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. Arango[1]
Kenneth Ng[2]
Timothy M. Ellmore[1,2]

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

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

Keywords: Working Memory, Visual Memory, Delay Activity, Rehearsal, Maintenance

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

Articulatory rehearsal during working memory (WM) maintenance facilitates subsequent retrieval, particularly for verbal material. Less is known about how rehearsal modulates WM delay activity during the maintenance of novel visual information. In the present study, 44 participants completed a Sternberg WM Task with either intact novel scenes (NS) or phase-scrambled versions (SS), 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 it (CR) or suppressed it (AS, i.e., repeat "the") during the delay. This was easy in the former condition 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 (CR vs. AS) and stimulus type (NS vs. SS). Performance on the WM task for NS revealed that CR neither improved short- or long-term memory. Delay activity revealed greater amplitude in the beta range in right parietal and centromedial regions for CR compared to AS. When task difficulty increased in the SS 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 task difficulty and cognitive strategy modulate the pattern of delay activity during maintenance of novel visual information with effects on subsequent memory.

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 & Oberauer, 2018), especially with regards to increasing list size and shorter presentation rates (Souza & Oberauer, 2018; Tan & Ward, 2008). 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 over again, decreases performance as compared with when someone rehearses (A. Baddeley, 2012; A. Baddeley, Lewis, & Vallar, 1984). 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.

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”). The word representation automatically links the visual stimulus with stored semantic representations. The semantic representation is often a rich representation that contains many features (i.e. sand and ocean) and associated knowledge (i.e. beaches are located in warm places and have palm trees). Complex visual stimuli are unique because they 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 (Craik & Lockhart, 1972; Ensor, Surprenant, & Neath, 2019; Nelson & Reed, 1976; Paivio, 1969). The novel features of the visual stimuli may also help to guide attention to salient features which facilitates encoding (Santangelo, 2015).

Given that complex pictures have rich representations that provide automatic deeper processing of the affiliated picture without much effort, it remains unclear if they would benefit from any additional encoding or maintenance processing. It has 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 & Reed, 1976). Few studies have addressed whether labeling and rehearsal for complex visual stimuli will benefit performance on a subsequent memory test. Research on simple stimuli, which lack deeper semantic representations, have suggested that rehearsal may benefit memory for visual stimuli. But the question remains, does rehearsal benefit memory for complex visual stimuli?

In order to study the memory for pure visual information, one needs to utilize a stimulus that does not have an automatic word representation and semantic association. Few studies have sought to study complex visual information that fits into this category, including abstract shapes (Mayer et al., 2007; Song & Jiang, 2006). A novel visual stimulus that has not been explored to our knowledge is the use of phase-scrambled images, which are complex and preserve a lot of the visual features of a nature scene. These phase-scrambled scenes are difficult to describe, specifically with

a one-word representation, and are often described based on their basic features (i.e. colors or line orientation). The difficult-to-describe nature of this stimuli makes it a suitable stimulus for studying visual memory and also whether or not maintenance mechanisms (i.e. articulatory rehearsal) can provide any additional benefit for storing and remembering the information.

Delay Activity and Working Memory

To understand the cognitive mechanisms that support maintenance of encoded information and successful retrieval, it is critical to examine the neural activity during the delay period (Sreenivasan & D'Esposito, 2019). Delay activity is characterized as a period of increased and sustained activation throughout the delay period (Sreenivasan, Curtis, & D'Esposito, 2014; Sreenivasan & 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 & 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, Burgess, & Frith, 2000), especially with regards to verbal stimuli (A. 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, Lundqvist, & Bastos, 2018; Sreenivasan & 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 few studies have characterized delay activity during

maintenance of complex visual stimuli. Controlling for these components of an experiment are critical for identifying the brain regions that support memory for visual information and how that changes when words and semantic meaning are associated with that visual information to support memory. 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 articulatory rehearsal influences short- and long-term memory for complex visual stimuli and the neural activity that supports it. 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 the type of complex visual stimulus, it is predicted that rehearsal will provide a behavioral advantage over preventing maintenance both in tests of working memory and immediate long-term memory. The delay activity during rehearsal will be continuous and sustained throughout the delay period representing active maintenance 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 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 consisted of 24 participants (age = 25.8 (8.6) years, range 18-56, 11 females).

Experiment 2

To confirm that the 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 (Sternberg, 1966). The task consisted of 2 working memory tasks (**Figure 1**; 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 the images, participants were instructed to generate a verbal label for the image (i.e. descriptive label like “beach”), and during 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 suppression, participants were discouraged from generating a verbal label and instructed to repeat the word "the" throughout the delay period (A. D. Baddeley, Thomson, & Buchanan, 1975; Landry & Bartling, 2011). Suppression is intended to block the ability to verbally rehearse by engaging the articulatory process of the phonological loop with an unrelated word or sound. The classic suppression task repeats a non-task related word such as “the” over and over again (A. D. Baddeley et al., 1975; Landry & Bartling, 2011; Ricker, Cowan, & Morey, 2010). This classic suppression task was chosen over a different task such as random number generation or a math problem because these alternatives 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 (Norris, Hall, Butterfield, & Page, 2019; Ricker et al., 2010).

Participants completed both the rehearsal and suppression conditions in a randomized order. Participants were given examples of verbal labels during a short 10-

trial practice set as well as the rate at which they should rehearse or suppress, before beginning the task. The participant made probe choices on a RB-530 response pad (Cedrus Inc). If a probe matched one of the previously presented images from the 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 if it was 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, Hays, Ehinger, Oliva, & Torralba, 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 for because phase-scrambling removes all semantic content. The images were Fourier phase-scrambled in Matlab v 2016.

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. The data was analyzed in Jasp v0.9.0.1. Paired-samples t-tests were used to compare behavioral accuracy between conditions (rehearsal vs. suppression) on the working memory and recognition tasks.

EEG Processing and Analysis

Continuous 64-channel EEG was collected at a sampling rate of 1000 Hz using an active electrode system with actiCHamp system (Brain Products). All electrodes were brought down to an impedance of 25 kOhms or lower, per the manufacturer's specifications. Channels with an 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 μV). 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 was conducted for all 64-scalp electrodes. In addition, a brain source montage was applied to the collected data which groups

neighboring electrodes into overlapping brain regions and TFA was run. The brain source montage consists of 15 discrete brain regions in the left hemisphere, right hemisphere, and along the central midline. This brain regions analysis works by calculating weighted combinations of the recorded scalp electrodes in order to reduce the amount of overlap and are intended to estimate a focal source for overlapping brain regions. If focal activity is not visible, it suggests that the underlying sources of brain activity are more widespread.

TFA absolute amplitude scalp-level, TFA brain regions, and temporal spectral analysis were generated in BESA Research. TFA absolute amplitude scalp-level, TFA brain regions, 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 and performance with corrections for multiple comparisons.

Results

Experiment 1

Behavioral. Examination of performance on this working memory 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 (**Supplemental Table 1**, $p < .05$). A cluster is a group of adjacent bins (sensor (<4 cm distance), time (100 msec), frequency (.50 Hz) bins), in which the difference in absolute amplitude between the two conditions is significantly different from a random permutation distribution (Maris & Oostenveld, 2007). The sensor-level analysis reveals two distinct patterns of activity for the rehearsal and suppression conditions (**Figure 4a**). For the rehearsal condition (**Figure 4b** – 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 4c** – 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 in the upper alpha and lower beta range (**Figure 5**; 500 msec to 3000 msec) and becomes desynchronous later in the delay period (4000 msec to 6000 msec). 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 recognition performance (p = .28).

Source-level analysis of the absolute amplitude revealed 57 significant clusters across 13 of the 15 brain regions. The main source of activity for the rehearsal condition was the central midline (CM_BR; 12 clusters, Time 100 to 6000 msec, Frequency 12-29 Hz), but overall activity was relatively diffuse with no clear focal point. For the suppression condition, 3 regions were identified as the focal source of activity, the temporal parietal right (TPR_BR; 8 clusters, Time 800 to 5400 msec, Frequency 10.5-17.5 Hz), the temporal parietal left (TPL_BR; 8 clusters, Time 0 to 5900 msec, Frequency 7-12.5 Hz), and the temporal anterior right (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 is mainly in the beta range.

