

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

Author names and affiliations:

Chelsea Reichert Plaska^{1,2}

Ashley M. Arango¹

Kenneth Ng²

Timothy M. Ellmore^{1,2}

¹The Behavioral and Cognitive Neuroscience Program, CUNY Graduate Center, ²Department of Psychology, The City College of New York

Corresponding Author: Timothy Ellmore, Ph.D. (tellmore@ccny.cuny.edu)

of figures - 5 Figures

of tables – 3 Tables

of words for abstract -247 words

of words for introduction – 650 words

of words for discussion – 1454 words

Conflict of Interest Statement: The authors declare no competing financial interests

Acknowledgements (Funding): The City University of New York Graduate Center Doctoral Student Research Fund, Round 12

Abstract

There is a rich behavioral literature on articulatory rehearsal for verbal stimuli, suggesting that rehearsal may facilitate memory, but few studies have examined the benefits for visual stimuli. Neural delay period studies have largely failed to control for the use of maintenance strategies, which make activity patterns during maintenance difficult to interpret. Forty-four participants completed a modified Sternberg Task with either novel scenes (NS) that contained semantic information or phase-scrambled scenes (SS) that lacked it. Participants were instructed to generate a descriptive label and covertly rehearse (CR) or suppress (AS, i.e., repeat “the”) during the delay period. Artifact-corrected delay period activity was compared as a function of maintenance strategy (CR vs. AS) and stimulus type (NS vs. SS). Performance on the working memory task for NS revealed that CR neither provided a short- nor long-term behavioral advantage on the delayed recognition task for CR. Interestingly, when task difficulty increased with SS, there was both a significant short-term as well as a long-term advantage. Comparison of sensor-level delay activity during the maintenance phase for NS and SS revealed two distinct patterns of neural activity for NS; there was greater amplitude in the beta range in the right parietal and centromedial regions. For SS, across all sensors during CR, the higher amplitude was observed in the upper alpha and beta ranges. The results suggest that rehearsal increased subsequent memory with SS but not NS. Moreover, neural modulation during the delay period depends on both task difficulty and maintenance strategy.

Introduction

Rehearsal and Working Memory

It has long been established that rehearsal benefits memory for verbal stimuli, such as words and numbers. It is often assumed that participants engage in cumulative rehearsal when confronted with a list of verbal stimuli to remember. However, recent research has suggested that rehearsal is less beneficial to memory (Souza and Oberauer, 2018), especially with regards to increasing list size and shorter presentation rates (Tan and Ward, 2008; Souza and Oberauer, 2018). Baddeley (1986) 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. Numerous studies support that blocking rehearsal with articulatory suppression, repeating a word such as “the” over and again, decreases performance as compared with when someone rehearses (Baddeley et al., 1984; Baddeley, 2012). Recently, Souza & Oberauer (2018) suggested that rehearsal may only provide a benefit for stimuli that have a simple phonological representation and an additional component like semantic representation. How does a conclusion like this apply to complex visual stimuli?

Complex visual stimuli contain rich details and are easy to provide a semantically meaningful label to (Wright et al., 1990). Combining of visual information with a semantic label may result in a deeper level of encoding because the stimulus is encoded in both the visual and verbal domains (Paivio, 1969; Craik and Lockhart, 1972; Nelson and Reed, 1976; Ensor et al., 2019). It has also been suggested that the addition of the verbal label to a visually encoded stimulus does not improve memory for the stimulus, rather the added benefit of labeling is dependent on whether or not semantic associations are automatically accessed without labeling (Nelson and Reed, 1976). Few studies have addressed whether rehearsal for complex visual stimuli will benefit performance on a subsequent memory test. Research on simple stimuli, which lack semantic representations, have suggested that rehearsal may benefit memory for visual stimuli. But the question remains, does rehearsal benefit memory for complex visual stimuli?

Delay Activity and Working Memory

To understand the mechanisms that support maintenance of encoded information and successful retrieval, it is critical to examine the neural activity during the delay period (Sreenivasan and D'Esposito, 2019). Delay activity is characterized as a period of increased

and sustained activation throughout the delay period (Sreenivasan et al., 2014; Sreenivasan and D'Esposito, 2019). This traditional view of delay activity suggests that it is supported by persistent neuronal firing, which represents that information is active until a response is made (Constantinidis et al., 2018). Maintenance strategies can differentially engage brain regions which support those strategies (Weiss and Mueller, 2012). Attentional refreshing involves directing attention inward to selectively keep information active and largely engages attentional mechanisms (Cowan et al., 2005), while rehearsal implicates language areas (Henson et al., 2000), especially with regards to verbal stimuli (Baddeley, 2003). If maintenance strategies are not controlled for, delay period activity is difficult to interpret and may explain the recent challenges to the established patterns (Miller et al., 2018; Sreenivasan and D'Esposito, 2019). Similar to the behavioral rehearsal literature, delay period activity has been examined during maintenance of verbal stimuli and simple visual stimuli, but no study has characterized delay activity during maintenance of complex visual stimuli. Thus, the question remains, how does rehearsal influence delay period activity to support memory for complex visual stimuli?

The purpose of Experiments 1 and 2 is to understand how rehearsal and task difficulty impacts performance on a working memory task using complex visual stimuli. It is hypothesized that controlling for the maintenance strategy, namely rehearsal versus suppressing rehearsal, will result in differences in the behavioral performance and delay period activity. Regardless of task difficulty, it is predicted that rehearsal will provide a behavioral advantage over suppressing rehearsal. The delay activity during rehearsal will be continuous and sustained throughout and correlated with performance.

Materials and Methods

Participants

The study was approved by the Institutional Review Board of the City College of New York Human Research Protection Program. A total of 54 participants signed the 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 was recorded as part of an EEG study and took approximately 2 hours to complete.

Experiment 1

One participant was excluded from Experiment 1 of the study because of failure to follow instructions. The final sample included in Experiment 1 of the study consisted of 29 participants

(age = 25.4 (8.1) years, 14 females). For the EEG analysis a total of 6 participants were excluded from Experiment 1 of the study, 5 participants were excluded for noisy EEG recordings or difficulty with data collection, and 1 participant was excluded for failing to follow instructions. The final sample for Experiment 1 of the study consisted of 24 participants (age = 25.8 (8.6) years, range 18-56, 11 females).

