Neurobiology of Learning and Memory 219 (2025) 108052

Contents lists available at ScienceDirect

Neurobiology of Learning and Memory

journal homepage: www.elsevier.com/locate/ynlme

Delayed emergence of EEG-based task-relevant representations

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ARTICLE INFO

Keywords:
Representation Learning
EEG
Wakeful rest
Generalization

ABSTRACT

This paper examines the effect of a period of quiet wakefulness (an “offline wake” state) on the performance of a decision making task. An initial feedback-based learning period using a subset of stimuli, was followed by (i) a “pre-test” phase using both “old” and “new” stimuli without feedback, (ii) a delay period of either active or offline wakefulness, and (iii) a “post-test” period, again without feedback. Behaviourally, we found that offline wakefulness significantly improved generalization — the ability to apply learned knowledge to novel stimuli. However, we did not find any EEG-based neural correlates of this generalization improvement. Rather, we found that task-relevant representations emerged only after the delay period, independently of whether the delay was active or offline.

1. Introduction

Recent experiments in humans have shown that a period of Quiet Wakefulness, also known as “Quiescence” or “Offline Wake State”, has beneficial effects on performance across a broad range of cognitive tasks. One body of work has focused on the effects of a period of Quiescence on memory for recently learned information. Memory performance of the Quiescence group is usually compared to an “Active” group who, instead of resting after learning, complete a distractor cognitive task. Findings revealed an improved memory performance in the Quiescence group, such as an increased memory strength (Dewar, Alber, Butler, Cowan, & Della Sala, 2012) or fine details within recently learned stories (Craig & Dewar, 2018). Overall, memory performance degrades over time but less so for participants assigned to Offline versus Active wake groups. This body of work extends previous studies which have shown that periods of sleep benefit memory when compared to typical waking activities (Axmacher, Elger, C., & Fell, 2008; Graveline, Y., Wamsley, & E., 2017; Lewis & Durrant, 2011; Löwe, Petzka, Tzegka, & Schuck, 2024; Petzka, Chatburn, Charest, Balanos, & Staresina, 2022; Petzka, Zika, Staresina, & Cairney, 2023; Schapiro et al., 2018).

Possible mechanisms underlying memory stabilization through quiescence have recently been uncovered by functional imaging experiments. These studies have, for example, found that neuronal activation patterns detected during encoding are reactivated during Offline Wake states (Tambini & Davachi, 2019a). These analyses were motivated by the findings of “pattern replay” (a temporally ordered sequence of reactivations) observed in rodent studies (Foster, 2017) that promote synaptic plasticity. Moreover, Neuroimaging studies have shown that memory reactivation during quiescence increases connectivity between cortical areas which is thought to distribute and reorganize memory representations across hippocampal and neocortical networks (Schlichting, L., Preston, & A., 2014; Tompary & Davachi, 2017).

A more recent body of work investigates the effects of Quiescence on cognitive tasks beyond memory (Tambini & Davachi, 2019b; Wamsley & Collins, 2024; Wamsley & J., 2019). Reactivation of encoded elements during quiescence is thought to facilitate feature selection, similarity extraction and pattern recognition, thereby promoting generalization and improvement in performance (Tambini & Davachi, 2019b). These improvements are supported by the learning of low dimensional representations that are useful for the task at hand, for example, a new discriminatory feature (Craiget al., 2018), a new cognitive map (Craig & Wolberset al., 2018), or a new higher-order rule (Quentin et al., 2020). Building upon these insights, our recent work in the lab (Menghi, Silvestrin, Pascolini, & Penny, 2023) employed EEG and Representational Similarity Analysis (Kriegeskorte, Mur, & Bandettini, 2008) to describe the neural dynamics of representations emerging during a decision-making task. We found that a low-dimensional, task-relevant representations emerged from 700 ms after stimulus presentation and are associated with performance. However, the role of quiescence in the development of these representations remains elusive.