Experiment 2

Behavioral. The results show that when task difficulty increased, there was both a significant short-term advantage of rehearsal (**Figure 6**) 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 naturalistic scenes as compared with the phase-scrambled scenes suggests that the task difficulty explains

the performance. These images were more difficult to generate a label for 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 participants would be engaging in the same maintenance activity and should engage the same set of brain regions.

Sensor-level examination 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. The pattern of delay activity appears to be both sustained and continuous throughout the entire delay period, specifically in the right parietal and occipital region (**Figure 7a** – P08 – orange cluster), as has been previously reported in the literature (Berger, Omer, Minarik, Sterr, & Sauseng, 2014; Jensen, Gelfand, Kounios, & Lisman, 2002; Khader, Jost, Ranganath, & Rösler, 2010; Tuladhar et al., 2007). There is also a brief period early on (Time 0 to 1800 msec) in the theta, alpha, and beta range in which greater amplitude is observed in the suppression condition.

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 (**Supplemental Table 3**). Additionally, temporal spectral analysis during rehearsal was significantly correlated with working memory performance (**Figure 7b**; 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 the absolute amplitude revealed 67 significant clusters across 11 of the 15 brain regions (**Figure 8a**). Of the significant clusters, a clear focus of activity for the rehearsal condition was observed in the temporal anterior left (TAL_BR; **Figure 8b**, 10 clusters, Time 0 to 6000 msec, Frequency 4-30 Hz), parietal left (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 as well as a later focal point in the theta range (4-8 Hz) in the same brain regions as well as the right frontal region (Time 3800 to 6000 msec).

Discussion

In Experiment 1, generating a meaningful label for novel scenes and the use of articulatory rehearsal during the maintenance phase of the working memory task neither provided a short- nor long-term behavioral advantage. Comparison of sensor-level delay activity during the maintenance phase revealed two distinct patterns of neural activity,

with greater activity in the beta range in the right parietal and centromedial regions for the rehearsal condition as compared with suppression. The pattern of sensor-level activity was not correlated with short- nor long-term memory. Source-level analysis using a brain regions montage revealed no clear focal source of activity for either condition. When task difficulty increased in Experiment 2 with phase-scrambled scenes, generating a meaningful label for and using articulatory rehearsal during the maintenance phase of the working memory task, provided both a significant short-term as well as a long-term advantage. Examination of sensor-level EEG activity during rehearsal revealed greater activity in the upper alpha and beta ranges throughout the delay period, specifically in the bilateral temporal, occipital and parietal regions and left frontal region. Additionally, the pattern of sensor-level activity for rehearsal was correlated with short-term memory, but not long-term memory. Source-level analysis with the brain regions montage revealed a focal point of activity for the rehearsal condition in the left anterior temporal and the left parietal regions.

The results of Experiment 1 suggest that in the rehearsal condition, “holding onto” the visual information was not as important as generating the label. Hence, reliance on the label and rehearsal may have been all that was necessary for successful probe choice. Specifically, if you were shown a beach and a graveyard and the probe was a park, it would be very easy to get the answer correct even if you couldn’t recall the specific details of the presented encoding images since you could easily determine a category mismatch between park, beach, and graveyard. Successful performance in the suppression condition, on the other hand, suggests that remembering visual information may rely on attentional mechanisms. When rehearsal is prevented,

attentional refreshing may have been the only means by which to keep the visual information in working memory.

Interestingly, when phase-scrambled scenes were used in Experiment 2, there is evidence of increased engagement of attentional systems as well as the maintenance via rehearsal, suggesting that the coupling of these two mechanisms may have together supported the behavioral advantage over suppression. In Experiment 2, reliance on the label alone was not possible because the label likely didn't provide any information about a category mismatch between the probe and the encoding images. Rather, the label would help you to refresh the associated visual stimulus to determine if the probe matches the stored encoding images.

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 complex visual stimuli.

Experiment 1 used intact, novel outdoor scenes that contained semantic information and were easy to generate a descriptive label for (i.e. a beach or a farm). In the rehearsal condition, the generation of the labels during encoding provided a dual means of encoding (Nelson & Reed, 1976; Paivio, 1969) in both the visual and verbal domains and was intended to benefit memory. However, there was no difference in performance on the short- nor 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); as a result, the association provides automatic deeper encoding (Craik & Lockhart, 1972). It has also been established that humans can remember thousands of images after only seeing the images for a brief time (Brady, Konkle, Alvarez, & Oliva, 2008; Standing, 1973; Standing, Conezio, & Haber, 1970). This ability has been termed the picture superiority effect (Stenberg, 2006) and may also account for the fact that performance for images was near ceiling regardless of the maintenance strategy. The results of Experiment 1 suggest that the automatic semantic associations are more important than recoding of the images into a verbal label and rehearsal (Ensor et al., 2019; Nelson & Reed, 1976). 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. 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 ensured that a deeper level-of-processing occurred with the phase-scrambled stimulus (Craik & 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 the type of stimulus. 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 & Lockhart, 1972; Ensor et al., 2019; Phaf &

Wolters, 1993). 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 & Reed, 1976). Whereas with the suppression condition participants engaged in more shallow encoding, relying solely on refreshing the visual information, and did not recode or rehearse; hence, the 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 (A. Baddeley, 2003; Hwang et al., 2005). Whereas, suppression results in the engagement of more frontal electrodes suggesting greater attentional demand (Camos, Mora, & Oberauer, 2011) as well as greater mental effort (Kopp, Schröger, & Lipka, 2006) involved in inhibiting rehearsal. The brain regions analysis revealed diffuse brain region activity for both the rehearsal and suppression conditions, which suggests no underlying focal source of delay activity.

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 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 (A. Baddeley, 2000; Hutchinson, Uncapher, & Wagner, 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 & 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 in the upper alpha and beta ranges 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 may suggest the engagement of the phonological loop (A. Baddeley, 2003; Hwang et al., 2005; Munk et al., 2002) and has also been implicated in the maintenance of non-spatial visual memory (Munk et al., 2002). Engagement of occipito-temporal and parietal regions are associated with both visual working memory and attentional selection (Mayer et al., 2007; Mayer, Kim, & Park, 2011). Parietal lobe involvement in maintenance has been linked to attentional selection (Munk et al., 2002) specifically with regards to novelty (Mayer et al., 2011) and may also play a role in the integration of

features in complex objects (Mayer et al., 2007). Because the phase-scrambled images were non-spatial, greater activation in these regions may actually reflect non-spatial visual maintenance (Munk et al., 2002).

The simplest explanation is that differences in delay activity between the two experiments can be attributed to differences in the task demands (Sreenivasan & D'Esposito, 2019). The stimuli used phase-scrambled scenes that were difficult to generate a label for. 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 (Ensor et al., 2019; Wright et al., 1990). The generation of a label in Experiment 2 was more effortful than in Experiment 1 (i.e., colors and feature-related) both during the recoding process and rehearsal and did not automatically produce a category label. 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 (Sreenivasan & D'Esposito, 2019). While it has long been established that sustained activity observed during the maintenance phase when stimuli are no longer being encoded represents both maintenance of encoded information and

focusing of attention inward, recent research has suggested that delay activity is more complex (Miller et al., 2018; Rose et al., 2016; Sreenivasan & 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 (Rose et al., 2016; Stokes, 2015).

Examination of the change in amplitude over time in both Experiments 1 and 2 suggests that when controlling for maintenance strategy, the pattern of delaying 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 & 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 & 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. 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 or alternated between rehearsal and 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. Both studies involved the confrontation of participants during the recognition task by the experimenter or a research assistant. All participants, except one who was excluded from the analysis, confirmed that they followed instructions and indicated the condition in which they saw the old images (i.e., rehearsal vs suppression). Future experiments that rely on covert maintenance mechanisms or suppression should include a response-based behavioral confirmation such as an immediate reporting of generated labels or the number of times the labels are rehearsed. Additionally, although the generated labels were reviewed during the recognition task to confirm compliance, they were not systematically analyzed for the depth of encoding. Future studies should examine the type of label generated as a function of stimulus type to see if the type of label (i.e., deeper descriptive label like "sunset" vs. shallower label like "white and blank lines") impacts subsequent memory.