Experiment 2

To confirm that ceiling effects were not biasing the findings of Experiment 1, Experiment 2 was conducted. Experiment 2 is a replication of Experiment 1 with different stimuli to reduce the overall performance. Four participants were excluded from Experiment 2 of the study because of computer malfunction while recording the behavioral responses. The final sample for Part 2 of the study consisted 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 Task (*Figure 1*; Sternberg, 1966). The task consisted of 2 working memory tasks (100 trials each) and a delayed recognition task (150 trials). During the working memory task, 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. During presentation of images, participants were instructed to generate a verbal label for the image, and the delay period they were instructed to rehearse covertly (i.e. using their inner voice) the verbal label throughout the entire delay period (termed Rehearsal) or were prevented from actively rehearsing (termed Suppression). For the later condition, participants were discouraged from generating a verbal label and instructed to repeat the word "the" throughout the delay period (Baddeley et al., 1975; Landry and Bartling, 2011). Participants were given examples of labels as well as the rate at which they should rehearse during practice trials before beginning.

Participants completed both the Rehearsal and Suppression conditions in a randomized order. The participant made probe choices on an RB-530 response pad (Cedrus Inc). If a probe matched one of the previously presented encoding set, the participant would press the green

(right) button on the response pad. If the probe did not match the encoding set, the participant would press the red (left) button. Participants completed the delayed recognition task approximately 10 minutes after the completion of the working memory tasks. During this short break, participants remained in the lab. The recognition task was a mix of any encoding image from either the Rehearsal and Suppression conditions (40 images from each condition), as well as new images (70 images). During the recognition task, the participant indicated if the image was presented in either of the working memory conditions (Rehearsal or Suppression) or a new image. If they indicated that they saw the image in one of the earlier working memory conditions, they were asked to indicate if they remembered labeling the image and verbally stated the label that was used. The experimenter recorded the verbal label.

Stimuli

In Experiment 1, the stimuli consisted of high-resolution, colored outdoor scenes, which did not contain any people's faces or words. The images were randomly selected from the SUN database (Xiao et al., 2010) and were resized to 800 by 600 pixels. Experiment 2 employed the same study design as Experiment 1 with phase-scrambled versions of the naturalistic scenes used in Experiment 1 (*Figure 2*). Importantly, the images contained the same colors and spatial frequencies as the images used in Experiment 1 but lacked in semantic content and were more challenging to generate labels because phase-scrambling removes all semantic content. The images were Fourier phase-scrambled in Matlab v9.1 (R2016b).

Behavioral Analysis

The behavioral data were processed in Python 3.0, and the corresponding figures were created using Seaborn 0.9.0 in Python 3.0. Statistical analysis was conducted using JASP v0.9.0.1. Paired-samples t-tests were used to compare behavioral accuracy between conditions on the WM tasks for both the Image and Scramble Study. Paired-samples t-tests were used to compare behavioral accuracy between the image types.

EEG Processing and Analysis

Continuous 64-channel EEG was collected at a sampling rate of 1 kHz using an active electrode system with actiCHamp system (Brain Products). All electrode impedances were lowered to 25 kOhms or below, per the manufacturer's specifications. Electrodes with impedance above 25 were interpolated. The raw EEG data was processed in BESA Research v 6.1. Data was re-referenced offline to the average reference. Participants were only included in

the EEG analysis if they had at least 50 delay periods that survived the artifact scan (amplitude less than 145 μ V). Time-frequency analysis (TFA) was conducted on artifact-corrected delay period epochs (0 to 6000 ms). TFA was bandpass filtered between 4 Hz and 30 Hz and generated with 100 ms/0.5 Hz steps.

TFA absolute amplitude and temporal spectral analysis were generated in BESA Research. TFA absolute amplitude and temporal spectral analysis were compared using paired-samples t-tests with corrections for multiple comparisons in BESA Statistics v 2.0. Additionally, correlations were run between TFA temporal spectral analysis and performance with corrections for multiple comparisons.

Results

Experiment 1 and Discussion

Behavioral. Examination of performance on this WM task revealed that there was no significant difference in performance between rehearsal and suppression (.95 proportion correct vs. .95), $t_{(28)} = .70$, $p = .49$, $d = .13$, suggesting that rehearsal did not provide a short-term behavioral advantage (*Figure 3*). Similarly, there was no long-term behavioral advantage on the delayed recognition task for rehearsal vs. suppression (.80 proportion correct vs. .78), $t_{(28)} = 1.38$, $p = .18$, $d = .23$.

The behavioral results suggest that complex scenes may not benefit from rehearsal. It is also possible that the task was not difficult enough to benefit from rehearsal.

EEG. Sensor-level changes in absolute amplitudes between the two conditions (n=24 subjects) with corrections for multiple comparisons revealed 100 significant clusters (*Table 1*, $p < .05$). A cluster is a group of adjacent bins (sensor (<4 cm distance), time (100 ms), frequency (.50 Hz) bins), in which the difference in absolute amplitude between the two conditions is significantly different from a random permutation distribution (Maris and Oostenveld, 2007). For the rehearsal condition (*Figure 4a* – P8 electrode - orange clusters), amplitude was greater in the theta and beta range for the left frontal, bilateral fronto-temporal, and central regions, suggesting engagement of the phonological loop (Baddeley, 2003; Hwang et al., 2005) and in the beta range for the right parietal region, throughout the delay period. For the suppression condition (*Figure 4b* – 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.

Review of the change in amplitude over time (temporal spectral analysis) suggests that activity is increased and synchronous early in the delay period and begins to decrease later in the delay period. There was no significant difference between temporal spectral analysis during rehearsal versus suppression ($p = .08$). Additionally, temporal spectral analysis during rehearsal was not significantly correlated with working memory ($p = .46$) nor with recognition performance ($p = .28$).

Overall, the significant sensor-level difference in absolute amplitude suggests that participants engaged in different maintenance strategies; however, the change in delay activity over time was similar.

Experiment 2 and Discussion

Behavioral. The results show that when task difficulty increased, there was both a significant short-term advantage of rehearsal (*Figure 5*) as compared with suppression (.85 proportion correct vs. .78, $t_{(19)} = 7.93$, $p < .001$, $d = 1.77$) as well as a long-term advantage for images from the rehearsal condition as compared with suppression (.71 proportion correct vs. .62, $t_{(19)} = 4.58$, $p < .001$, $d = 1.02$).

