Effects of context changes on memory reactivation

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Abstract

The efficient utilization of limited working memory (WM) resources involves transferring task-relevant information to long-term memory (LTM) through repetition. While the interaction between context and LTM has been extensively studied, its influence on the dynamics between WM and LTM is less understood. In this study, we explored these dynamics using a delayed match-to-sample task, where human participants (6 Male, 16 Female) encountered the same target object across six consecutive trials, facilitating the transition from WM to LTM. Notably, during half of these target repetitions, the background color changed. To measure the WM storage of the target, we analyzed the contralateral delay activity (CDA) in electroencephalography (EEG). Our results showed that a task-irrelevant context change triggers the reactivation of LTM in WM. This reactivation may be attributed to content-context binding in WM and hippocampal pattern separation.

Significance Statement

In our research, we investigated how our brain efficiently manages information to achieve tasks. Humans have a limited "working memory," like a temporary mental notepad. Previous research shows that repeating important information can help it stick to our long-term memory. We investigated how context can influence this process. We used electroencephalography to show that even when we are not paying attention to the background, a change in it can trigger our long-term memory to be reactivated in working memory. This memory reactivation seems to be linked to how our brain connects information with the context it is in. Understanding this process could lead to improved learning and memory techniques, which could benefit us in various aspects of our lives.

Introduction

Task settings determine the relevancy of information. For example, while driving, we need to represent information regarding pedals, mirrors, other vehicles, and traffic lights. Working memory (WM) is crucial for maintaining this task-relevant information (Baddeley, 2003, 2010; Carlisle et al., 2011; Cowan, 2017). With repeated exposure and use, long-term memory (LTM) gradually takes over the role of preserving this information (Anderson, 1983; Carlisle et al., 2011; Gruber et al,. 2016; Logan, 1988). Notably, LTM is strongly intertwined with the specific context in which memories are formed and utilized (Godden & (Baddeley, 1975; Robin et al., 2016; Tulving & Thomson, 1973). However, despite our understanding of the relationship between contextual factors and LTM formation and utilization, how context impacts the interplay between WM and LTM remains unclear.

The influence of context on the encoding and retrieval of LTM has been extensively documented. For example, retrieval is more successful when it shares the same context with encoding (Godden & Baddeley, 1975; Tulving & Thomson, 1973). Moreover, any provided context (e.g., location), even if different from the encoding context, improves recall compared to not receiving a context even (Robin et al., 2016). These results highlight the importance of forming item-context bindings for remembering items. Changes in context also determine the structure of episodic memories. We experience the world continuously but perceive and store events that are segmented into meaningful parts (Zacks & Swallow, 2007). This segmentation in episodic memory reflects changes in contextual features such as background color, sound, location, or task rules (Clewett et al., 2017; Heusser et al., 2018; Horner et al., 2016; Raccah et al., 2022; Wang et al., 2022; Güler et al., 2023; Güler et al., 2024; Nolden et al., 2024). These findings suggest that contextual changes influence how an item is preserved in LTM.

Even though the effects of context on LTM encoding and retrieval are well established, its influence on the interaction between WM and LTM remains more obscure. In daily life, context is intimately linked with task-relevant information. For instance, a red light may signal the need to stop on the road but indicate brewing coffee in your kitchen. With each change in context, internal representations need to be adapted to facilitate correct interpretation and responses. Given that WM stores task-relevant representations, we hypothesize that WM should serve as the platform to adapt to a novel context even for information stored in LTM. WM reactivation has been observed in response to alterations in task-relevant aspects such as task rules (Şentürk et al., 2024) and reward values (Reinhart et al., 2016), which implies the possibility that

reactivation may also occur in response to task-irrelevant contextual changes, indicating a broader scope for its triggering mechanisms. Furthermore, the role of WM in storing item-context bindings is established when dealing with novel information (Artuso & Palladino, 2011; Cai 2020), which suggests that it may be capable of reactivating context information handed off to LTM as well. Various context adaptation processes in LTM such as hippocampal pattern separation (Amer & Davachi, 2023; O'Reilly & McClelland, 1994; Yassa & Stark, 2011), which enhance the differentiation and integration of memories, can take place via cortical reactivation (Wimber et al., 2015). Given the role of sustained cortical activity for WM storage, these results could imply that the active representation of information in WM is critical for individuating similar memories, possibly via enabling associating each memory with a unique context. Consequently, we propose that a similarly intricate relationship with context is likely to be as integral to WM as it is to LTM.

Exploring the relationship between context and WM can be approached by examining the effects of contextual changes on WM reactivation. The storage of task-relevant information hands off from WM to LTM with repeated exposure (Carlisle et al., 2011; Gunseli et al., 2014ab, Grubert et al., 2016; Reinhart et al., 2014; Reinhart & Woodman, 2014; Reinhart et al., 2016; Şentürk et al., 2024). Considering that LTM is reactivated in WM to adapt to changes in the environment (Artuso & Palladino, 2011; Cai 2020; Şentürk et al., 2024) and that adaptation processes like hippocampal pattern separation may take place via cortical reactivation associated with WM (Wimber et al, 2015), we hypothesize context shifts would trigger the reactivation of information handed off to LTM back in WM. Observing memory reactivation for background color changes would suggest that task-irrelevant contextual changes promote memory reactivation. On the other hand, if WM operates independently of the context, then information handed off to LTM should remain in LTM without being reactivated in WM despite contextual shifts. This would suggest that reactivation of task-relevant items might be triggered solely by changes in task-relevant features.