Conclusions

Examination of beneficial cognitive strategies and underlying neural processes that are associated with the maintenance of visual information are critical for understanding how this type of information is stored in working memory. The present study sought to understand how the type of complex visual information in combination with controlling for maintenance, namely rehearsal versus suppressing rehearsal, would

influence delay activity. The results provide evidence that rehearsal and the ability to associate semantic information with the visual stimuli both impact memory and modulate the pattern of delay period activity. Moreover, the results suggest that rehearsal enhances both short- and long-term memory for visual stimuli, but only when semantic connections are not automatically associated with the visual stimuli.

References

Baddeley, A. (2000). The episodic buffer: a new component of working memory? *Trends in cognitive sciences, 4*(11), 417-423.

Baddeley, A. (2003). Working memory: looking back and looking forward. *Nature reviews neuroscience, 4*(10), 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*(2), 233-252.

Baddeley, A., Logie, R., Bressi, S., Sala, S. D., & Spinnler, H. (1986). Dementia and working memory. *The Quarterly Journal of Experimental Psychology, 38*(4), 603-618.

Baddeley, A. D., Thomson, N., & Buchanan, M. (1975). Word length and the structure of short-term memory. *Journal of verbal learning and verbal behavior, 14*(6), 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), 1-16.

Brady, T. F., Konkle, T., Alvarez, G. A., & Oliva, A. (2008). Visual long-term memory has a massive storage capacity for object details. *Proceedings of the National Academy of Sciences, 105*(38), 14325-14329.

Camos, V., Mora, G., & Oberauer, K. (2011). Adaptive choice between articulatory rehearsal and attentional refreshing in verbal working memory. *Memory & Cognition, 39*(2), 231-244.

Cermak, G. W. (1971). Short-term recognition memory for complex free-form figures. *Psychonomic Science, 25*(4), 209-211.

Constantinidis, C., Funahashi, S., Lee, D., Murray, J. D., Qi, X.-L., Wang, M., et al. (2018). Persistent spiking activity underlies working memory. *Journal of Neuroscience, 38*(32), 7020-7028.

Cowan, N., Elliott, E. M., Saults, J. S., Morey, C. C., Mattox, S., Hismjatullina, A., et al. (2005). On the capacity of attention: Its estimation and its role in working memory and cognitive aptitudes. *Cognitive psychology, 51*(1), 42-100.

Craik, F. I., & Lockhart, R. S. (1972). Levels of processing: A framework for memory research. *Journal of verbal learning and verbal behavior, 11*(6), 671-684.

Ensor, T. M., Surprenant, A. M., & Neath, I. (2019). Increasing word distinctiveness eliminates the picture superiority effect in recognition: Evidence for the physical-distinctiveness account. *Memory & cognition, 47*(1), 182-193.

Henson, R., Burgess, N., & Frith, C. D. (2000). Recoding, storage, rehearsal and grouping in verbal short-term memory: an fMRI study. *Neuropsychologia, 38*(4), 426-440.

Hutchinson, J. B., Uncapher, M. R., & Wagner, A. D. (2009). Posterior parietal cortex and episodic retrieval: convergent and divergent effects of attention and memory. *Learning & Memory, 16*(6), 343-356.

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

Jensen, O., Gelfand, J., Kounios, J., & Lisman, J. E. (2002). Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral cortex, 12*(8), 877-882.

Khader, P. H., Jost, K., Ranganath, C., & Rösler, F. (2010). Theta and alpha oscillations during working-memory maintenance predict successful long-term memory encoding. *Neuroscience letters, 468*(3), 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*(2), 188-203.

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

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG-and MEG-data. *Journal of neuroscience methods, 164*(1), 177-190.

Mayer, J. S., Bittner, R. A., Nikolić, D., Bledowski, C., Goebel, R., & Linden, D. E. (2007). Common neural substrates for visual working memory and attention. *Neuroimage, 36*(2), 441-453.

Mayer, J. S., Kim, J., & Park, S. (2011). Enhancing visual working memory encoding: The role of target novelty. *Visual cognition, 19*(7), 863-885.

Miller, E. K., Lundqvist, M., & Bastos, A. M. (2018). Working Memory 2.0. *Neuron, 100*(2), 463-475.

Munk, M. H., Linden, D. E., Muckli, L., Lanfermann, H., Zanella, F. E., Singer, W., et al. (2002). Distributed cortical systems in visual short-term memory revealed by event-related functional magnetic resonance imaging. *Cerebral Cortex, 12*(8), 866-876.

Nelson, D. L., & Reed, V. S. (1976). On the nature of pictorial encoding: A levels-of-processing analysis. *Journal of Experimental Psychology: Human Learning and Memory, 2*(1), 49.

Norris, D., Hall, J., Butterfield, S., & Page, M. P. (2019). The effect of processing load on loss of information from short-term memory. *Memory, 27*(2), 192-197.

Paivio, A. (1969). Mental imagery in associative learning and memory. *Psychological review, 76*(3), 241.

Phaf, R. H., & Wolters, G. (1993). Attentional shifts in maintenance rehearsal. *The American journal of psychology*, 353-382.

Ricker, T. J., Cowan, N., & Morey, C. C. (2010). Visual working memory is disrupted by covert verbal retrieval. *Psychonomic Bulletin & Review, 17*(4), 516-521.

Rose, N. S., LaRocque, J. J., Riggall, A. C., Gosseries, O., Starrett, M. J., Meyering, E. E., et al. (2016). Reactivation of latent working memories with transcranial magnetic stimulation. *Science, 354*(6316), 1136-1139.

Santangelo, V. (2015). Forced to remember: when memory is biased by salient information. *Behavioural brain research, 283*, 1-10.

Song, J.-H., & Jiang, Y. (2006). Visual working memory for simple and complex features: An fMRI study. *Neuroimage, 30*(3), 963-972.

Souza, A. S., & Oberauer, K. (2018). Does articulatory rehearsal help immediate serial recall? *Cognitive psychology, 107*, 1-21.

Sreenivasan, K. K., Curtis, C. E., & D'Esposito, M. (2014). Revisiting the role of persistent neural activity during working memory. *Trends in cognitive sciences, 18*(2), 82-89.

Sreenivasan, K. K., & D'Esposito, M. (2019). The what, where and how of delay activity. *Nature Reviews Neuroscience*, 1.

Standing, L. (1973). Learning 10000 pictures. *The Quarterly journal of experimental psychology, 25*(2), 207-222.

Standing, L., Conezio, J., & Haber, R. N. (1970). Perception and memory for pictures: Single-trial learning of 2500 visual stimuli. *Psychonomic Science, 19*(2), 73-74.

Stenberg, G. (2006). Conceptual and perceptual factors in the picture superiority effect. *European Journal of Cognitive Psychology, 18*(6), 813-847.

Sternberg, S. (1966). High-speed scanning in human memory. *Science, 153*(3736), 652-654.

Stokes, M. G. (2015). ‘Activity-silent’working memory in prefrontal cortex: a dynamic coding framework. *Trends in Cognitive Sciences, 19*(7), 394-405.

Tan, L., & Ward, G. (2008). Rehearsal in immediate serial recall. *Psychonomic Bulletin & Review, 15*(3), 535-542.

Tuladhar, A. M., Huurne, N. t., Schoffelen, J. M., 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*(8), 785-792.

Weiss, S., & Mueller, H. M. (2012). “Too many betas do not spoil the broth”: the role of beta brain oscillations in language processing. *Frontiers in Psychology, 3*.

Wright, A. A., Cook, R. G., Rivera, J. J., Shyan, M. R., Neiworth, J. J., & Jitsumori, M. (1990). Naming, rehearsal, and interstimulus interval effects in memory processing. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 16*(6), 1043.