The lack of behavioral difference for the complex scenes as compared with the phased-scrambled scenes suggests that the task difficulty explains the performance. These images were more difficult to generate a label because they lacked semantic content; therefore, this eliminated the automatic semantic association.

EEG. It was predicted that rehearsal and suppression would produce similar EEG delay period activity to the Experiment 1 sensor-level analysis since the task was the same.

Sensor-level examination of the absolute amplitude between the two conditions ($n = 20$ subjects) with corrections for multiple comparisons revealed 15 significant clusters (*Table 2*, $p < .05$). Greater amplitude was observed in the upper alpha and beta ranges across all sensors for the rehearsal condition (*Figure 6a* – P08 – orange cluster), as compared with the suppression condition. The pattern of delay activity appears to be both sustained and continuous throughout the entire delay period, as has been previously reported in the literature (Jensen et al., 2002; Tuladhar et al., 2007; Khader et al., 2010; Berger et al., 2014).

Review of the sensor-level temporal spectral analysis suggests that it is transient in nature, similar to the delay activity observed in Experiment 1. Activity is increased and synchronous in the early part of the delay period and begins to decrease later in the delay period. Comparison of the temporal spectral analysis between the rehearsal and suppression

conditions revealed 3 clusters of significantly different activity (*Table 3*). Additionally, temporal spectral analysis during rehearsal was significantly correlated with working memory performance (*Figure 6b*; Cluster 1: blue, cluster value = -38801.2, $p = .005$, Cluster 2: orange, Cluster value = 20445.5, $p = .065$), but not performance on the recognition task ($p = .62$).

The significant sensor-level difference in absolute amplitude and temporal spectral analysis suggests that delay activity was modulated by maintenance strategy.

Discussion

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 of rehearsal) influenced the short- and long-term memory for visual stimuli.

Experiment 1 used intact, novel outdoor scenes that contained semantic information (i.e. a beach or a farm) which were intended to elicit stored semantic associations automatically. 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 (Ensor et al., 2019) which provide automatic deeper encoding (Craik and Lockhart, 1972). Consequently, the addition of rehearsing with a generated label offers no more benefit than accessing those stored associations. It is also plausible that task difficulty modulated the benefit of a maintenance strategy like rehearsal. Participants saw two images and within 6 seconds responded to whether or not the image was old or new. It has been established that humans can remember thousands of images after only seeing the images for a brief time (Standing et al., 1970; Standing, 1973; Brady et al., 2008). This ability has been termed the picture superiority effect (Stenberg, 2006) and may account for the fact that generating a semantic label and rehearsing provided no additional benefit. While it has been suggested that the addition of the semantic label provides a dual means of encoding (Paivio, 1969; Nelson and Reed, 1976), these results suggest that the semantic associations are automatically generated without recoding and rehearsal (Nelson and Reed, 1976; Ensor et al., 2019). Thus, it is not surprising that the performance was near ceiling.

Experiment 2 was conducted to increase task difficulty by using phase-scrambled images that lacked semantic content. While an automatic association of a label to a picture results in deeper encoding, this automatic association fails to occur with phase-scrambled

stimuli; therefore, the process of generating a label during encoding ensures that a deeper level-of-processing occurs (Craik and Lockhart, 1972; Ensor et al., 2019). Performance in Experiment 2 provides support for the assumption that the benefit of rehearsal on complex visual stimuli is modulated by task difficulty. More specifically, when participants generated a semantic label and rehearsed throughout the delay period, they engaged in deeper encoding and elaborative rehearsal (Cermak, 1971; Craik and Lockhart, 1972; Phaf and Wolters, 1993; Ensor et al., 2019). These findings are consistent with the idea that generating a label is only beneficial to visual stimuli when semantic information is not automatically accessed (Nelson and Reed, 1976). Whereas with the suppression condition participants engaged in more shallow encoding, relying solely on the visual information, and did not recode or rehearse; hence, performance was lower.

Delay Activity and Rehearsal

The delay period is a critical time during a working memory task when encoded information is maintained. Experiments 1 and 2 sought to understand how delay activity would change as a function of task difficulty (intact novel scenes vs. phase-scrambled scenes) and 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, which suggests the engagement of the phonological loop (Baddeley, 2003; Hwang et al., 2005). Whereas, suppression results in the engagement of more frontal electrodes suggesting greater attentional demand (Camos et al., 2011) as well as greater mental effort (Kopp et al., 2006) involved in inhibiting rehearsal. Engagement of the parietal electrodes for both conditions may indicate storage of the images in a temporary visuospatial store (Baddeley, 2003). Delay activity during a WM task is often associated with the engagement of either the prefrontal cortex or the posterior parietal regions but has been established in studies that often fail to control for maintenance strategy. Activity in the parietal region has been suggested as the storage place for visual information during the maintenance phase of a working memory task. It serves as the buffer in which information lives until it is needed for retrieval, analogous to the verbal information store. 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 hypothesis (Baddeley, 2000; Hutchinson, 2009). Activation in these regions, regardless of the connections with attentional networks, likely does not only reflect attentional processes (Hutchinson et al., 2009). The results of this study confirm that controlling

for maintenance strategy, hence controlling for the cognitive domains that are involved, will recruit different brain regions (Sreenivasan and D'Esposito, 2019).

In experiment 2 the patterns of delay activity were different than the patterns observed in Experiment 1. For the rehearsal condition, activity was greater for all sensors, as compared with suppression. The simplest explanation is that differences in delay activity between the two studies can be attributed to differences in the task demands (Sreenivasan and D'Esposito, 2019). The stimuli used phase-scrambled scenes that were difficult to generate a label to. Although difficult-to-label images 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 a definitive semantic association and a verbal label (Wright et al., 1990; Ensor et al., 2019). The generation of a label in Experiment 2 was more effortful than in Experiment 1, and often shallower in nature (i.e., colors and feature-related) both during the recoding process and rehearsal. Thus, the differential pattern of delay activity, particularly in the frontal regions during rehearsal, represents the process of recoding difficult-to-label images (i.e., engagement of bilateral fronto-temporal regions) and a more attention-demanding rehearsal period (i.e., engagement of centro-frontal regions).