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https://doi.org/10.1016/j.nlm.2025.108052
Received 16 July 2024; Received in revised form 13 January 2025; Accepted 31 March 2025
Available online 15 April 2025

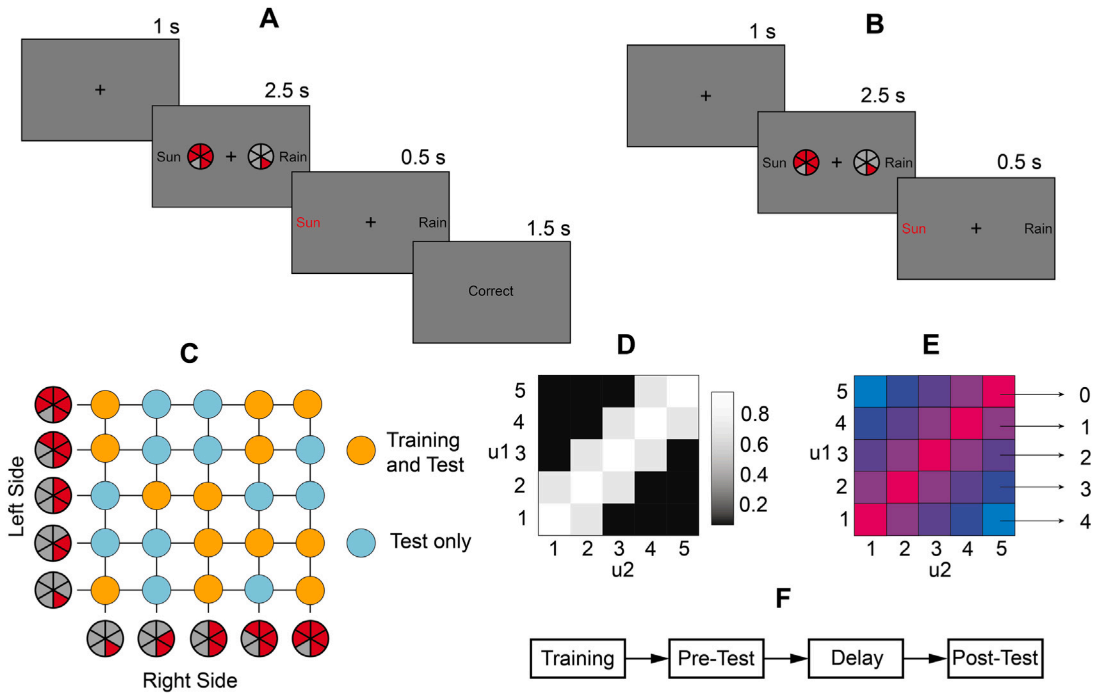

Fig. 1. (A) Training Trial structure. (B) Testing Trial structure. (C) Stimuli (D) Stimulus-Outcome Mappings (E) Feature Values (F) Procedure (A) Each trial started with a fixation cross. Afterwards, two pies appeared (the “stimulus”) and participants had up to 2.5 s to respond. Confirmation of the choice was then given and feedback was provided. (B) Test blocks were identical to training blocks except that feedback was not provided. (C) Experimental stimuli. Each pie on the left side can be combined with each pie on the right side, creating 25 unique configurations (stimuli), 13 of which are used during training and testing phases, and 12 during the testing phases only. (D) The gray scale image plots the Sun Outcome probability (given button press “sun”), as a function of the number of red slices in the right side pie, u_1, and left side pie, u_2. (E) The task structure can be described by a one-dimensional manifold determined by the subtraction feature value computed over the number of slices of the two pies, u_1 and u_2. (F) Shows the overall experimental structure.

