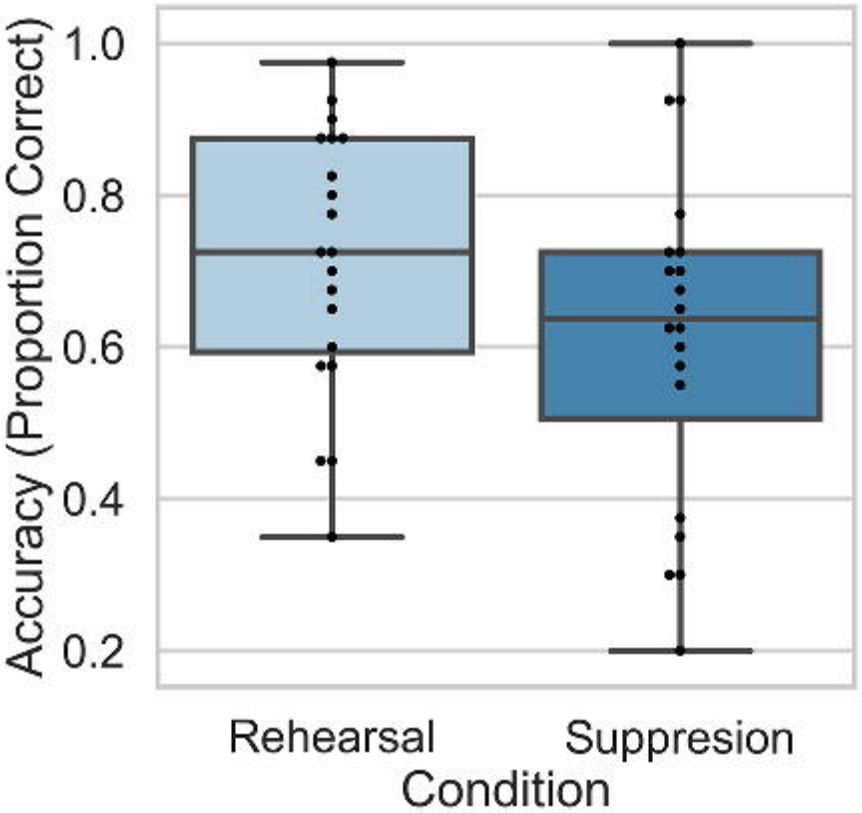

Accuracy (Proportion Correct)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
Rehearsal
Suppresion
Condition

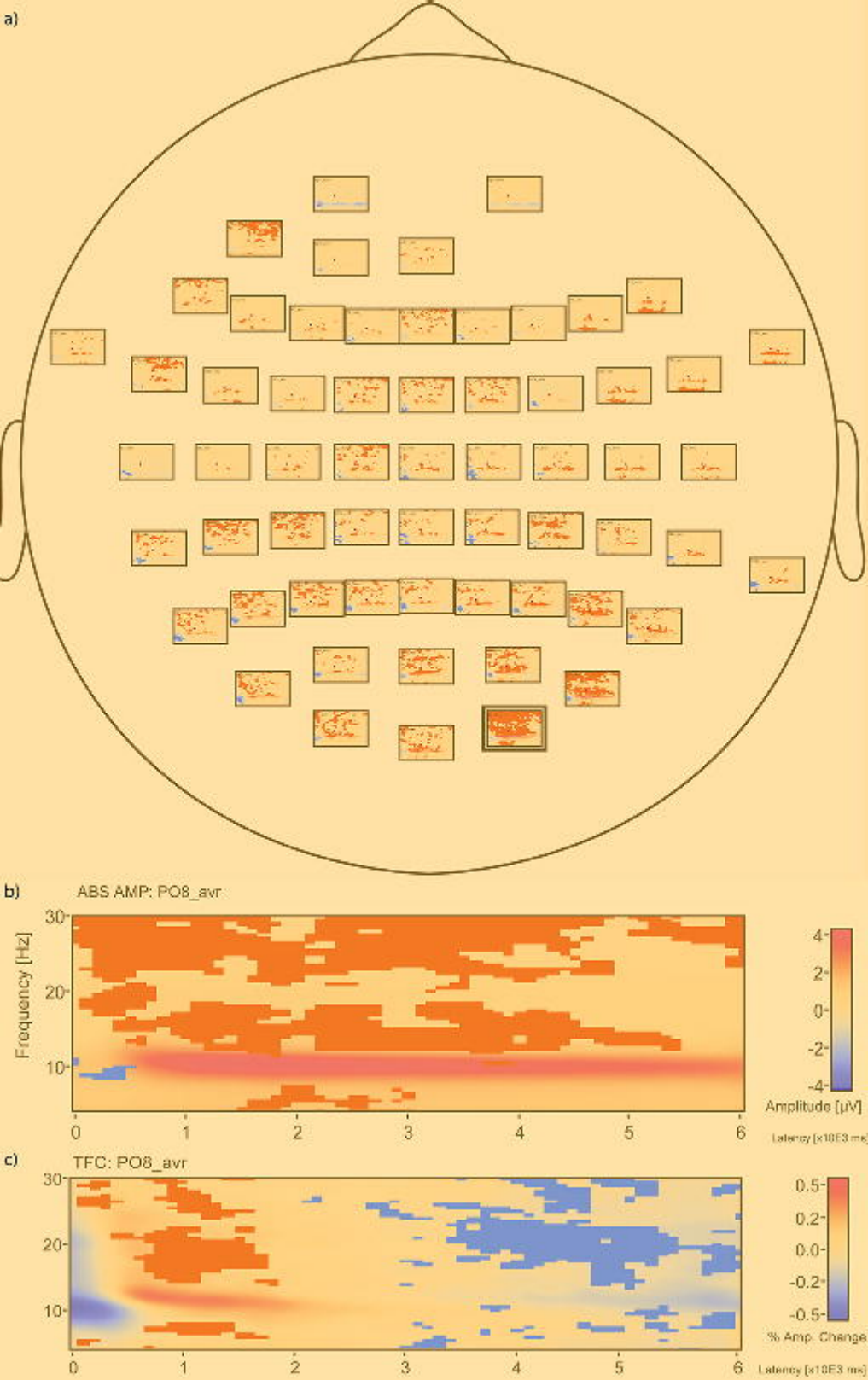

B)
F1_avr: Delay Period
Frequency [Hz]
30
20
10
0
1
2
3
4
5
6
Latency [x10E3 ms]
0.2
0.1
0.0
-0.1
-0.2
Amplitude [µV]
A)
C)
P8_avr: Delay Period
Frequency [Hz]
30
20
10
0
1
2
3
4
5
6
Latency [x10E3 ms]
0.2
0.1
0.0
-0.1
-0.2
Amplitude [µV]

a)


Accuracy (Proportion Correct)
0.9
0.8
0.7
0.6
0.5
Rehearsal
Suppresion
Condition

b)


Accuracy (Proportion Correct)
1.0
0.8
0.6
0.4
0.2
Rehearsal
Suppresion
Condition


a)
b)
ABS AMP: PO8_avr
Frequency [Hz]
30
20
10
0
1
2
3
4
5
6
4
2
0
-2
-4
Amplitude [µV]
Latency [x10E3 ms]
c)
TFC: PO8_avr
30
20
10
0
1
2
3
4
5
6
0.5
0.2
0.0
-0.2
-0.5
% Amp. Change
Latency [x10E3 ms]