Transient vs. Sustained Delay Activity

Elucidating the pattern of delay activity is the current focus in the working memory literature (Nature, 2019). While it has long been established that sustained activity observed during the maintenance phase when stimuli are no longer being encoded represented both maintenance of encoded information and focusing of attention inward, recent research has suggested that delay activity is more complex (Rose et al., 2016; Miller et al., 2018; Sreenivasan and D'Esposito, 2019). 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 (Stokes, 2015; Rose et al., 2016). 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) followed by a period of desynchronous activity, regardless of stimulus type. This pattern of activity is consistent with recent reports that maintenance is not necessarily supported by persistent delay activity in prefrontal regions (Miller et al., 2018; Sreenivasan and D'Esposito, 2019); instead delay activity may reflect more complex processes going on throughout the cortex and deeper 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 (Cowan et al., 2005). Thus, delay activity is a function of the strategy that is employed to maintain information (Sreenivasan and D'Esposito, 2019) as well as the task difficulty.

Limitations

Participants engaged in covert rehearsal and suppression to reduce the amount of noise introduced into the EEG signals. Thus, task compliance is based on participant confirmation during the recognition task (i.e., reported their generated labels). Additionally, the generated labels were reviewed during the recognition task to confirm compliance and were not systematically analyzed for the depth of encoding. Future studies should include a post-trial component during the working memory tasks to confirm task compliance when covert maintenance strategies are used.

Significance Statement

Rehearsal is a maintenance technique that is purported to benefit memory. Despite decades of research affirming the positive effect of rehearsal on memory, the benefit may be limited to certain types of stimuli. Understanding the neural process that underlie maintenance is also a critical area of research. Interestingly, few studies that examine neural patterns of maintenance, control for the technique used. The present study sought to understand how controlling for maintenance, namely rehearsal versus suppressing rehearsal, would influence delay activity. The results provide evidence that rehearsal and task difficulty both modulate the pattern of delay period activity. Moreover, the results suggest that rehearsal may only benefit complex visual stimuli that lack semantic content.

References

- Baddeley A (2003) Working memory: looking back and looking forward. *Nature reviews neuroscience* 4:829-839.
- Baddeley A (2012) Working memory: theories, models, and controversies. *Annual review of psychology* 63:1-29.
- Baddeley A, Lewis V, Vallar G (1984) Exploring the articulatory loop. *The Quarterly journal of experimental psychology* 36:233-252.
- Baddeley A, Logie R, Bressi S, Sala SD, Spinnler H (1986) Dementia and working memory. *The Quarterly Journal of Experimental Psychology* 38:603-618.
- Baddeley AD, Thomson N, Buchanan M (1975) Word length and the structure of short-term memory. *Journal of verbal learning and verbal behavior* 14:575-589.
- Berger B, Omer S, Minarik T, Sterr A, Sauseng P (2014) Interacting Memory Systems—Does EEG Alpha Activity Respond to Semantic Long-Term Memory Access in a Working Memory Task? *Biology* 4:1-16.
- Brady TF, Konkle T, Alvarez GA, Oliva A (2008) Visual long-term memory has a massive storage capacity for object details. *Proceedings of the National Academy of Sciences* 105:14325-14329.
- Camos V, Mora G, Oberauer K (2011) Adaptive choice between articulatory rehearsal and attentional refreshing in verbal working memory. *Memory & Cognition* 39:231-244.
- Cermak GW (1971) Short-term recognition memory for complex free-form figures. *Psychonomic Science* 25:209-211.
- Constantinidis C, Funahashi S, Lee D, Murray JD, Qi X-L, Wang M, Arnsten AF (2018) Persistent spiking activity underlies working memory. *Journal of Neuroscience* 38:7020-7028.
- Cowan N, Elliott EM, Saults JS, Morey CC, Mattox S, Hismjatullina A, Conway AR (2005) On the capacity of attention: Its estimation and its role in working memory and cognitive aptitudes. *Cognitive psychology* 51:42-100.
- Craik FI, Lockhart RS (1972) Levels of processing: A framework for memory research. *Journal of verbal learning and verbal behavior* 11:671-684.
- Ensor TM, Surprenant AM, Neath I (2019) Increasing word distinctiveness eliminates the picture superiority effect in recognition: Evidence for the physical-distinctiveness account. *Memory & cognition* 47:182-193.
- Henson R, Burgess N, Frith CD (2000) Recoding, storage, rehearsal and grouping in verbal short-term memory: an fMRI study. *Neuropsychologia* 38:426-440.

- Hutchinson JB, Uncapher MR, Wagner AD (2009) Posterior parietal cortex and episodic retrieval: convergent and divergent effects of attention and memory. *Learning & Memory* 16:343-356.
- Hwang G, Jacobs J, Geller A, Danker J, Sekuler R, Kahana MJ (2005) EEG correlates of verbal and nonverbal working memory. *Behavioral and Brain Functions* 1:20.
- Jensen O, Gelfand J, Kounios J, Lisman JE (2002) Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral cortex* 12:877-882.
- Khader PH, Jost K, Ranganath C, Rösler F (2010) Theta and alpha oscillations during working-memory maintenance predict successful long-term memory encoding. *Neuroscience letters* 468:339-343.
- Kopp F, Schröger E, Lipka S (2006) Synchronized brain activity during rehearsal and short-term memory disruption by irrelevant speech is affected by recall mode. *International Journal of Psychophysiology* 61:188-203.
- Landry P, Bartling C (2011) The Phonological Loop and Articulatory Suppression. *American Journal of Psychological Research* 7:79-86.
- Maris E, Oostenveld R (2007) Nonparametric statistical testing of EEG-and MEG-data. *Journal of neuroscience methods* 164:177-190.
- Miller EK, Lundqvist M, Bastos AM (2018) Working Memory 2.0. *Neuron* 100:463-475.
- Nelson DL, Reed VS (1976) On the nature of pictorial encoding: A levels-of-processing analysis. *Journal of Experimental Psychology: Human Learning and Memory* 2:49.
- Paivio A (1969) Mental imagery in associative learning and memory. *Psychological review* 76:241.
- Phaf RH, Wolters G (1993) Attentional shifts in maintenance rehearsal. *The American journal of psychology*:353-382.
- Rose NS, LaRocque JJ, Riggall AC, Gosseries O, Starrett MJ, Meyering EE, Postle BR (2016) Reactivation of latent working memories with transcranial magnetic stimulation. *Science* 354:1136-1139.
- Souza AS, Oberauer K (2018) Does articulatory rehearsal help immediate serial recall? *Cognitive psychology* 107:1-21.
- Sreenivasan KK, D'Esposito M (2019) The what, where and how of delay activity. *Nature Reviews Neuroscience*:1.
- Sreenivasan KK, Curtis CE, D'Esposito M (2014) Revisiting the role of persistent neural activity during working memory. *Trends in cognitive sciences* 18:82-89.
- Standing L (1973) Learning 10000 pictures. *The Quarterly journal of experimental psychology* 25:207-222.