The present study therefore assesses the effect of context changes on the relative involvement of WM and LTM in storing task-relevant information. To achieve this, participants performed a WM task in which the target object was repeated across trials. The repetition of the target object is expected to result in its handoff from WM to LTM (Carlisle et al., 2011; Gunseli et al., 2014b; Reinhart et al., 2016). During this repetition, the context, which is the background color, occasionally changed. The context was completely task-irrelevant, as it didn't predict

the correct response. We used contralateral delay activity (CDA), a widely used EEG index of WM storage (Luria et al., 2016; Vogel et al., 2005) to assess the involvement of WM in storing information available in LTM. Previous research showed that CDA scales with the number of items kept in WM and reaches an asymptote at individuals' WM capacity (Luria et al., 2016; Vogel & Machizawa, 2004; Vogel et al., 2005). Moreover, it has been shown to reflect the number of items in WM and not their complexity (Ikkai et al., 2010). Furthermore, CDA decreases when the same item is repeatedly stored in WM, reflecting the handoff of the item's representation from WM to LTM (Carlisle et al., 2011; Gunseli et al., 2014ab, Grubert et al., 2016; Reinhart et al., 2014; Reinhart & Woodman, 2014; Reinhart et al., 2016; Şentürk et al., 2024). Thus, it is a suitable tool to measure WM involvement in storing items. Here, we anticipate that the CDA will decrease with the repetitions of the same item across trials as previously shown (Carlisle et al., 2011; Gunseli et al., 2014ab, Grubert et al., 2016; Reinhart et al., 2014; Reinhart & Woodman, 2014; Reinhart et al., 2016; Şentürk et al., 2024). To test our main hypothesis, we evaluated the CDA for such repeated items when the context changes. Our results showed that the CDA decreased with repetition as a sign of transition to LTM and recovered when the context changed despite the same target being repeated. This outcome suggests that task-irrelevant contextual changes trigger an automatic reactivation of task-relevant items that have been transferred to LTM. By doing so, it informs our understanding of how previously learned information is represented in memory for novel contexts.

Methods

Participants

29 students from Sabancı University participated for course credits in this study, and 7 participants were excluded from further analysis due to exclusion criteria (explained below). The analyses were conducted with 22 participants ($Mean_{age}$ = 21.7, SD = 2.9), 6 males and 16 females. We determined the target participant number based on our previous work that used a similar experimental design (Şentürk et al., 2024). Effect sizes from four studies that used CDA as a memory load measure were averaged (Berggren & Eimer, 2016; Gunseli et al., 2014b; Reinhart et al., 2016; Xie & Zhang, 2018). Following the guidelines by Schönbrodt and Wagenmakers (2018) and Dienes (2021), and the associated R package by Schönbrodt & Stefan (2019) (github.com/nicebread/BFDA), a sequential design approach was conducted. Cauchy distribution as an uninformed and objective distribution was chosen as prior with half of the estimated effect size as the scaling parameter (Dienes, 2021). We calculated the

minimum number of participants as 20 by estimating the number of participants needed for a power of .90, and a false positive rate of .02 under the estimated effect size d=1.12. The number of participants as a stopping rule was estimated as 70 with the smallest effect size in the abovementioned studies, which is d= 0.48. Bayes Factor was planned to be calculated first when the number of participants reaches 20 then aimed to be calculated after every 5 new participants.

Data collection was decided to continue until the Bayes Factor is between 1/6 and 6 or the number of participants reaches 70. We collected 22 participants in total after exclusion. Because we were late in checking the statistical analyses of 20 participants, we exceeded the specified number of 20 without calculating the Bayes Factor. We realized the mistake with 22 participants. We first calculated the BF for the first 20 participants and the result was above 6, then we calculated the BF again with all 22 participants and the results were still similar (above 6) so we stopped the data collection at 22 participants.

Since color served as context in this study, before the experiment, each participant took an online Ishihara Color Blindness test, which is suggested to be as efficient as traditional paper tests (Marey et al., 2015). Participants viewed plates, which consist of solid circles of various colors and sizes that form a number or a pattern. They indicated the number written on the plate or counted the number of lines on the pattern. If they respond correctly to less than 13 plates out of 38, they are excluded from the experiment due to red-green color vision deficiency (Marey et al., 2015).

After the EEG data artifact rejection process (see below), participants who had less than 60 non-rejected trials per condition or with accuracies lower than 80% were excluded from further analysis. New participants were recruited to replace excluded participants. This study was approved by the Sabancı University Ethical Committee. All participants signed a consent form to participate in the study.

Ethics Statement

This study was performed in line with the principles of the Declaration of Helsinki. The ethics approval was granted by the Sabancı University Research Ethics Committee.

Stimuli

Images that were used in the current study (Şentürk et al., 2024) were brought together with

additionally collected images to create a set of 2880 images of real-world objects (Konkle et al., 2010; Konkle & Caramazza, 2013; Konkle & Oliva, 2012; Google Images) in total. Images were resized to contain approximately the same number of non-transparent pixels. Half of the images were selected as target objects and the other half were selected as non-target. Target objects were separated into two groups, animate and inanimate. Animate and inanimate groups contained 60 object categories, each category consisting of 12 pictures, thus making 1440 target objects in total. Each object (7.1° x 7.1°) was presented once as a target throughout the experiment. Each category became a target twice. Two objects from each object category were used as targets during the experiment.

Each trial was presented with a color as a context. Context color could be either red (HSL: 228, 44, 146) or green (H:71, S:67, L:145). The context color was presented as a rectangular frame surrounding the center of the screen (16.7° x 10°). The experiment had 1440 trials. Each target object was repeated for 6 trials in a row. Through these repetition series, the context could change in the 1st and/or 5th repetition. Participants viewed the experiment 85 cm away from the computer screen. The background color of the experiment was grey. The location cue was a vertically halved, bicolored circle (0.35° x 0.35°), with one side being navy blue (H:240, S:100, L:25) and the other side orange (H:38,5, S:100, L:50). For a given participant, a particular color indicated the side of the screen on which the target was presented, and it was counterbalanced across participants.

Design and Procedure

Trial design

The trial design is depicted in Figure 1. The task was to indicate if the probe item matches the target item. Each trial started with a presentation of the context color for 1250 ms. Then, the location cue appeared for a jittered duration of 800-1400 ms and remained on the screen until the probe was at the center of the screen. Following the location cue, two objects were presented. One of the objects was presented at the left and one to the right of the location cue, for 500 ms. Participants were instructed to memorize the target presented on the cued side. They were instructed to fixate on the location cue. Next, there was a retention interval of 900 ms during which the cue remained on the screen. After the retention interval, the probe was shown at the center of the screen. On each side of the probe, there were two response labels, “Same” and “Different” (0.7°). Participants pressed the left or right arrow key on a Turkish QWERTY computer keyboard to indicate their response (Figure 1; e.g., the left arrow to

respond Same and the right arrow to respond Different). The locations of each response label were counterbalanced across participants. The probe remained on the screen until response or up to 1600 ms. Participants received visual feedback upon their response ('correct' or 'incorrect') or after 1600 ms ('miss'). The feedback was shown at the center of the screen for 300 ms (5° x 5°). Lastly, a blank inter-trial interval was jittered between 300 and 700 ms. The context color frame was presented in the background (16.7° x 10°) throughout the trial except the inter-trial interval.