1.1. Current study

The main goal of the current study was to assess the effects of an offline-wake period on generalization and memorization. Additionally, we wanted to investigate the differences in the emergence of task-relevant representations, reflecting abstraction processes and rules extraction, during quiescence and active periods. The task used in the present study is adapted from the “subtraction” task previously used in the lab (Menghi et al., 2023). Briefly, participants learnt associations between configurations of virtual pies and a weather outcome (sun or rain) as shown in Fig. 1D. The structure of this mapping is shown in Fig. 1D and participants should learn to choose “Sun” when the number of slices of the two pies presented is similar. Good performance in this task can be achieved by learning a new representation which could take the form of (i) a logical or verbal rule (Ballard, Miller, Piantadosi, & Goodman, 2017), (ii) identification of a discriminatory feature (u_1-u_2) (Menghi, Kacar, & Penny, 2021), or (iii) identification of homogeneous clusters of exemplars (one along the diagonal, and one on either side) (Sanborn, Griffiths, & Navarro, 2010).

In more detail, participants were trained on a set of pies (Training) and then tested (Pre-Test) on the same set (old configurations) plus a new test set (new configurations; Fig. 1A and B). Participants were assigned either to the offline wake group, in which case they closed their eyes and were asked to rest during the delay block, or to the active wake group, in which case they did a spot-the-difference task during the delay block. Then, participants completed a final test (Post-Test; Fig. 1E). During the testing blocks, participants received no feedback.

Since participants were tested on configurations of pies they were trained on (“old stimuli”), and new configurations of pies they had not seen before (“new stimuli”), it was possible to separately assess both memorization and generalization performance.

We hypothesized that the active wake condition would disrupt the representation learning process that results in generalization and that this would be reflected both in behavioural performance and the emergence of task-based representations. We also expected that memory performance, and accuracy for old configurations, would be less degraded in the offline wake condition.

2. Materials and methods

2.1. Participants

A total of 42 volunteers from the University of East Anglia (mean age = 25.07, SD = 7.15, 15 male, 27 female) were recruited through the SONA System (https://uea-uk.sona-systems.com/); 21 assigned to Active Wake, 21 to Offline Wake. Data from 3 participants were discarded because they did not respond to more than 20% of the trials. Data from a further 3 participants were discarded from behavioural analyses because their performance was below chance level during the first testing session. Analyses were performed on 36 participants, 18 assigned to Active Wake and 18 to Offline Wake (mean age = 25.41, SD = 7.42, 13 male, 23 female). Of the 18 participants assigned to the Active Wake condition, the first 5 participants completed the spot-the-difference task for 15 min due to a coding error. After identifying this issue, the task duration was corrected to 10 min for the remaining 13 participants. Data from a further participant belonging to the active wake condition was excluded from the EEG data analyses because of poor EEG data quality. All participants were naive to the purpose of the experiment. At the end of the experiment, participants received credits for their participation. The study was approved by the University of East Anglia School of Psychology Research Ethics Committee (PSY-REC) and all participants provided consent at the beginning of the experiment.

2.2. EEG acquisition and preprocessing

A BrainProduct actiCAP was used to record EEG signals from 32 electrodes, placed according to the standard 32-channel arrangement, FT9 was used as hEOG, electrode impedances were kept below 25 kΩ, signals were recorded at a sampling rate of 1000 Hz, and preprocessing was carried out using the Fieldtrip toolbox for MATLAB (Oostenveld, Fries, Maris, & Schoffelen, 2011). Continuous data were highpass filtered at 0.5 Hz and re-referenced to the common average. The data were epoched from 500 ms before the onset of the stimulus (see Fig. 1A) to 1.5 s following it. We visually inspected these epochs to remove trials containing muscle activity or electrical artefacts and identified bad electrodes which were then interpolated to the weighted average of neighbouring electrodes. On average 7% of the 341 total trials were discarded. A maximum of 2 non-neighbouring electrodes were interpolated per participant. Fast Independent Component Analysis (fastICA) (Comon, 1994) was then applied to the epoched data, components were visually inspected to reject eye blinks, eye movements and sustained high-frequency noise. EEG epochs were then low-pass filtered with a cut-off of 30 Hz. Furthermore, we performed baseline correction based on the pre-onset period. Finally, we visually reinspected the epochs to ensure no artefact remained. Rejected trials and EOG signals were excluded from all further analyses.