- Standing L, Conezio J, Haber RN (1970) Perception and memory for pictures: Single-trial learning of 2500 visual stimuli. *Psychonomic Science* 19:73-74.
- Stenberg G (2006) Conceptual and perceptual factors in the picture superiority effect. *European Journal of Cognitive Psychology* 18:813-847.
- Stokes MG (2015) 'Activity-silent' working memory in prefrontal cortex: a dynamic coding framework. *Trends in Cognitive Sciences* 19:394-405.
- Tan L, Ward G (2008) Rehearsal in immediate serial recall. *Psychonomic Bulletin & Review* 15:535-542.
- Tuladhar AM, Huurne Nt, Schoffelen JM, Maris E, Oostenveld R, Jensen O (2007) Parieto-occipital sources account for the increase in alpha activity with working memory load. *Human brain mapping* 28:785-792.
- Weiss S, Mueller HM (2012) "Too many betas do not spoil the broth": the role of beta brain oscillations in language processing. *Frontiers in Psychology* 3.
- Wright AA, Cook RG, Rivera JJ, Shyan MR, Neiworth JJ, Jitsumori M (1990) Naming, rehearsal, and interstimulus interval effects in memory processing. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 16:1043.
- Xiao J, Hays J, Ehinger KA, Oliva A, Torralba A (2010) Sun database: Large-scale scene recognition from abbey to zoo. In: *Computer vision and pattern recognition (CVPR), 2010 IEEE conference on*, pp 3485-3492: IEEE.

Figure Legends

Figure 1. Example trial of the modified Sternberg working memory task from Experiment 1. The task consisted of a low cognitive load (2 images) that consists of encoding, delay period, probe choice, and scramble images. 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. Example trial of the modified Sternberg working memory task from Experiment 2. The task consisted of a low cognitive load (2 images) that consists of encoding, delay period, probe choice, and black screen. An example of a rehearsal trial in which participants generate the label for each phase-scrambled image and rehearse during the delay period.

Figure 3. Examination of performance on the working memory and recognition tasks from Experiment 1 suggest that 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 4. Absolute Amplitude comparison of delay period activity in Experiment 1 reveals differential pattern of activity 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) 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. b) 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 5. Comparison of performance on the working memory and recognition tasks from Experiment 2 suggest that rehearsal does benefit 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 6. Time Frequency Analysis of delay period activity in Experiment 2 reveals greater activity for rehearsal and correlation with performance. The y-axis is frequency (Hz); x-axis is the time in sec. a) Absolute amplitude plot for the PO8 electrode during the 6-sec delay period. 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, $p < 0.05$). b) 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, $p = .005$).

Tables and Legends

Table 1.

Cluster	p-value	Cluster value	Start Time (ms)	End Time (ms)	Start Frequency (Hz)	End Frequency (Hz)
Cluster 1	0	-3219.72	0	5700	4	12.5
Cluster 2	0	1291.89	0	3100	23	30
Cluster 3	0.001	908.429	4400	6000	23	30
Cluster 4	0.001	866.052	3000	4500	21	30
Cluster 5	0.001	815.945	2200	4800	12	18
Cluster 6	0.002	-682.507	4500	6000	10.5	16
Cluster 7	0.001	606.747	0	1500	10.5	22
Cluster 8	0.002	-515.507	900	3400	10	17.5
Cluster 9	0.002	-433.786	3700	6000	4	9
Cluster 10	0.001	432.653	3200	6000	4	5
Cluster 11	0.002	-383.992	0	600	18.5	22.5
Cluster 12	0.002	367.796	5100	6000	12.5	17
Cluster 13	0.002	328.387	4700	6000	16.5	20
Cluster 14	0.002	295.663	3100	4300	17.5	20
Cluster 15	0.002	285.702	2100	2900	4	5.5
Cluster 16	0.002	258.945	4400	5600	4	7
Cluster 17	0.002	245.497	3200	4400	19.5	28
Cluster 18	0.002	227.926	1600	3000	19	27
Cluster 19	0.002	217.322	0	1000	22.5	29.5
Cluster 20	0.002	-202.478	3400	4400	11	13.5
Cluster 21	0.002	173.824	2000	3700	23.5	27.5
Cluster 22	0.003	-162.489	600	1800	14	20
Cluster 23	0.003	-153.869	1500	3000	10.5	14.5
Cluster 24	0.002	142.727	2400	3000	4	7
Cluster 25	0.003	-135.422	3700	4800	11.5	13.5
Cluster 26	0.002	132.326	3800	4400	25	29.5
Cluster 27	0.003	-131.546	5100	5800	20	22
Cluster 28	0.002	105.412	0	700	24	30
Cluster 29	0.003	101.524	2700	3500	8.5	10.5
Cluster 30	0.003	99.7788	0	1000	15	18.5
Cluster 31	0.003	96.6672	2300	2600	14	16.5
Cluster 32	0.003	91.5141	5300	6000	18	23
Cluster 33	0.004	-83.2616	0	800	12.5	16.5
Cluster 34	0.004	82.7652	500	900	13	16