Xiao, J., Hays, J., Ehinger, K. A., Oliva, A., & Torralba, A. (2010). *Sun database: Large-scale scene recognition from abbey to zoo.* Paper presented at the Computer vision and pattern recognition (CVPR), 2010 IEEE conference on.

Figure 1. Example Working Memory Trial in Experiment 1 (Intact Scenes). 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 Working Memory Trial in Experiment 2 (Scrambled Scenes). 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 (a). An example of a suppression trial in which participants suppress during the delay period (b).

Figure 3. 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 4. 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. b) 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. c) 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. Delay Period Time Frequency Analysis for Experiment 1 Reveals a Transient Pattern of Activity. Time Frequency Analysis plot for the PO4 electrode from the rehearsal condition during the 6-sec delay period in a whole window analysis. There was no significant difference between rehearsal and condition for the Time Frequency Analysis. The overall pattern of delay activity is transient with an early period of increased synchronous activity in the upper alpha and beta (500 msec to 3000 msec) followed by a period of desynchronous activity in the same frequency bands (4000 msec to 6000 msec).

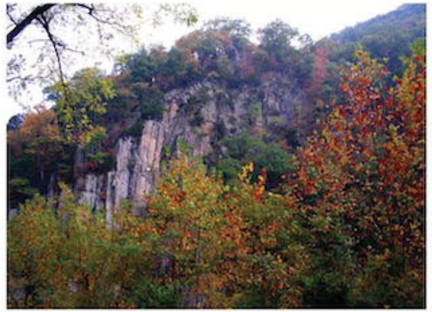
Figure 6. Working Memory and Recognition Performance in Experiment 2 (Scrambled Scenes) Suggests that Rehearsal Benefits Both Short- and Long-Term Memory. Boxplots of performance accuracy, each dot represents a single participant (n = 20). a) Examination of performance on the working memory task shows 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 7. 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) 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, $p = .005$).

Figure 8. Delay Period Activity Brain Region Analysis in Experiment 2 (Scrambled Scenes) Reveals a Left Anterior Temporal Source during Maintenance Rehearsal. 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 grouped by brain region. Orange clusters represent rehearsal delay activity greater than suppression and blue clusters represent suppression delay activity greater than rehearsal. A clear focal point of activity for the rehearsal condition is found in the left anterior temporal region (TAL_BR) and the left posterior region (PL_BR) which suggests that these regions are the source of delay activity for articulatory rehearsal. No clear focal point of activity emerged for the suppression condition, which suggests that the source of activity is more diffuse. b) Absolute amplitude plot for the TAL_BR region 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 (10 clusters, Time 0 to 6000 msec, Frequency 4-30 Hz).

a) Rehearsal

Trial Start

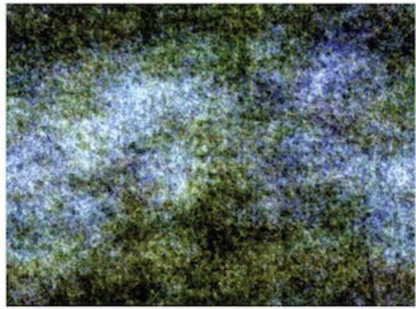


Generate a label:
Mountain

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

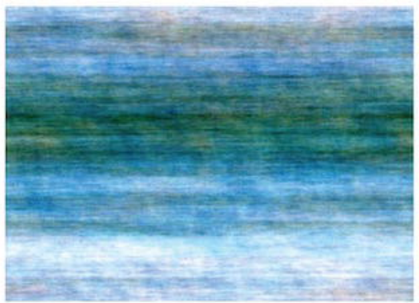
Trial Start

Look at the image &
do not generate a label

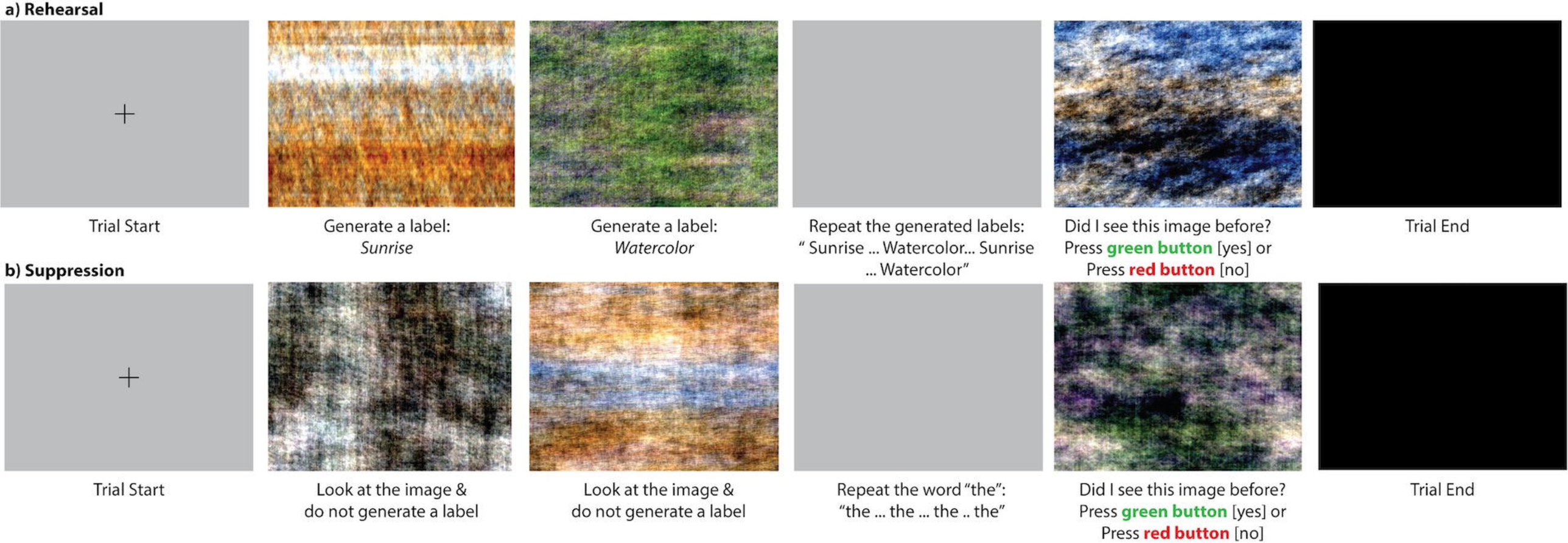
Look at the image &
do not generate a label