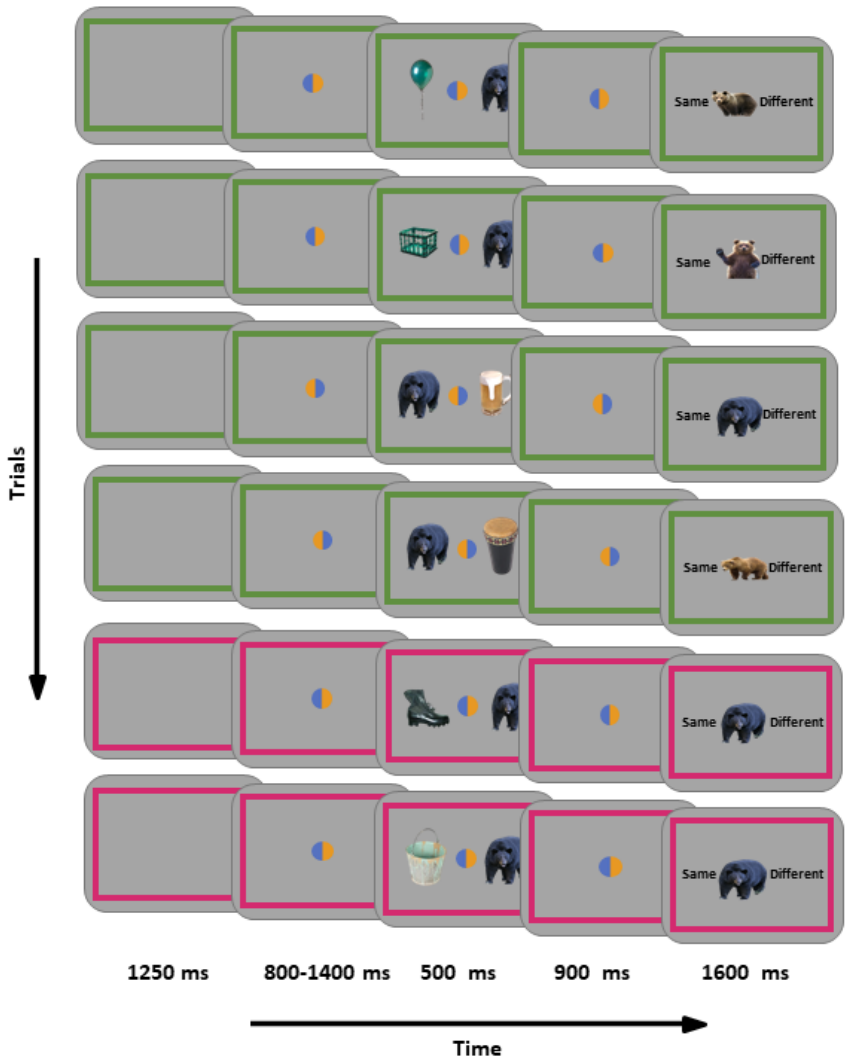

Figure 1. Illustration of the experimental procedure. Each trial will start with the presentation of context, i.e., the background color, which will be filled in the real experiment but shown here only as a frame for illustration purposes. Then, participants will see the location cue that indicates which object will be the target object. Following the location cue, the target object was shown at the indicated side and the non-target object was at the contralateral side. After a brief retention interval, participants will be shown a probe object and will indicate if it is the same as the target.

Trial distribution & block design

On each trial, the probe and the target were from the same object category. For each condition, the target was equally likely to be on the left or right on the target display. The target type was equally likely to be animate or inanimate. The experiment began with a practice session of 25 trials minimum. The objects used during practice weren't shown in the main experiment. The practice session was repeated until participants achieved at least 80% accuracy. The experimental session was divided into 38 to 42 blocks of approximately 40 trials. The block and trial numbers varied to ensure each block starts with a new context and a new target. At the end of each block, participants were informed about their accuracy and were able to take a self-paced break.

Behavioral analysis

Our main hypotheses concern the EEG data and are not directly related to the behavioral performance pattern. However, as in previous studies using this protocol, we expected to observe a decrease in reaction time with target repetition (Carlisle et al., 2011; Gunseli et al., 2014a). To test this, we performed a Bayesian paired sample t-test to compare reaction times of 1st and 5th target repetitions in old context trials.

EEG recording and registered analysis

The electroencephalogram (EEG) was recorded from 32 sintered - AG/AgCl electrodes. The electrodes were positioned at International 10/20 System sites and mounted in an elastic cap using Brain Products actiCHamp (actiCHamp Plus, Brain Products GmbH, Gilching, Germany). The vertical EOG electrodes were located at 2 cm above and below the right eye, and the horizontal EOG electrodes were located at 1 cm lateral to the external canthi. We performed the analysis of the EEG data using MATLAB (2022), the EEGLAB toolbox (Delorme & Makeig, 2004), and custom code. Trials containing ocular artifacts that are recorded by EOG, and EEG noise such as blocking, muscle noise, saturation, etc., were detected manually via visual inspection. Trials with such artifacts were excluded from further analysis. We applied a filter to EEG data by IIR Butterworth filter with a band-pass of 0.1-40 Hz using the *pop_eegfiltnew.m* function of EEGLAB. The online reference electrode was located in the right mastoid, and then the data was re-referenced offline to the average of left and right mastoids. A baseline period of 200 ms prior to stimulus onset was included in the ERP analysis.

The CDA was computed at P7/8, PO3/4, PO7/8, and O1/2 electrodes (Günseli et al., 2019; Ikkai et al., 2010; Vogel & Machizawa, 2004; Vogel et al., 2005) by subtracting the activity of ipsilateral channels from the contralateral ones relative to the target position between 400 to 1400 ms after target onset (retention interval). To test if new targets are stored in WM (Carlisle et al., 2011; Gunseli et al., 2014a,b; Reinhart et al., 2016), the CDA in new target trials were compared against zero using two one-sample t-tests, one for new contexts and the other for old contexts.