2.3. Apparatus and stimuli

The experiment was performed in a dimly lit room with participants seated approximately 60 cm away from a computer display. Stimuli were presented on a 23-inch HP Elite Display 240c monitor using the Psychophysics Toolbox (http://psychtoolbox.org/) (Brainard, 1997) for Matlab (Mathworks) running on Windows 7. Two virtual "pies", equidistant from the fixation point, were displayed. Each pie was divided into six slices with from one up to five slices that could be filled with red colour making a total of twenty-five combinations, see Fig. 1 (panel A). The stimuli were presented on a dark grey background.

2.4. Procedure

The overall experimental procedure is shown in Fig. 1F. The experiment comprised one training block (91 trials with 7 repetitions of the 13 different training stimuli), and two test blocks; one before the delay period ("pre-test") and one after ("post-test"). Each test block comprised 125 trials with 5 repetitions of each training stimulus, and 5 repetitions of each test stimulus. During the delay period half of the participants were assigned to the distractor task ("Active Wake"), the other half to a period of quiescence ("Offline Wake").

In Fig. 1 (panel A), in the training block, each trial started with a black fixation cross presented at the centre of the screen for 1000 ms. Afterwards, the stimuli appeared and stayed on screen for 2500 ms, or until response. Responses were made on a standard keyboard, the "a" indicated sun prediction and "l" indicated rain. Responses not given within the required time constitute "missed trials". After button press, confirmation of the choice, by highlighting choice in red, was given for 500 ms. Finally, feedback was provided, indicating "correct" if the prediction was correct, "incorrect" if it was not and "too slow" if they missed the trial. In the pre-test and post-test blocks, the trial structure was identical to the training block but without feedback (see Fig. 1 panel B). Participants were explicitly instructed to maintain their gaze fixed on the central fixation cross throughout the task. This instruction was reinforced before the task began, and participants were reminded to avoid unnecessary eye movements.

During the delay, subjects in the quiescence condition were asked to close their eyes and relax for 10 min (Craiget al., 2018). Offline, using an automatic sleep stage model (Perslev et al., 2021), we checked if participants fell asleep during this time. Three participants spent more than 5 min in sleep stage N2 during the quiescence period. The remaining fifteen participants spent the whole quiescence period awake. Subjects in the active condition completed a distractor task, a spot the difference task similar to that described in Craiget al. (2018). On each trial, participants were presented with a pair of real-world photos on the computer screen which were identical other than for two discrete differences and participants were asked to find these differences and indicate them with the mouse. After the delay participants were presented with the instructions for the final test block (post-test) and were asked to press a button to start. The overall experiment took about thirty minutes to complete.

We assess the effect of Offline versus Active Wake conditions using a between-subjects design in which 18 participants were assigned to the offline group and 18 participants to the active group. During training, 13 configurations of stimuli were presented and subjects received feedback about whether their decisions were correct or not. There were 7 repetitions of each trial type making 91 trials in all. During testing (both pre-test and post-test), these same stimuli were again presented ("old stimuli") along with 12 new stimuli that had not been presented during training ("new stimuli") in a random order. Each trial type was repeated 5 times making 125 trials in all. A "memorization" score could then be computed based on the correct decision rate over old stimuli categorized with feedback in the initial training phase, and a "generalization" score on the correct decision rate over new stimuli.

In previous work Menghi et al. (2023) participants were trained on 10 repetitions of each of the 25 different stimuli, making 250 training trials in total, whereas in the current study the training period comprised only 91 trials (7 repetitions of the 13 "old" stimuli). We specified this reduced training regime for two reasons (i) so participants did not reach ceiling thereby giving them room for improvement during the delay period and (ii) to hold out some stimuli for testing so that we could separately measure generalization versus memorization.