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

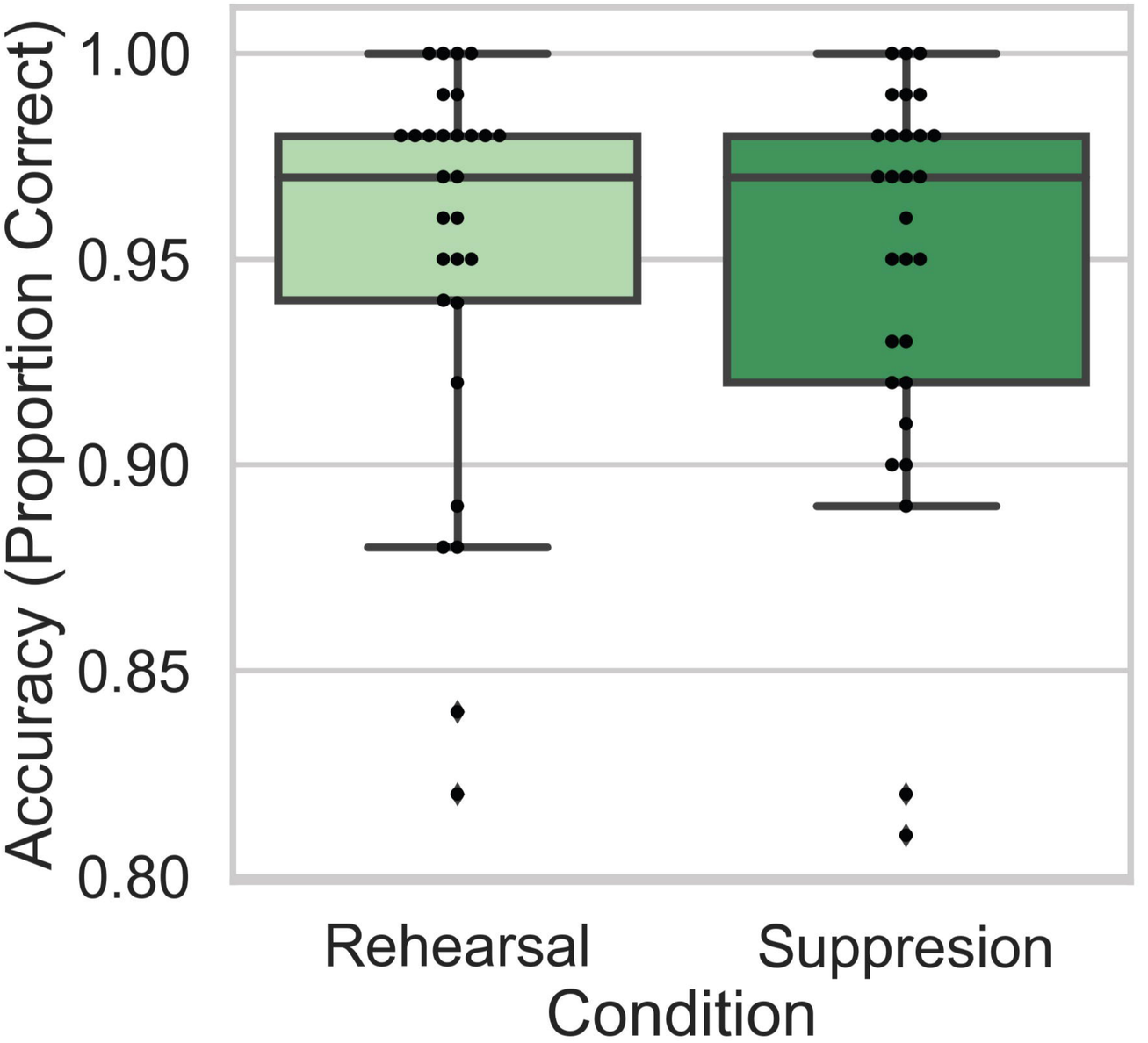
Did I see this image before?
Press **green button** [yes] or
Press **red button** [no]