Next, to test if repeated targets are being handed off from WM to LTM (Carlisle et al., 2011; Gunseli et al., 2014ab, Grubert et al., 2016; Reinhart et al., 2014; Reinhart & Woodman, 2014; Reinhart et al., 2016; Şentürk et al., 2024), we compared the 1st and the 5th target repetitions using a Bayesian paired-samples t-test. For this analysis, we used old context trials only. To assess if this difference showed a linear or a quadratic CDA trend through a target repetition series (Figure 2), a trend analysis with repeated measures ANOVA was conducted. Last and importantly, to assess whether a context change results in the targets stored in LTM being reactivated in WM, we used a Bayesian paired samples t-test to compare the CDA in new vs. old context trials only for the 5th target repetition where a handoff to LTM is expected based on previous literature (Carlisle et al., 2011; Gunseli et al., 2014 a,b; Reinhart et al., 2016).

Exploratory analysis

We calculated the N2pc, which is an index of attentional selection (Eimer, 1996; Hickey et al., 2009). Similar to CDA, N2pc was calculated as a difference between contralateral and ipsilateral activity regarding the target position, time-locked to the onset of the memory item. This difference was calculated between 250 ms and 350 ms based on visual exploration of our data and our previous study with a similar design (Şentürk et al., 2024). Time-frequency analysis was conducted to explore the involvement of attentional processes in memory reactivation (Fukuda & Woodman, 2017; Günseli et al., 2019). Bilateral and contralateral alpha-band suppression were analyzed in the time course between 500-1200 ms. The same channels with the CDA analysis (P7/8, PO7/8, and O1/2) were used in the calculation. We analyzed the power of frequencies between 4 and 50 Hz to see if the effects we observed were alpha band specific or propagated to other frequencies. To calculate bilateral alpha-band suppression, we defined our frequencies between 8-12 Hz (Günseli et al., 2019; Woodman et al., 2012) on a logarithmic scale. For each frequency, a sinusoid (ei2ft) was created then these sinusoids were converted to Morlet wavelets by being tapered with a Gaussian (n (e-t2/2s2; s

is the width of the Gaussian; s = /(2f); denotes for number of cycles created for wavelet). We padded zero to the beginning and the end of our data as half of the length of our Morlet wavelets. Our epoched data were rearranged as one continuous EEG data. Fast Fourier Transform (FFT) was applied to both the EEG and Morlet waves. The dot product of the Fourier-transformed EEG data and Fourier-transformed Morlet wavelet was calculated for each frequency. Then inverse FFT was applied to each dot product. With this procedure, the EEG data became convoluted for each Morlet wavelet. Then, we performed baseline normalization and decibel (dB) conversion. Each baseline was calculated by averaging the power activity between 500-200 ms before the memory item onset of all trials. The power activity in each trial was divided by this baseline and converted to dB. Then, for the analysis regarding the alpha band suppression, we averaged the dB values between 8-12 Hz, and 400-1200 ms, over trials for each condition. We have chosen a slightly shorter time window compared to the CDA calculation to prevent probe-related activity from contaminating the power due to the temporal smearing caused by convolution.

A similar procedure was applied to calculate the contralateral alpha suppression. However, for contralateral alpha suppression, the baseline was calculated between 500-200 ms before the location cue rather than the memory onset. Since the location cue was given before the memory representation, lateralization can be expected in the baseline time window that reflects the expected attention (Ikkai et al., 2016). This might result in the cancellation of lateralization in the retention interval due to baseline removal with a lateralized baseline. This difference in baseline time range was applied to get a clear baseline without lateralization. This baseline normalization was applied to each condition separately, unlike the bilateral time-frequency decomposition. Then the power values from the selected channels (P7/8, PO7/8, and O1/2) that are contralateral to the target item position were subtracted from the ipsilateral channels (Günseli et al., 2019).

Results

Behavioral Results

2.3.1.1 Reaction times

There was anecdotal evidence for no difference in reaction times across target repetition 1 and target repetition 5 (old context TR1 vs old context TR5, $BF_{10} = 0.669$; $t(21) = 1.597$, $p=.125$). Moreover, there was also anecdotal evidence for equal reaction times at the new and old context

trials' first repetitions (BF_{10}=0.225; t(21)= 0.132, p=0.896). Also, there was anecdotal evidence for an increase in RT with a change in context at the 5th repetition (BF_{10} = 1.536; t(21) = 2.164, p=.042). When we conducted a trend analysis with repeated measures ANOVA, repetition showed no linear contrast (t(105) = -1.357; p = .178). These results suggest that RT was mostly unaffected by target repetitions and contextual shifts.

Accuracy

We found strong evidence for an increase in accuracy with repetition (old context TR1 vs old context TR5, BF_{10} = 91.247; t(21)=-4.265, p<.001; linear contrast with repetition, t(105)=5.923, p<.001). Also, there was anecdotal evidence for equal accuracy at the 5th repetition between change in context (M=.96, SD=.02) and old context (M=.96, SD=.02; BF_{10}= 0.243; t(21) =0.432, p=.67). Thus, while accuracy improved across target repetitions, it was mostly unaffected by context shifts.

EEG Results

Contralateral delay activity

We compared the CDA amplitudes of the 1st repetition trials against 0 to test whether there is a CDA when a novel object is presented. As depicted in Figure 2A, the 1st repetition trials' CDA values were more negative than 0 (old context, BF_{10}=34470; t=-7.134, p<.001; new context, BF_{10}=43375; t(21)=-7.252, p<.001). Then we compared the 1st and 5th repetitions of old context trials to test the transition of the item from WM to LTM. Results showed strong evidence that the CDA amplitude of the 5th repetition was different from the 1st (BF_{10}=2406; t(21)=-5.815, p<.001), which suggests the representation of the target item was transferred to LTM with repetition of the same task and item (linear trend, t(105) =6.859, p<.001).