Cluster 35	0.004	-70.5906	4200	4400	22.5	23.5
Cluster 36	0.005	65.3972	3600	4100	4	5
Cluster 37	0.007	56.7185	4900	5300	15.5	17.5
Cluster 38	0.007	52.1515	3800	4200	22	24
Cluster 39	0.008	49.348	3800	4100	26	28.5
Cluster 40	0.009	46.2967	3400	3700	15	18
Cluster 41	0.01	-46.2615	1000	1800	7	8.5
Cluster 42	0.011	-43.4175	1500	2100	11.5	12
Cluster 43	0.011	43.2112	4500	4800	9.5	12.5
Cluster 44	0.011	-40.4913	4500	4800	18	19.5
Cluster 45	0.011	-40.2886	1800	2100	22.5	23.5
Cluster 46	0.014	39.017	5800	6000	9.5	10.5
Cluster 47	0.011	-38.0149	1400	1700	19	22
Cluster 48	0.014	37.8078	2800	3300	12.5	14
Cluster 49	0.014	37.7062	1500	2100	29	30
Cluster 50	0.011	-36.7765	1000	1200	7	8
Cluster 51	0.011	-36.2723	5000	5400	17.5	18.5
Cluster 52	0.016	34.0853	5400	5900	26.5	28
Cluster 53	0.014	-34.0646	3900	4200	15.5	16.5
Cluster 54	0.016	33.1684	2800	3200	13.5	15.5
Cluster 55	0.017	32.9503	5900	6000	9	11
Cluster 56	0.017	32.3299	5500	6000	19	20
Cluster 57	0.023	27.6824	4400	4900	9.5	10
Cluster 58	0.023	27.334	1800	2100	4	4.5
Cluster 59	0.022	-26.0868	900	1300	5	6.5
Cluster 60	0.023	25.9468	2300	2700	15.5	17
Cluster 61	0.022	-25.9459	0	100	4	5.5
Cluster 62	0.022	-25.6374	2700	2900	22.5	24
Cluster 63	0.023	25.2349	500	600	4	4.5
Cluster 64	0.023	-25.1243	5900	6000	7	8.5
Cluster 65	0.023	24.0365	2800	3100	29	30
Cluster 66	0.025	23.0386	5000	5300	29	30
Cluster 67	0.025	22.8883	100	500	29.5	30
Cluster 68	0.025	22.5738	4500	5000	26	27
Cluster 69	0.027	21.7288	600	900	19.5	20.5
Cluster 70	0.027	21.6794	5400	5700	26.5	27.5
Cluster 71	0.027	21.6689	2400	2600	20	21
Cluster 72	0.028	21.2652	5700	6000	26.5	27.5
Cluster 73	0.026	-20.4767	2100	2400	8	9
Cluster 74	0.028	20.3423	5000	5300	25	26.5

Cluster 75	0.026	-20.2277	4300	4500	4	5.5
Cluster 76	0.028	19.2269	5800	6000	4	4.5
Cluster 77	0.028	-19.1831	3200	3400	7.5	8
Cluster 78	0.029	-18.7855	2200	2400	8.5	9.5
Cluster 79	0.028	18.5465	4100	4300	21	22
Cluster 80	0.028	18.401	3400	3600	29	30
Cluster 81	0.029	-17.9053	2200	2400	15.5	16.5
Cluster 82	0.028	17.889	4000	4200	18.5	19.5
Cluster 83	0.028	17.6837	700	1000	21.5	22.5
Cluster 84	0.03	17.0372	1600	1900	26.5	27
Cluster 85	0.03	16.4397	5900	6000	24.5	26
Cluster 86	0.03	16.0846	1300	1500	26	27
Cluster 87	0.031	15.7391	1300	1600	10	11
Cluster 88	0.031	15.6284	4800	5000	21	22
Cluster 89	0.033	15.2976	3800	4100	23.5	24.5
Cluster 90	0.035	14.728	3700	4000	9	9.5
Cluster 91	0.035	13.4996	5900	6000	24.5	26
Cluster 92	0.035	13.32	2500	2700	20.5	21
Cluster 93	0.036	13.1822	4000	4200	29	29.5
Cluster 94	0.037	13.048	1500	1600	23	24.5
Cluster 95	0.037	12.4223	3200	3400	5	5.5
Cluster 96	0.044	-11.9081	4400	4500	22.5	23
Cluster 97	0.044	-11.7014	1500	1700	7	7.5
Cluster 98	0.044	-11.6741	3700	3800	7	8
Cluster 99	0.045	-11.4642	3900	4100	4	4.5
Cluster 100	0.045	-11.3412	2100	2300	27.5	28
Cluster 101	0.045	-11.339	5000	5200	16.5	17
Cluster 102	0.037	11.3019	3100	3400	19	19.5
Cluster 103	0.049	-10.9901	5000	5300	15.5	16
Cluster 104	0.046	9.96535	1700	1900	13.5	14
Cluster 105	0.046	9.92858	5200	5300	25	25.5
Cluster 106	0.046	9.82327	1600	1800	25.5	26

Table 1. Clusters of significantly different absolute amplitude bins between the rehearsal and suppression conditions in Experiment 1. Each cluster has a start and stop time during the delay period (between 0-6000 msec), a start and stop frequency (between 4-30 Hz), and lists the electrodes that were involved in the cluster.

Table 2.

Cluster	p-value	Cluster value	Start Time (ms)	End Time (ms)	Start Frequency (Hz)	End Frequency (Hz)
Cluster 1	0	44900	0	6000	10	30
Cluster 2	0	-4108.68	0	1800	4	23.5
Cluster 3	0.001	2704.99	1100	4200	4	9
Cluster 4	0.016	218.701	3300	4100	4	6
Cluster 5	0.023	130.246	2200	2900	5	7.5
Cluster 6	0.025	115.592	5000	6000	16.5	19.5
Cluster 7	0.025	110.125	2000	3100	21.5	24.5
Cluster 8	0.027	97.6974	1300	2200	4	6.5
Cluster 9	0.031	82.398	5300	5800	21.5	23.5
Cluster 10	0.036	-78.2282	5300	6000	4	6.5
Cluster 11	0.035	75.0621	1400	2000	7	9
Cluster 12	0.041	-63.1014	4900	5600	7.5	8.5
Cluster 13	0.046	-56.2702	4500	5000	4	5
Cluster 14	0.046	46.3749	5600	6000	17	19
Cluster 15	0.047	45.6369	5400	6000	20.5	22.5

Table 2. Clusters of significantly different absolute amplitude bins between the rehearsal and suppression conditions in Experiment 2. Each cluster has a start and stop time during the delay period (between 0-6000 msec), a start and stop frequency (between 4-30 Hz), and lists the electrodes that were involved in the cluster.