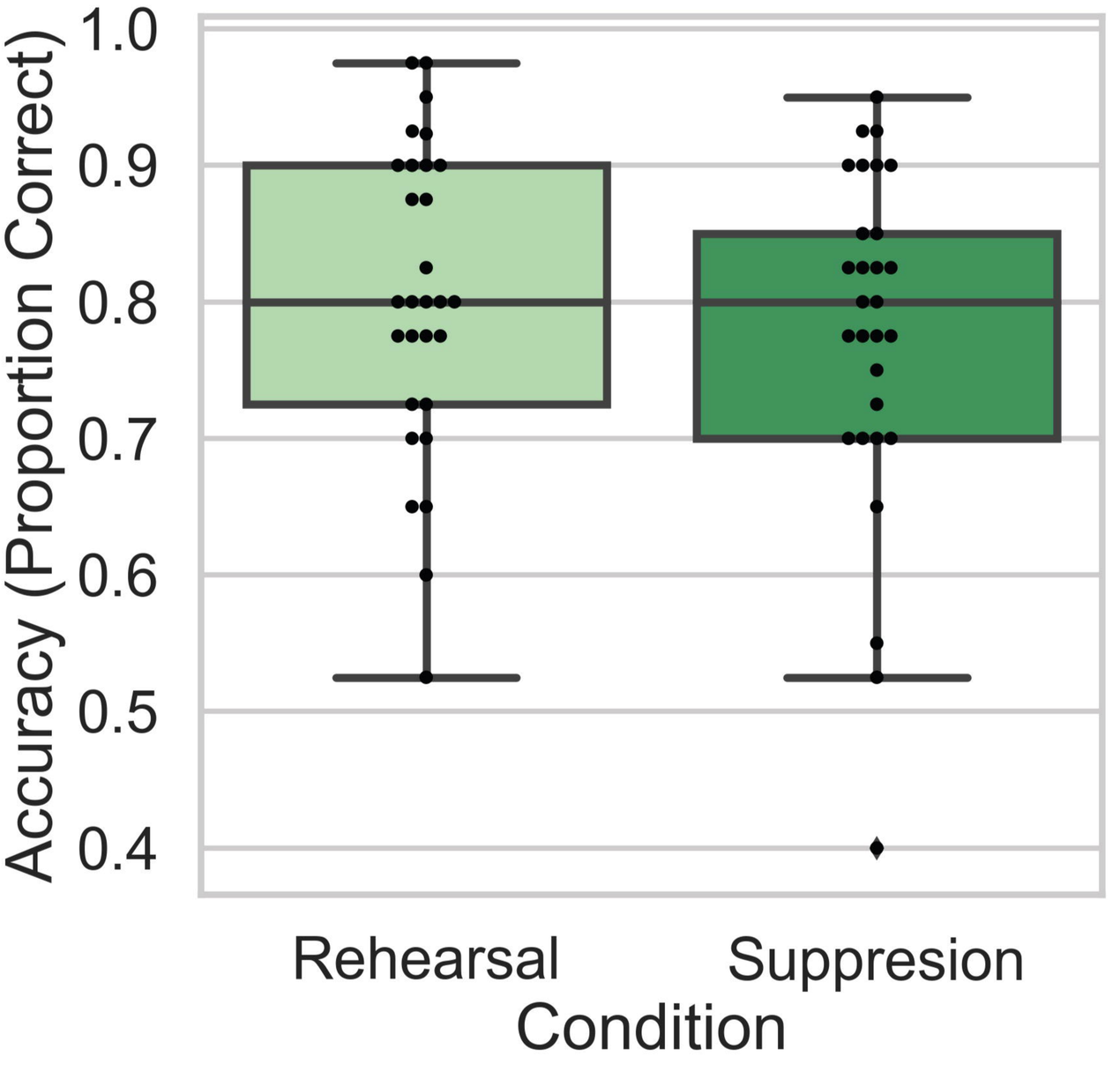
Trial End

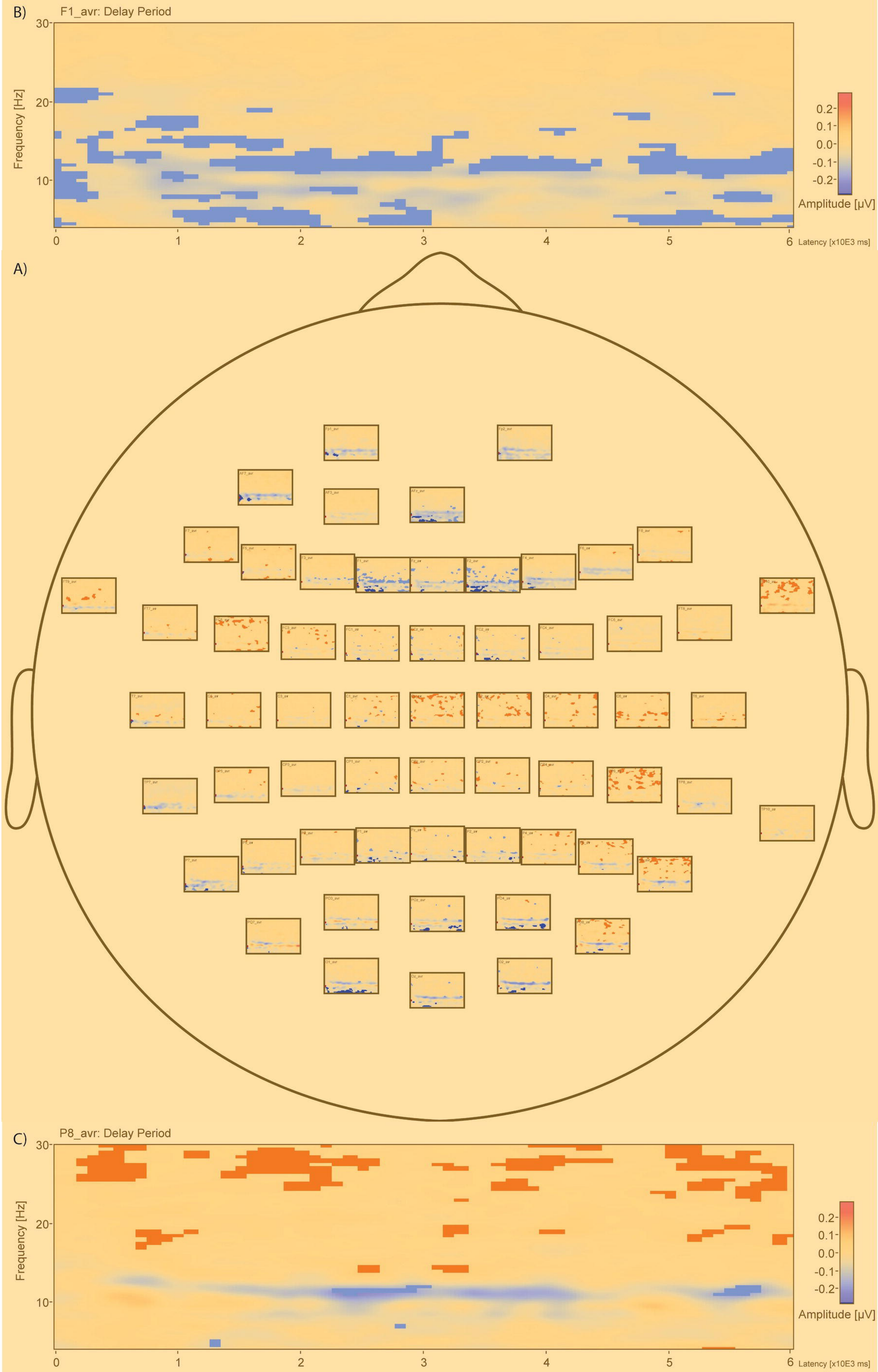

a) Rehearsal
Trial Start
Generate a label:
Sunrise
Generate a label:
Watercolor
Repeat the generated labels:
" Sunrise ... Watercolor... Sunrise
... Watercolor"
Did I see this image before?
Press green button [yes] or
Press red button [no]
Trial End
b) Suppression
Trial Start
Look at the image &
do not 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

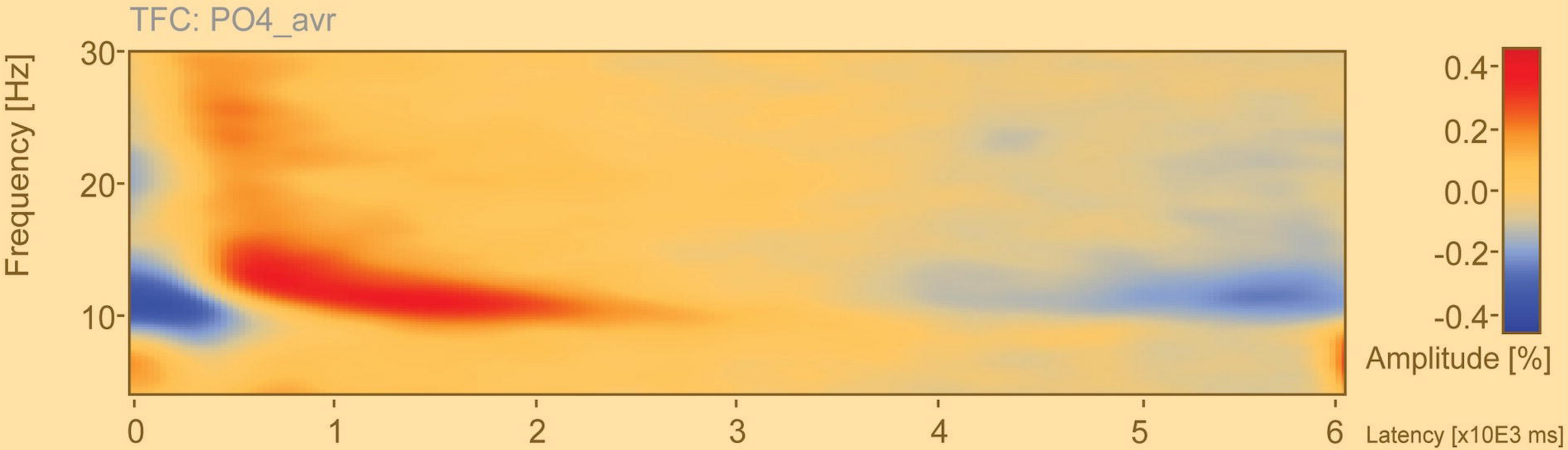
a)


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

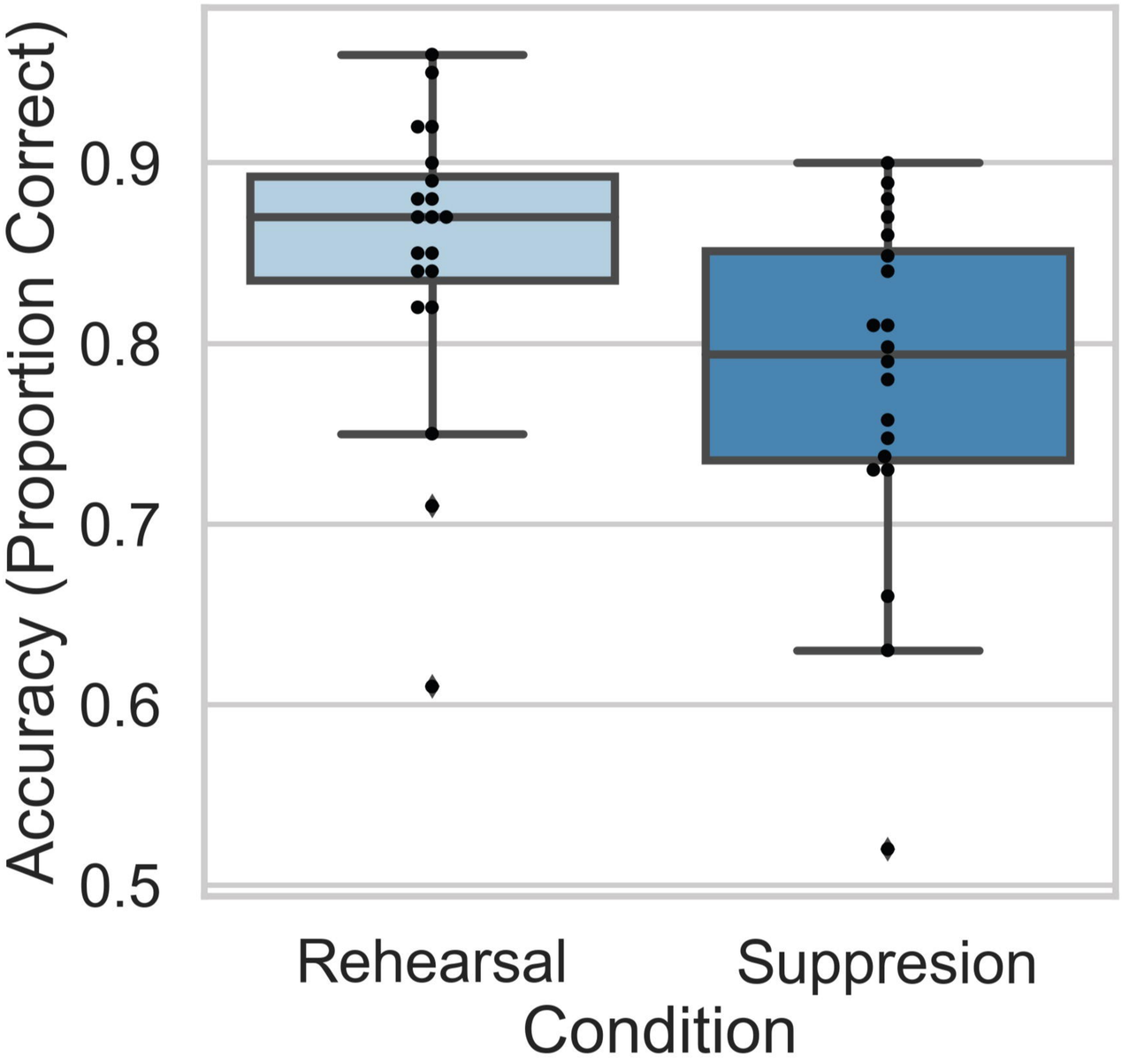
b)