Then, we compared the 5th repetition trial regarding whether there was a change in context or not. When there was a change in background color, we observed strong evidence for a recovery in the CDA (BF_{10}=8.858; t(21)=-3.131, p<.01; Figure 2.B). We conclude that a change in context triggers the reactivation of the task-relevant item in WM. Lastly, we tested if a similar increase is present for novel targets. The CDA for novel targets did not differ for old context and new context trials (BF = 0.326). This finding suggests that a CDA increase via a contextual shift at target repetition 5 is unlikely to represent a non-reactivation-related cognitive boost, as a similar shift should have been present for contextual shifts at target repetition 1.

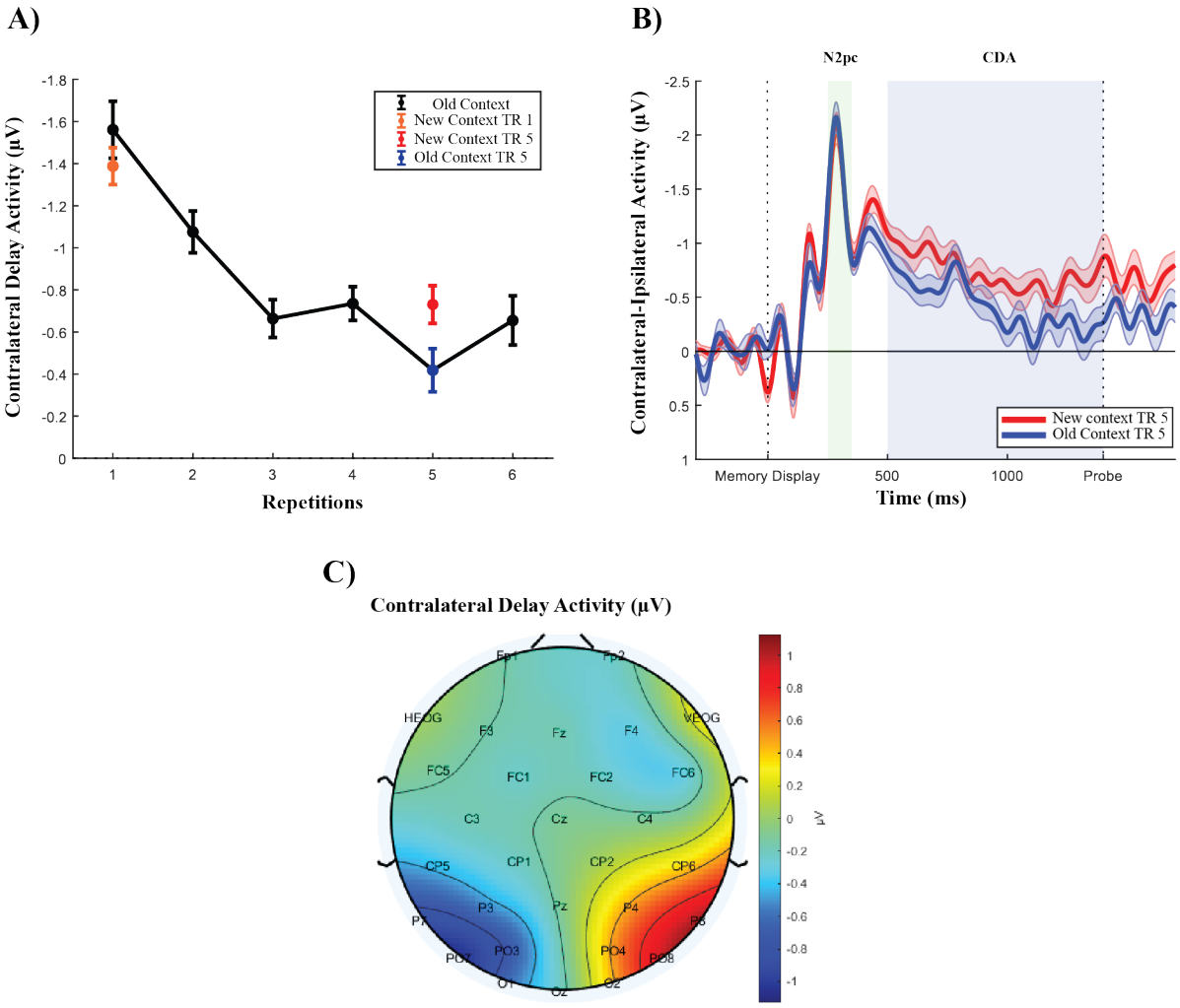

Figure 2. Contralateral delay activity. A) CDA changes through repetitions.We observed a decrease in CDA amplitude with target repetition. CDA was recovered at the 5th repetition when there was a contextual change. B) CDA and N2pc comparison between new and old context trials at the fifth repetition of the target item. We observed the recovery of CDA when there was a change in context, but this effect was absent for N2pc. C) Through retention interval, contralateral negativity on the scalp

N2pc

For a new target, there was strong evidence for an N2pc (BF_{10}=767.442, t(21)=-5.269, p<.001) suggesting that the memory item was attended at the memory display. N2pc didn't show any changes regarding the contextual changes. However, with the first repetition, we observed a

strong increase in N2pc (BF_{10}=55.982; t(21)=4.033, p<.001) (Figure 3.A). After this increase, it didn't show any changes due to context changes (BF_{10}=; 0.240 t(21)=0.401, p=.692).

Alpha-band suppression

The alpha-band suppression provided a pattern similar to the CDA (Figure 3C). For a new target, there was strong evidence for a bilateral alpha-band suppression (BF_{10}=5899.886, t(21)=-6.250, p<.001). Moreover, there was a decrease with the repetition of the same target (old context TR1 vs old context TR5, BF_{10}=396.46; t(21)=-4.957, p<.001), which was further supported by the linear trend observed with repetition (ANOVA linear contrast, t(105)=8.023, p<.001). Lastly, the comparison between old-context and new-context trials at the 5th repetition showed that the alpha-band suppression recovered (BF=1830; t(21)=-5.683, p<.001). These results suggested that overall attentional resources declined with repetition and recovered with a contextual change (Reinhart & Woodman, 2014; Şentürk et al., 2024). This increase in alpha suppression could reflect memory reactivation of the task-relevant item or the novel context (Fukuda & Woodman, 2017) given that the global alpha suppression explored here is not specific to the hemisphere that represents the memory item.