Table 3.

Cluster	p-Value	Cluster Value	Start Time (ms)	End Time (ms)	Start Frequency (Hz)	End Frequency (Hz)
Cluster 1	0	-13147.60	0	1400	4	26.5
Cluster 2	0	+11959.00	1100	4600	4	18.5
Cluster 3	.0003	-8012.79	3900	6000	4	28.5

Table 3. Clusters of significantly different temporal spectral amplitude bins between the rehearsal and suppression conditions in Experiment 1. Each cluster has a start and stop time during the delay period (between 0-6000 msec), a start and stop frequency (between 4-30 Hz), and lists the electrodes that were involved in the cluster.

a) Rehearsal



Trial Start



Generate a label:
Mountain



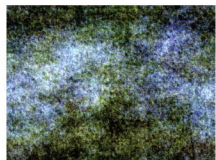
Generate a label:
Lake



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



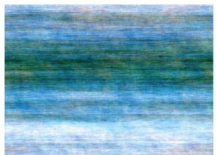
Look at the image &
do not generate a label



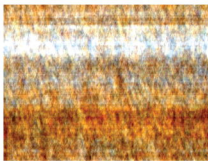
Repeat the word "the":
"the ... the ... the .. the"



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



Trial End



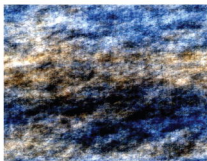
Generate a label:
Orange Sky



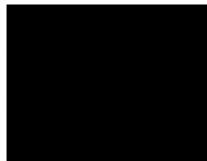
Generate a label:
Lilly Pond

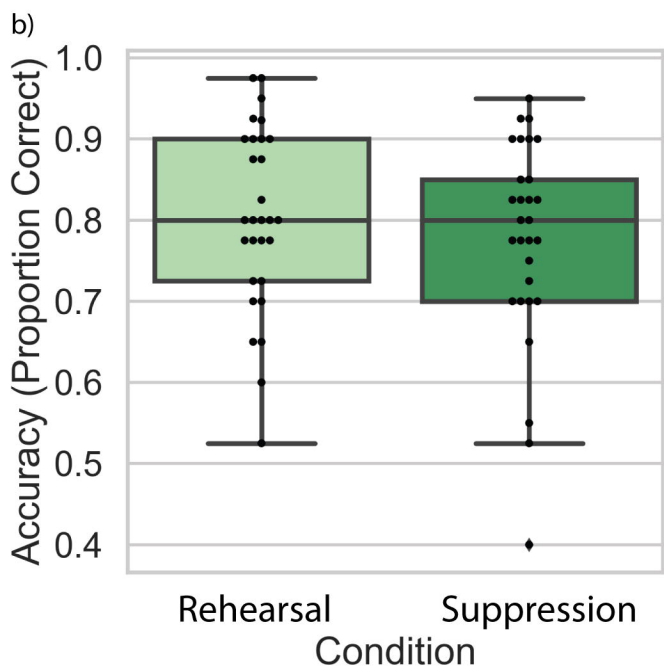
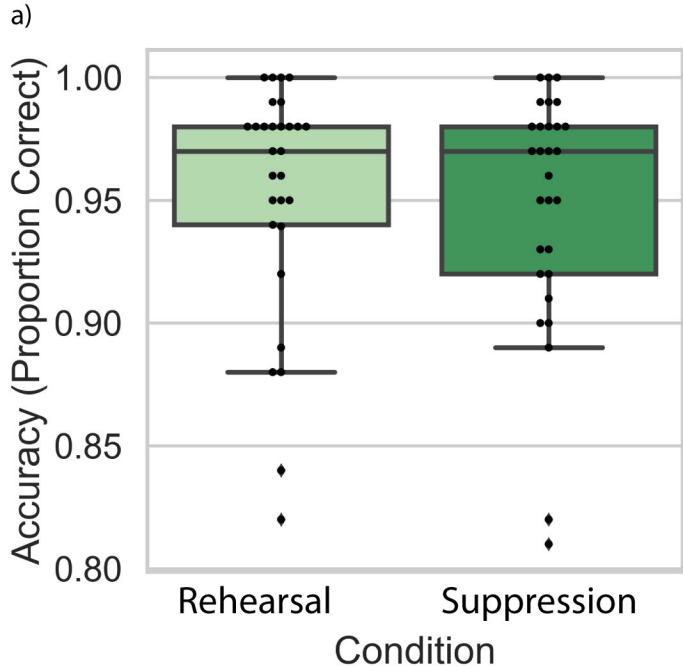