2.5. Stimulus-outcome mappings

The probabilistic structure of the task, y_t, was defined by making the log-odds of the outcome a quadratic function of stimulus characteristics, u_t (number of red slices) resulting in the mapping shown in Fig. 1 panel D.

$$\begin{aligned}
\log\left[\frac{p(y_t=1)}{p(y_t=0)}\right] &= (u_t-\mu)^T W (u_t-\mu) + w_0 \qquad (1)\\
W &= 2.4 \times \begin{bmatrix} -0.71 & 0.70 \\ 0.70 & -0.71 \end{bmatrix}\\
\mu &= [3,3]^T\\
w_0 &= 4\\
u_t &= [u_t(1), u_t(2)]^T
\end{aligned}$$

If, for each cue, subjects choose the option with the highest probability, then the correct classification rate would be 95%. This map is identical to that used in our previous work Menghi et al. (2023) (referred to as the "subtraction" task) and can be approximately described by the verbal rule "choose Sun if the pies have a similar number of slices". The above parameters μ, W and w_0 have been set to produce the stimulus-outcome mapping shown in Fig. 1, panel D.

3. EEG data analysis

3.1. ERP

We performed three cluster-based permutation tests contrasting ERPs for within condition new versus old cues and between conditions active wake and offline wake and the interaction between old and new cues in the two delay conditions. Cluster-based permutation testing on all the electrodes and the whole epoch was implemented using the FieldTrip software (Maris & Oostenveld, 2007). The cluster-forming threshold and the threshold for statistical testing were both set to a two-tailed alpha level of 0.05. Condition labels were randomly permuted 1000 times with the Monte Carlo method, following the default method implemented in FieldTrip. This provides an automatic method for finding significant clusters, corrected for multiple comparisons, that does not depend on a priori selection of time window and electrodes.

3.2. Representational similarity analysis

As shown in Fig. 1, our experiment used 13 different stimulus configurations (C) during training and $C = 25$ during test, each being a unique combination of number of slices in the left and right 'pies'. We used Representational Similarity Analysis (RSA) (Kriegeskorte et al., 2008) to identify the relationship between these configurations and the multivariate (31-channel) EEG signals as they evolved over time. We downsampled the EEG epochs to 250 Hz and selected the peri-stimulus signal from −200 ms to 1500 ms with respect to stimulus onset. Here we first compute a dissimilarity matrix (DM) for the task-representation model, D_T, and the stimulus-representation model, D_S. The i,jth entry in these matrices is the Euclidian distance between stimulus i and stimulus j in the 1-dimensional feature space for D_T (see Fig. 1, Panel E), and the 2-dimensional input space for D_S.

For example, consider the point i at $[u_1, u_2] = [4, 5]$ and the point j at $[u_1, u_2] = [1, 2]$. Here the distance in input space is $D_S(i,j) = \sqrt{(4-1)^2 + (5-2)^2} = 4.24$. Whereas the distance in task-representation space is $D_T(i,j) = 1 - 1 = 0$ (both i and j have feature value 1 as indicated by the purple shading in Fig. 1, Panel E).

We then computed a neural DM for each subject's ERP data at each point in peristimulus time, with the i,jth entry now being the Euclidian distance between the 31-dimensional ERP vectors (for stimulus i and j). Finally, we computed the Spearman correlation over subjects between neural DMs and the model DMs (partialling out the effect of the other model DM). For all time points, statistical significance was determined non-parametrically at the group level by a cluster-based permutation approach (cluster-forming threshold of $p < 0.05$ two tailed), corrected significance level $p < 0.05$ (two tailed) (Maris & Oostenveld, 2007). We calculated the clusters of time points in which configurations could be discriminated.

4. Results

To assess the emergence of task representation in offline and active wake period, we divided the analysis into two parts. First, in our analysis of the behavioural data, we compared participant "improvement scores", post-test minus the pre-test scores, computed separately for memorization and generalization. We expected that an offline wake period, as compared with a period of active wake, would facilitate consolidation, thereby promoting memory and generalization. Second, for our analysis of the EEG data, we employed RSA to establish links between the neural representations and participants' behavioural results.