Contralateral alpha-band suppression

We analyzed the spatial lateralization in the alpha-band suppression regarding the object position (Figure 3E). For a new target, there was strong evidence for a contralateral alpha-band suppression (BF_{10}=29.585, t(21)=-3.727, p=.001) suggesting that the memory item was attended during its storage within WM. Alpha band suppression showed moderate evidence for no change regarding the repetition of the target or contextual changes (BF_{10}=0.223, t(21)=0.048, p=.96). This result suggests that participants continued to attend the memory items location across repetitions. This contrast between CDA and lateral alpha is in line with our previous findings and highlights a dissociation between selective attention and storage within WM (Günseli et al., 2019; Hakim et al., 2019; Şentürk et al., 2024; van Driel et al., 2017).

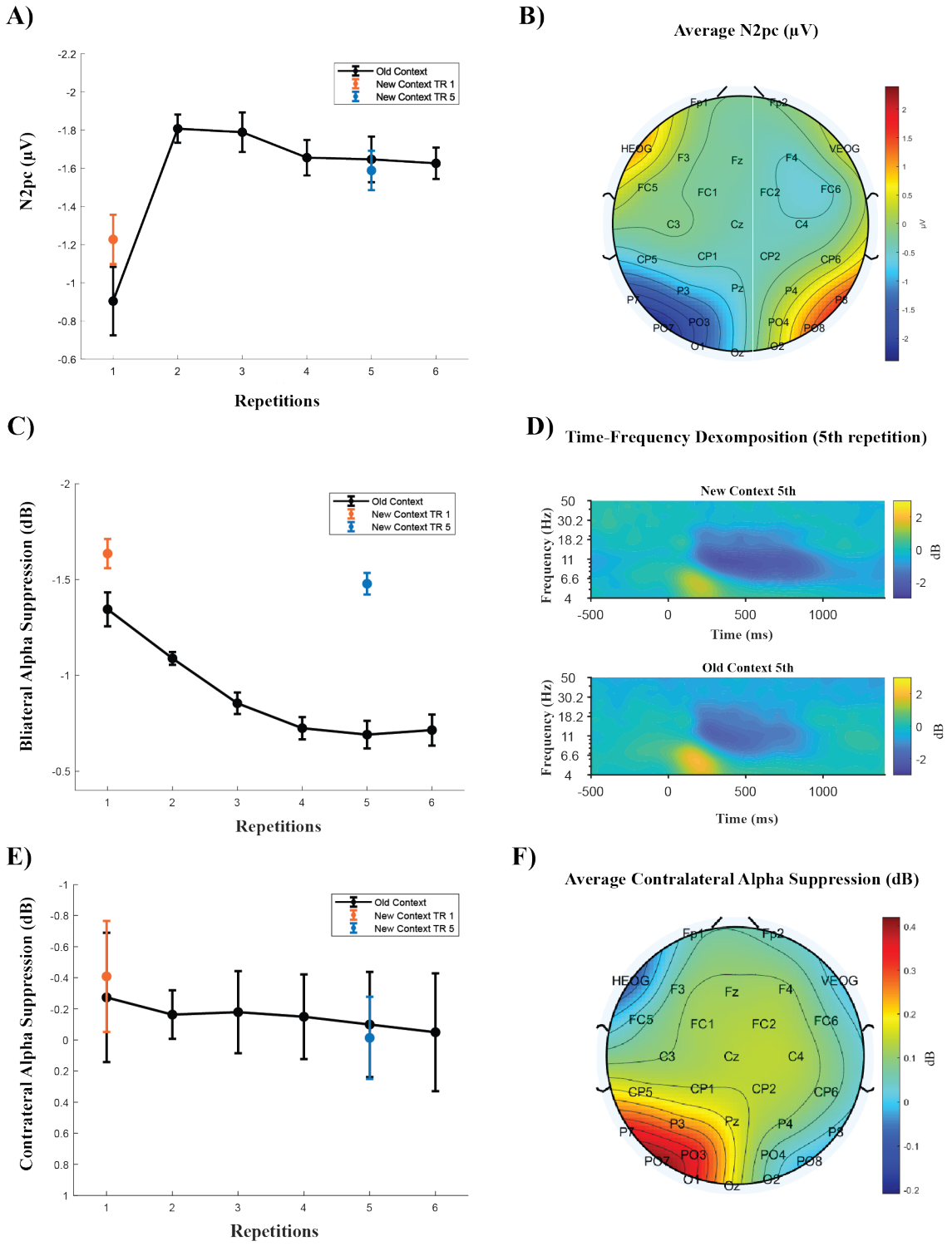

Figure 3. Exploratory analysis. A) Changes in N2pc through repetitions. N2pc only shows a strong increase with the first repetition, but then responds neither to repetition nor the contextual changes. B) The topography of N2pc averaged over trials. C) Bilateral Alpha Suppression through repetitions. Bilateral Alpha Suppression shows a decreasing pattern with repetition of the target item in the absence of a change in context, but recovers with a context change at the 5th repetition of the target item. D) Bilateral Alpha Suppression at the fifth

repetition, new vs. old context conditions. Figure shows the increased suppression of the alpha activity with a context change at the 5th repetition of the target item. E) Changes in Contralateral Alpha Suppression through repetitions. Contralateral Alpha Suppression doesn't show any changes regarding the repetition or the contextual changes. F) The topography of contralateral alpha suppression averaged over trials.

EEG-Behavioral relations

We examined whether the reactivation in WM predicts any behavioral performance of the participants. To achieve this, we subtracted the CDA amplitudes at the 5th repetition old-context trials from the 5th repetition new-context trials. Similarly, we subtracted the reaction times and accuracies at the 5th repetition of old-context trials from the 5th repetition of new-context trials. Then when we checked whether the changes in CDA due to contextual changes predict any behavioral performance by analyzing correlations. CDA differences with contextual changes predicted neither a difference in accuracy nor in reaction times (CDA-RT, Pearson's r=-0.267, p=.23, CDA-Accuracy, Pearson's r=-0.087, p=.701).