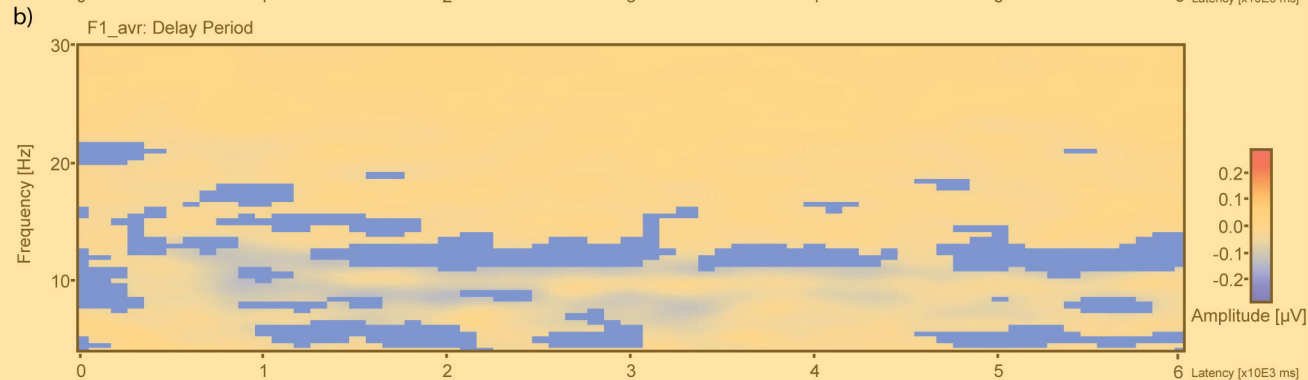
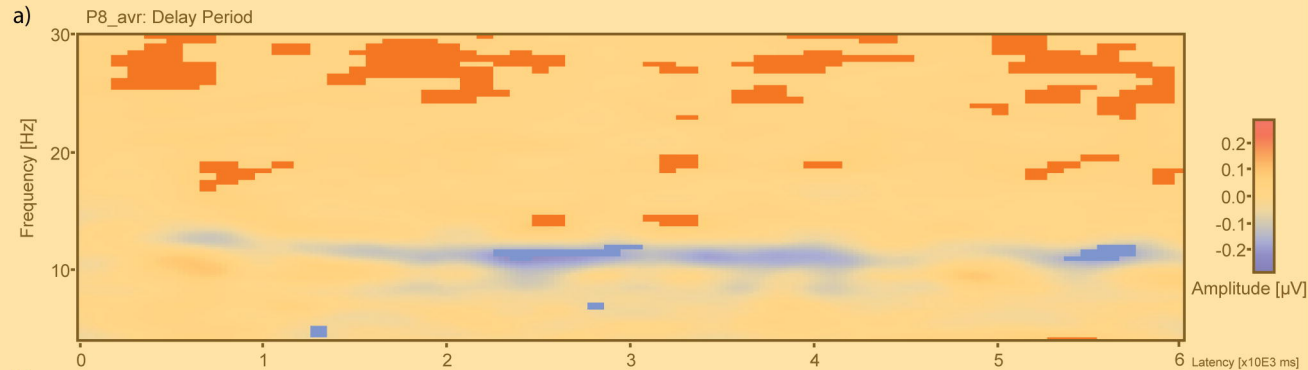
Repeat the generated labels:
"Orange sky...lilly pond...orange
sky...lilly pond"

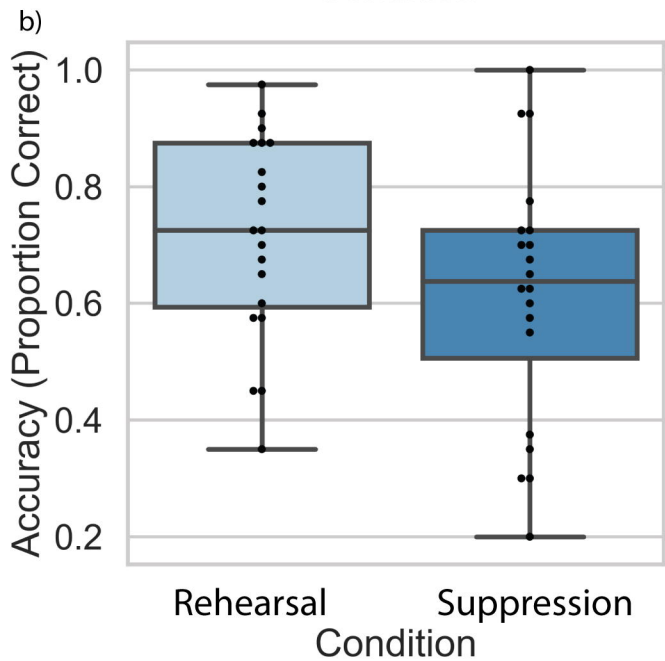
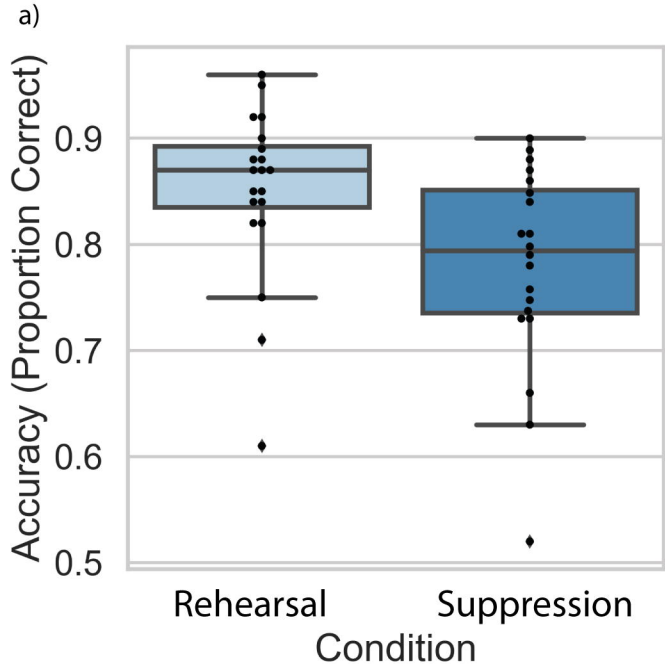


Did I see this image before?
Press **green button** [yes] or
Press **red button** [no]

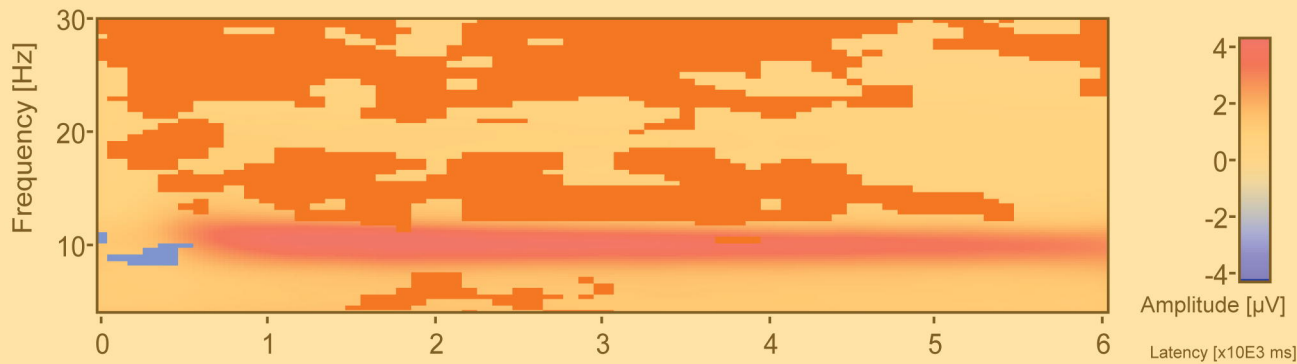








a) ABS AMP: PO8_avr



b) TFC: PO8_avr