4.1. Behavioural results

Improvement score were computed as the difference in proportion of correct responses over trials in the post-test minus the pre-test, computed separately for old (memorization) and new (generalization) stimuli. We performed a 2x2 mixed-design ANOVA, with between-subjects factor the group (Active Wake and Offline Wake) and within-subject factor the novelty (Old vs New) on the improvement scores. We found a significant interaction (F(1,34) = 4.559,p = 0.040), but no main effects (Group: F(1,1) = 0.321,p = 0.574; Novelty: F(1,34) = 0.0006,p = 0.98). To explore the source of the interaction, we conducted follow-up t-tests. While participants memorization for old configurations was not affected by the different wake conditions ($t(34) = -0.7743, p = 0.444$), participants in the offline wake conditions showed a trend towards an improvement in generalization compared to the participants in the active wake condition ($t(34) = 1.72, p = 0.094$), such effect would be significant with a one-sided test in the direction of the hypothesis ($p = 0.047$.), as motivated by previous studies (see introduction) (see Fig. 2).

4.2. ERP analysis of novelty effect in pre and post-delay test epoch

In our investigation, we conducted five cluster-based permutation tests during stimulus epochs. We tested for the effect of old versus new averaged over pre versus post epochs. We also tested for this effect in each of the different phases (pre and post). Between-subject conditions at the averaged activity of different wake conditions and their interaction with novelty. We did not find any significant clusters.

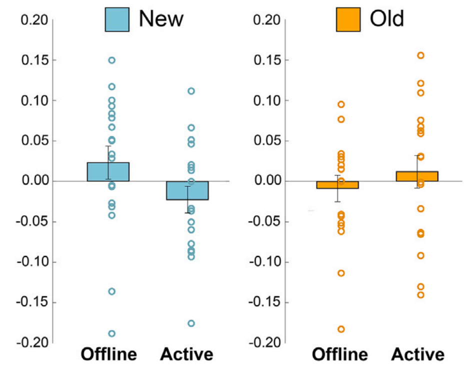

Fig. 2. Improvement Scores *The figure shows the improvement scores for old and new stimuli for both Offline and Active Wake groups. Changes in accuracy related to new stimuli correspond to generalization effects, and old stimuli to memorization effects. The error bars indicate the standard error of the mean.*

4.3. Representation similarity analysis

We analysed the neural similarity between stimulus-bound representations of the stimuli during the pre-test and post-test phases. Fig. 3 shows the correlation between the neural, stimulus-bound and task-relevant dissimilarity matrices during the testing sessions. Importantly, these results are based on data from all subjects in the study (i.e. both active and offline wake groups). Before and just after stimulus presentation, grand average decoding accuracy fluctuated around the chance level. During pre-test, the stimulus-bound representation reached significance 337 ms (337–361 ms), followed by five significant clusters (373–401 ms; 481–501 ms; 581–621 ms; 1219–1243 ms; 1411–1431 ms). The task-relevant representation did not reach significance. During post-test, the stimulus-bound representation reached significance 120 ms (120–145 ms), followed by three significant clusters (305–341 ms; 1187–1223 ms; 1367–1387 ms). The task-relevant representation reached significance at 577 ms (577–650 ms), followed by three significant clusters (962–990 ms; 1195–1243 ms; 1379–1399 ms). We did not find any difference between groups (active versus offline wake) in the emergence of stimulus-bound or task-representations. Furthermore, we split participants within each group into good and bad performers based on their behavioural outcomes and compared these subgroups. This analysis also revealed no significant differences, possibly because of the reduced sample size.

Thus, multivariate analysis of EEG data revealed the temporal dynamics of the task representation. First, a stimulus-bound representation emerges, providing a reconstruction of the stimulus map. This is evident during both test phases of the experiment. Second, a task-based representation emerges but only in the post-test epoch (not pre-test).