Discussion

We examined whether task-irrelevant changes in context result in memory reactivation. Considering that WM reactivation may be crucial for adjusting to the novel settings signaled by a new context (Şentürk et al., 2024; Reinhart et al., 2016), establishing novel item-context bindings (Artuso & Palladino, 2011; Cai 2020), and facilitating hippocampal and cortical pattern separation (Wimber et al, 2015), we hypothesized that contextual changes, although task-irrelevant, should reactivate task-related information from LTM into WM. Our EEG index of WM, the CDA, was present for novel targets but diminished for repeated targets, replicating previous work that demonstrated a rapid handoff from WM to LTM (Carlisle et al., 2011; Gunseli et al., 2014ab, Grubert et al., 2016; Reinhart et al., 2014; Reinhart & Woodman, 2014; Reinhart et al., 2016; Şentürk et al., 2024). Importantly, with a change in context (background color), a CDA re-emerged, indicating that the change in task-irrelevant context elicited the reactivation of task-relevant memories.

Why are memories reactivated following contextual changes?

What could be the reason behind context-change-dependent memory reactivation? Previously, Reinhart and colleagues found that memories are reactivated when participants were instructed for better performance (2014) or signaled high reward (Reinhart et al., 2016), suggesting that

high stakes facilitate memory reactivation. However, using behavioral indices, Mızrak and Oberauer (2021) suggested that reactivation was reserved for memories that partially overlap with former memories, in line with the proposed role of WM to resolve proactive interference (Engle, 2002). These studies align in their claims regarding reactivation being specific to particular task settings, namely, high stakes and high proactive interference. However, we recently demonstrated that repeated items are reactivated in WM if there is a change in task rules, rather than solely for a particular task setting itself. In the present study, we extend these findings to show that changes in task-irrelevant information also entail memory reactivation. Together with the results of Şentürk et al. (2024), our findings suggest that memory reactivation has a role in adapting to novel settings.

If memory reactivation reflects adaptive mechanisms, what adaptive functions does it serve? We propose two beneficial outcomes of memory reactivation elicited by contextual changes. One of these outcomes is hippocampal pattern separation. Similar memories are represented with similar neural patterns. However, the hippocampus separates the representations of similar events to prevent interference between them (Amer & Davachi, 2023; O'Reilly & McClelland, 1994; Yassa & Stark, 2011). Although this theory primarily focuses on episodic memories, here we argue that WM-driven processes might be crucial to achieving pattern separation. First, the CA3 subregion of the hippocampus is associated with both pattern separation and spatial WM (Kesner, 2013). Second, given that reinstated memories can be stored in a transformed format (Favila et al., 2020; Sahan et al., 2020), reactivation might serve as a medium to achieve the transformation associated with generating a distinct representation for the memory item when it is associated with a new context. In our experiment, encountering the same item in a different context might have signaled that it is a distinct event, thus encouraging pattern separation, which requires neural reinstatement associated with working memory. Future studies that focus on hippocampal-driven pattern separation and its relationship with memory reactivation can better specify the role of WM in pattern separation.

The second mechanism that might necessitate the reactivation of an item in WM due to a change in context is contextual binding in WM (Artuso & Palladino, 2011; Borders et al., 2022; Cai et al., 2022; Oberauer & Vockenberg, 2009). This process establishes associations between context and the related content in WM. Previous binding studies found that spatial, color, or temporal context affected behavioral performance (Artuso & Palladino, 2011; Cai et al., 2022; Oberauer & Vockenberg, 2009). For instance, Oberauer & Vockenberg (2009) showed that

participants recognized an item quicker when it appeared at the same location as before despite being intervened by other items. This was taken as evidence to support the lingering item-context binding benefiting the formation of the novel binding in WM. If WM establishes item-context bindings by default, the change in background color in our study might have triggered the reactivation of the item in WM to establish the binding of the item with the new context. While we cannot test this claim due to the task-irrelevancy of the context preventing meaningful behavioral effects, future studies might explore if the reactivation predicts any benefit of contextual binding to see whether these two processes interact. Our design doesn't enable us to further explore this relationship because our task doesn't necessitate participants to use context binding to achieve better performance and doesn't enable us to observe if content and context are associated in representational space.

Given the relationship between context change and memory reactivation, an important question is whether this reactivation is involuntary. We argue that our data supports so. Our cognitive systems use their resources in the most cost-effective ways (Mızrak & Oberauer, 2021; Stokes, 2015). For example, previous studies have shown that the neural cost of WM is avoided or diminished when stimuli are available in the external world, and thus can be recovered from perceptual input (Chota et al., 2023; Draschkow et al., 2021). In our experiment, the reactivation regarding the contextual changes showed neither a benefit in behavioral performance nor predicted it. Besides, the neural cost of this reactivation was observed as an increase in the CDA and alpha band activity suppression. This metabolic cost in the absence of behavioral benefits suggests that memory reactivation might not be a strategic choice but rather involuntary.

The independence of internal attention and storage in working memory.

In our study, contralateral alpha-band suppression did not differ across repetitions or contextual changes. Typically, contralateral alpha suppression is associated with the allocation of spatial attention (Günseli et al., 2019; Woodman et al., 2022). Given the decline in the CDA and bilateral alpha suppression, the indices of WM and attention within WM, respectively, one would have expected a decline also in the contralateral alpha suppression. The dissociation between CDA and contralateral alpha suppression implies a differentiation between the mechanisms of attentional resource allocation and WM storage. While some literature posits WM as a manifestation of endogenous attention (Gazzaley & Nobre, 2012; Kiyonaga & Egner, 2013), our evidence supports the notion that WM is a distinct cognitive mechanism, rather than

simply another term for attentional distribution. Our findings indicate reactivating memories does not necessarily involve the reallocation of spatial attention to them.

Eliminating alternative explanations.

In the present study, we interpreted the decline in CDA as indicative of a transition to LTM (Carlisle et al., 2011; Gunseli et al., 2014ab, Grubert et al., 2016; Reinhart et al., 2014; Reinhart & Woodman, 2014; Reinhart et al., 2016; Şentürk et al., 2024). Accordingly, we took the resurgence of the CDA as a sign of reactivating an LTM back in WM (Reinhart et al., 2014; Reinhart et al., 2016; Şentürk 2024). Below, we will discuss and eliminate three alternative explanations regarding this conclusion.