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

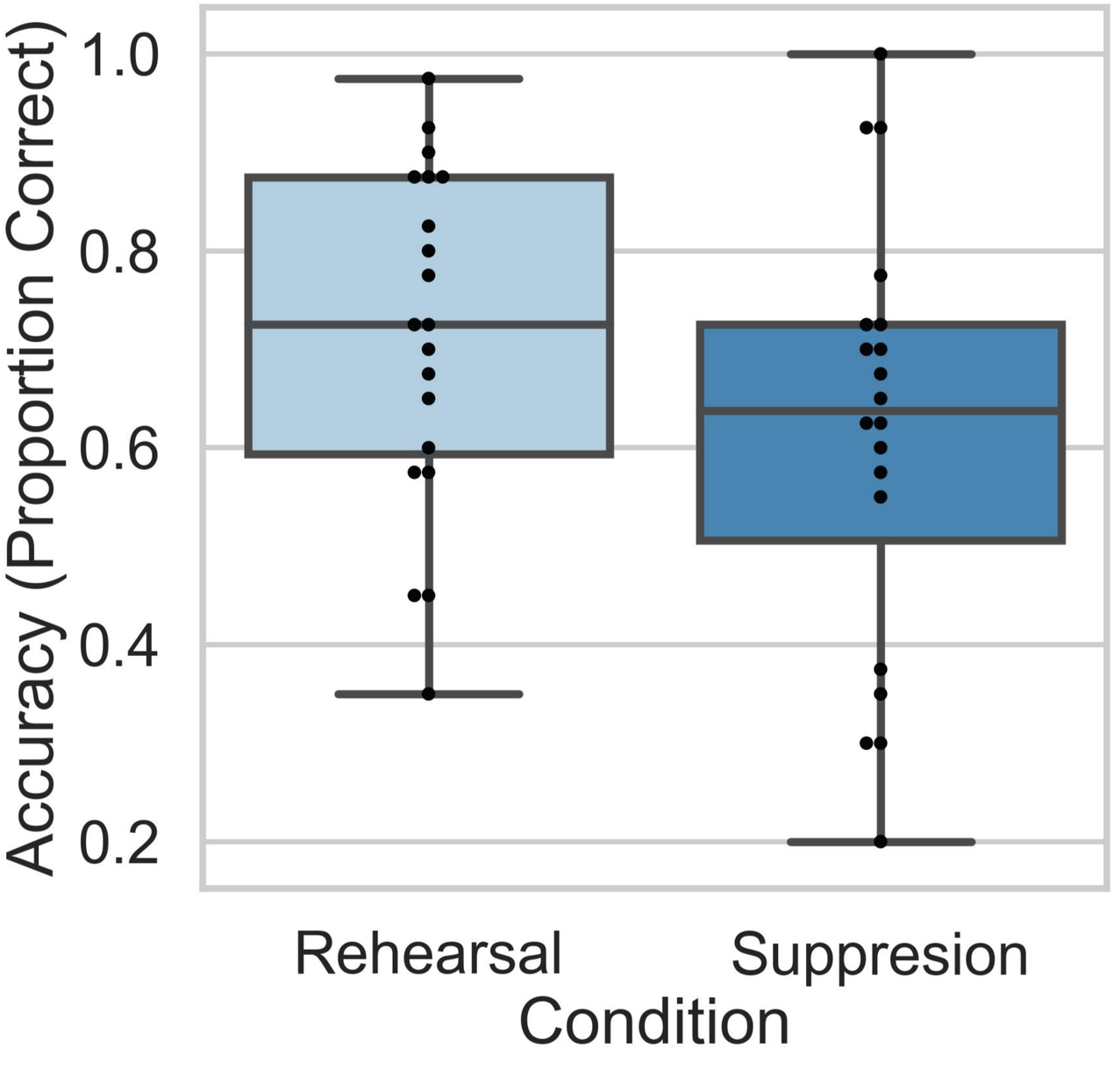

B)
F1_avr: Delay Period
Frequency [Hz]
30
20
10
0
1
2
3
4
5
6
Latency [x10E3 ms]
0.2
0.1
0.0
-0.1
-0.2
Amplitude [µV]
A)
C)
P8_avr: Delay Period
Frequency [Hz]
30
20
10
0
1
2
3
4
5
6
Latency [x10E3 ms]
0.2
0.1
0.0
-0.1
-0.2
Amplitude [µV]