The first possibility is that the decreasing CDA via target repetition reflects the decline in the allocation of attention to the repeated item rather than the transition to LTM. However, this possibility is contradicted by the absence of a decline in contralateral alpha suppression and N2pc, which are indices of selective attention both in the external world and within visual working memory (Eimer, 1996; Hickey et al., 2009). This dissociation between the patterns of CDA and contralateral alpha suppression is consistent with our previous work showing that the CDA is sensitive to storage in WM and is mostly unaffected by attentional resource allocation within WM, which is tracked via contralateral alpha-band power suppression (Günseli et al., 2019; Hakim et al., 2019; van Driel et al., 2017). Thus, it appears unlikely that diminishing attentional resources to the memory item can account for the observed CDA pattern here. Maybe above all, even if the CDA did reflect decreasing attention to the memory item, our interpretation of a decline in active maintenance holds. This is because a decrease in attention coupled with an increase in accuracy would not be possible without a handoff to LTM.

The second alternative is that the increase in CDA with a new context reflects increased WM activation due to the enhanced processing of the memory display rather than retrieval from LTM. However, the lack of a corresponding increase in N2pc and contralateral alpha suppression, both well-established indices of selective attention (Eimer, 1996; Hickey et al., 2009), argues against stronger encoding accounts, as stronger encoding requires stronger attention (Boynton, 2005; Carrasco, 2018; Mangun, 1995; Posner, 1980; Reynolds & Chelazzi, 2004; Treisman & Geffen, 1967). Importantly, regardless of whether the source is stronger encoding or stronger retrieval from LTM, WM representations were clearly reactivated when there was a context change despite the item also being available in LTM. In

other words, our interpretation of a context-driven activation of WM representations holds, irrespective of whether this activation arises from reencoding the memory display or retrieving the item from LTM.

The third alternative could be that the CDA increase with a context change reflects increased arousal or increased attention to the task. However, this is unlikely, for three reasons. First, task rules are abstract representations and arousal is a global state, neither of which would be expected to be lateralized. Therefore, they cannot account for a larger CDA, which is the difference between contralateral and ipsilateral signals in response to the memory item. In line with this, previous studies found the CDA to be immune to confounds from global effects like arousal or attention (Feldmann-Wüstefeld et al., 2018; Ikkai et al., 2010). Second, previous studies have documented that the CDA is unaffected by the difficulty of an upcoming task (Gunseli et al., 2014ab; Ikkai et al, 2010; Luria et al., 2016; Şentürk et al., 2014), making it a reliable tool to assess lateralized, representation-specific activity. Third, if the CDA increase with context change were due to increased attention to the task, this increase should also have been evident for context changes at repetition 1, which was not the case (also see Şentürk et al., 2024). Taken together, a global increase in attention or arousal levels are therefore not convincing candidates for explaining the CDA increase with a context change.

The fourth concern related to the interpretation of the CDA decline as transfer to LTM might be the lack of an effect of target repetition on reaction times. However, this was neither unexpected nor do we believe it is crucial. Firstly, the decline in reaction time over target repetitions is task-dependent, with the strongest effects observed in effortful search tasks and absent in recognition tasks (Carlisle et al., 2011; Gunseli et al., 2014ab). In our study, we replicate the latter. Secondly, the accuracy score did improve with repeated targets, which implies learning (Adam & Vogel, 2018; Olson et al., 2005). Thirdly, our primary outcome measure CDA, which has been consistently shown to index WM load (Roy & Faubert, 2022; Adam et al., 2018; Kang & Woodman, 2014; Feldmann-Wüstefeld et al., 2018; Hakim et al., 2019; Günseli et al., 2019, Luria et al., 2016; Vogel & Machizawa, 2005; Ikkai et al., 2010; McCollough et al., 2007), thus serves as a more direct indicator of the memory representation's status than reaction time, decreased across repetitions, and substantial evidence now correlates the decline in CDA with learning (Carlisle et al., 2011; Gunseli et al., 2014ab, Grubert et al., 2016; Reinhart et al., 2014; Reinhart & Woodman, 2014; Reinhart et al., 2016; Şentürk et al., 2024). Arguably, the memory performance not worsening despite

weakening neural indices of mental representations is sufficient to support long-term memory taking over given that the other alternative, forgetting would predict declining performance.

Besides the clear decrease in CDA with repetition, we observed a recovery in CDA at the 6th repetition compared to the 5th repetition. This can evoke the question of why participants would allocate more WM resources to maintaining the same information after transferring it to LTM. However, prior research has repeatedly demonstrated CDA recovery at the end of the learning curve, indicating some form of preparedness for the introduction of a new item (Gunseli et al., 2014ab; Carlisle et al., 2011; Reinhart & Woodman, 2014; Şentürk et al., 2024). In our study, the fixed number of 6 repetitions provides participants with an expectation of when a new item will be introduced. Therefore, it is plausible that the CDA increase on repetition 6 reflects preparatory WM activation. Importantly, this observation does not invalidate our core finding and conclusions; namely, that the CDA on repetition 5 differs between old and new context trials, documenting that individuals rely on LTM when the same context repeats and on WM when the context switches.

Conclusion.

In summary, our findings demonstrate that contextual shifts prompt the reactivation of memories. Specifically, items transferred to LTM through repeated storage are reactivated in WM upon encountering a change in the task-irrelevant context. Given the neural costs of this reactivation and the lack of observable behavioral benefits, we claim that context-dependent reactivation is involuntary. This underscores the automatic nature of memory reactivation in response to environmental changes, even when they are not directly related to the task at hand.

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Data Availability

All data and materials are shared publicly on Open Science (https://osf.io/xhrb9/?view_only=6ce0380db484406ea2070d8dbbf6ba93). Data is shared anonymously without any risk of lack of privacy.

Code Availability

All codes of the study are shared publicly on Open Science (https://osf.io/xhrb9/?view_only=6ce0380db484406ea2070d8dbbf6ba93).

Author Contributions

All authors contributed to the conceptualizing and the design processes of the study. Ş.Ö., Y.Ş., N.Ü. and E.G., prepared the experiment. All authors wrote the manuscript. Ş.Ö. collected the data. Ş.Ö. and E.G., conducted the data analysis. All authors discussed the interpretation of the results.

Competing Interests

The authors declare no competing interests.