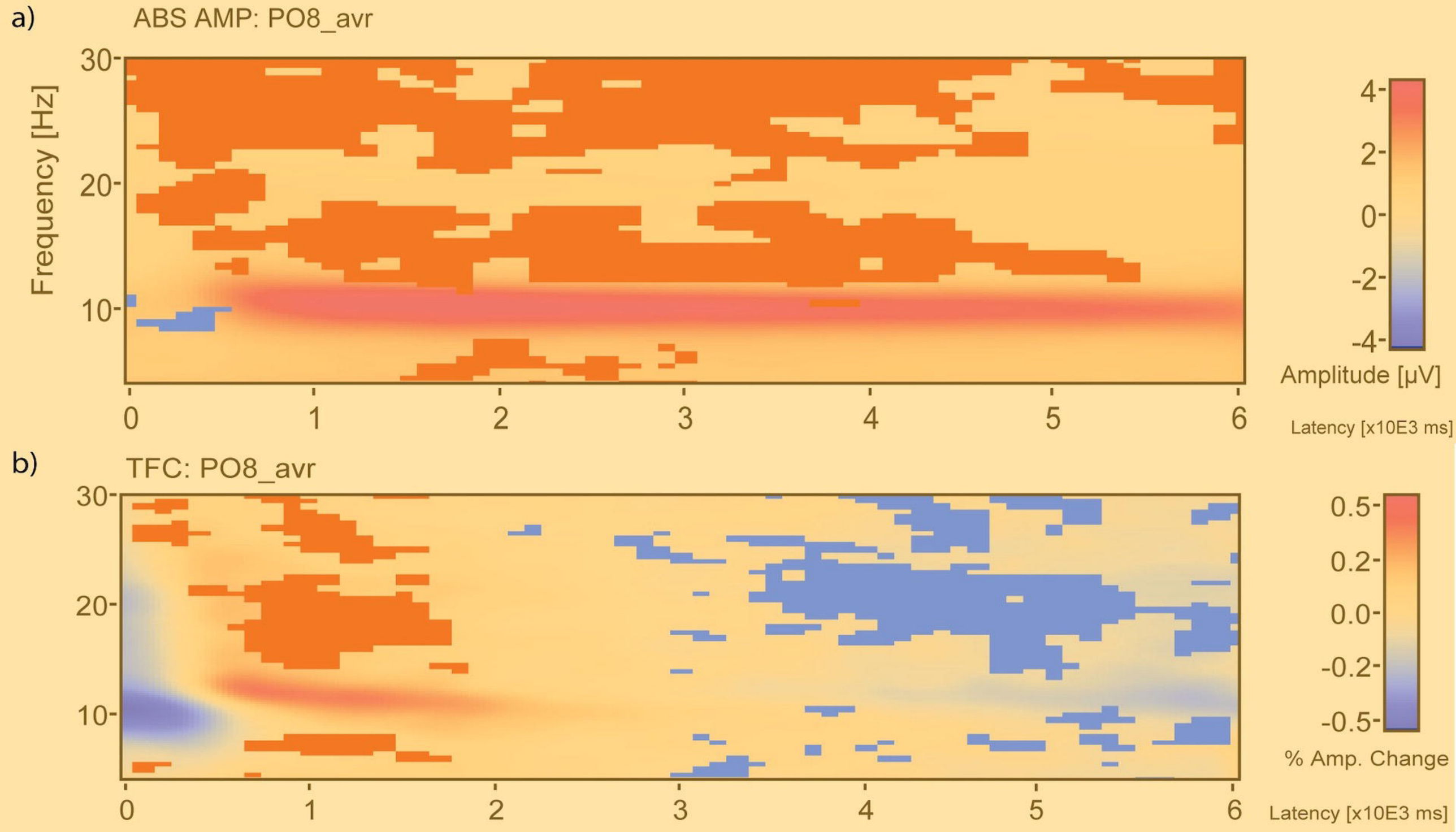

TFC: PO4_avr
Frequency [Hz]
30
20
10
0
1
2
3
4
5
6
Latency [x10E3 ms]
0.4
0.2
0.0
-0.2
-0.4
Amplitude [%]

a)

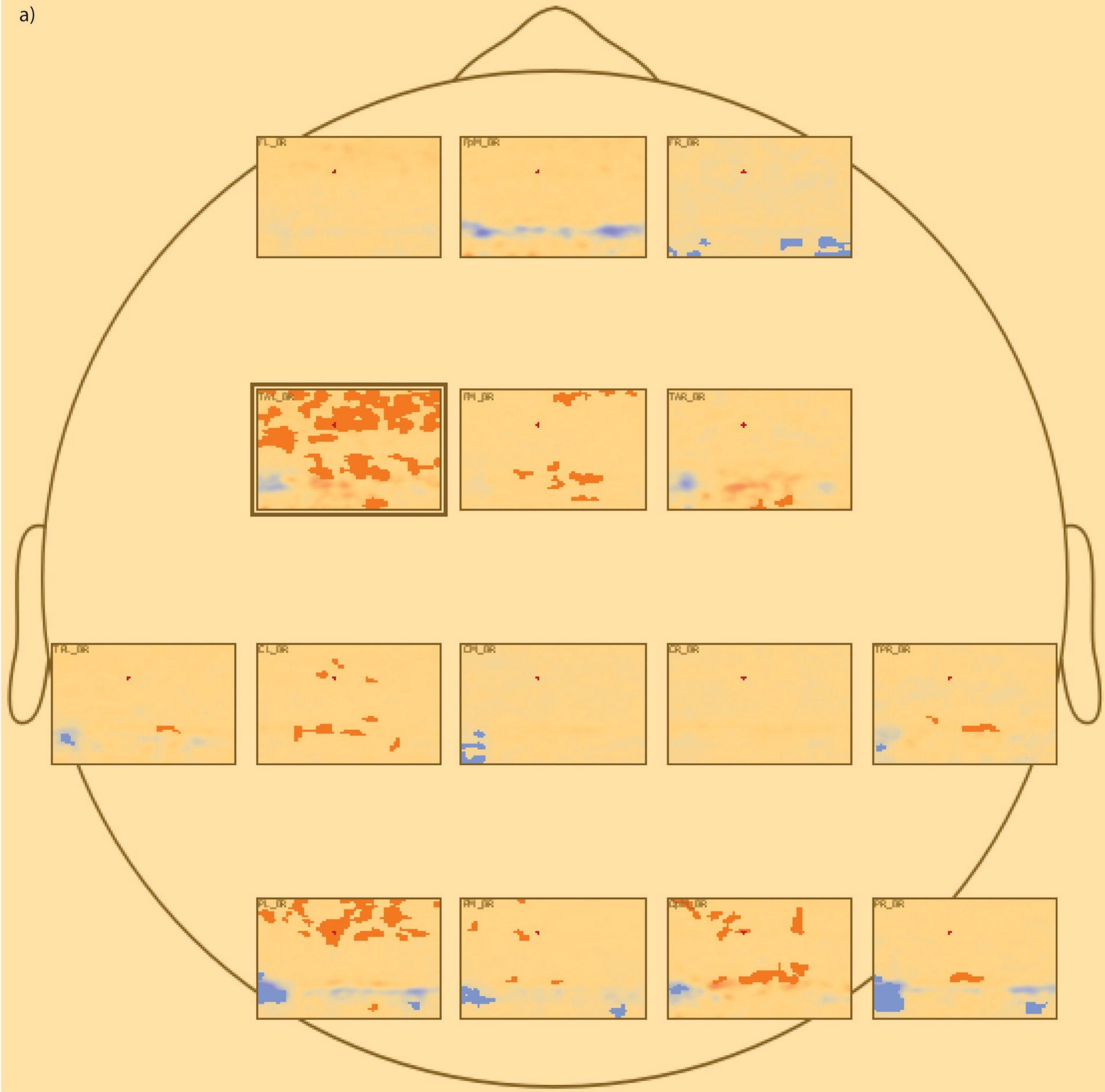

Accuracy (Proportion Correct)
0.9
0.8
0.7
0.6
0.5
Rehearsal
Suppresion
Condition

b)

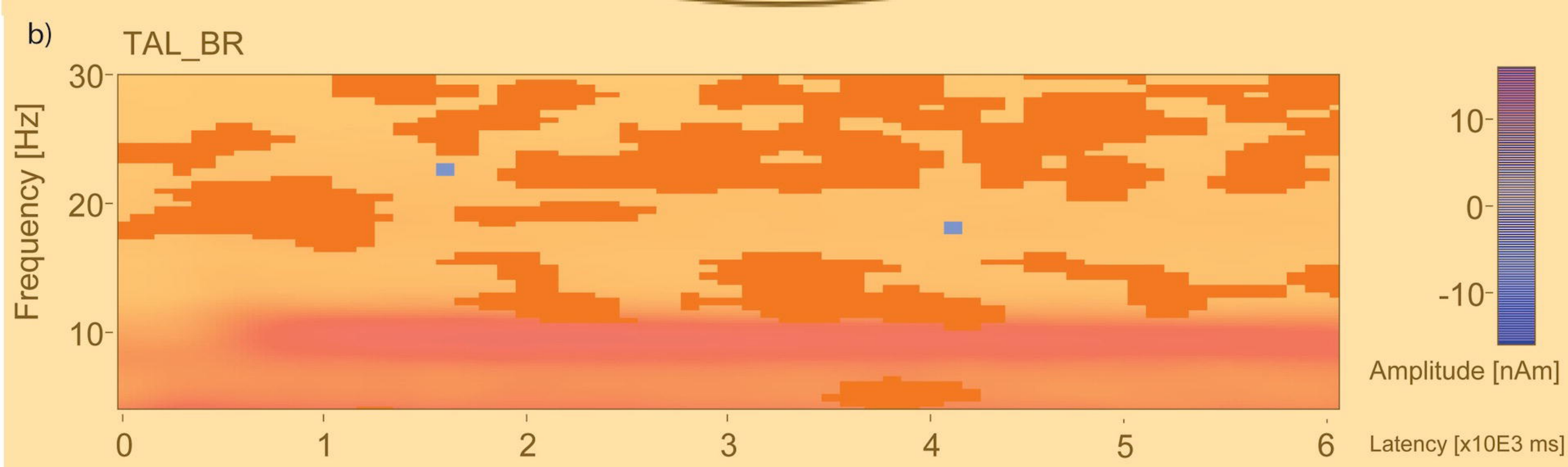

Accuracy (Proportion Correct)
1.0
0.8
0.6
0.4
0.2
Rehearsal
Suppresion
Condition


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

a)



b)


TAL_BR
Frequency [Hz]
30
20
10
0
1
2
3
4
5
6
Latency [x10E3 ms]
10
0
-10
Amplitude [nAm]