5. Discussion

This study investigated the impact of an offline versus online wake period on both generalization and memorization. Behaviourally, we found better generalization performance, represented by better accuracy for novel stimuli, in the active wake group compared to the offline wake group. This result supports our hypothesis that generalization processes are facilitated by an offline wake period. Contrary to expectations, we did not observe improved memory retention in the Offline group compared to the Active group. This finding is inconsistent with prior research indicating enhanced memory recall in

Fig. 3. Stimulus-bound and task-relevant representations *Time course of the correlation between neural and stimulus-bound dissimilarity matrices (green) and neural and task-relevant dissimilarity matrices (pink). The two panels show separate results for pre-test and post-test epochs. These results are based on data from all subjects in the study (i.e. both active and offline wake groups).*

similar contexts (Craig & Dewar, 2018; Dewar et al., 2012). This inconsistency may be due to differences in task design. While previous studies utilized tasks such as story recall (Dewar et al., 2012) or picture recognition (Craig & Dewar, 2018), our paradigm studied associations between stimuli (combinations of symbols in a combinatorial space) and optimal responses to those stimuli. Additionally, our experimental design encouraged participants to learn the underlying structure of the task rather than simply memorizing individual configurations. This might lead participants to use such representation for both old and new stimuli. However, this would suggest a similar performance between old and new stimuli, that we did not find (see supplementary materials). Finally, while our findings are consistent with the hypothesis that quiet rest facilitates generalization, it is important to interpret these results with caution given the risk of both Type II and Type I errors associated with small sample sizes as suggested in prior meta-analytic work on the effects of rest on verbal memory (see Humiston, Tucker, Summer, and Wamsley (2019)), our design may have been underpowered to reliably detect such effects.

With regard to the EEG data, we did not find any EEG-based neural correlates associated with the observed improvement in generalization. First, we did not find any ERP differences between active versus wake conditions, novel versus old stimuli, or the interaction between group and novelty. The lack of a novelty effect may be due to the high degree of similarity among stimulus configurations. Second, we did not find any group-related differences in the RSA analyses. One potential explanation for the lack of findings is that this study may be underpowered, having 18 participants in each group compared to, for example, 30 in Craig et al. (2018).

More positively, we found that task-relevant representations emerged after the delay period and that this occurred regardless of whether participants were in the active or offline groups. Notably, task-relevant representations emerged at comparable latencies to those observed in previous work (from 600 ms) (Menghi et al., 2023). Moreover, consistent with both our prior research and other studies (Luyckx, Nili, Spitzer, & Summerfield, 2019; Menghi et al., 2025), we observed both faster (stimulus-bound) and slower (task-relevant and abstracted) processes. Here, the stimulus-bound representations were observed both before and after the delay, whereas the task-relevant representations could only be detected after the delay.

In our previous study (Menghi et al., 2023) we found that task-relevant representations emerged during the training period whereas this was not the case in the current study. However, in that previous work participants were trained on more repetitions of each stimulus (10 versus 7) and more stimuli (25 versus 13). One reason for reducing the training regime in the current study was to avoid ceiling effects so that participants had room for improvement during the delay period. However, in retrospect, it may have been better to continue training for each participant until they reached a specific threshold of performance (e.g. 65% correct). It could also be that one factor governing the emergence of task-relevant representations is the number of configurations to be learned. A larger number of configurations might prompt participants to focus on learning the task's structure, while a smaller set may facilitate memorization of associations.

In this paper, and in earlier work in the field, "offline" and "online" states have been operationalized using cognitive tasks or a lack thereof, such as spot-the-difference ("online") versus eyes-close rest ("offline"). However, more recent studies acknowledge the high degree of temporal variability in factors such as the internal versus external focus of attention and show that offline versus online states can be more precisely defined using electrophysiological measures. For example, Wamsley et al. (2024) (Wamsley & Collins, 2024) use machine learning based on data from EEG, pupil diameter, reaction time and occasional subjective reports to identify two types of offline states. Similarly, Lacaux et al. (2021) use spectral analyses of EEG data and find that participants who entered the N1 stage of sleep (but not deeper) spontaneously improve on a number reduction task. Future work based on the experimental paradigm in this paper might therefore benefit from having a single participant group but with offline versus online states identified post-hoc using electrophysiological measures.

Concluding, we found that offline wake periods enhanced generalization. No EEG correlates were associated with generalization improvements, possibly due to methodological constraints. However, task-relevant representations emerged post-delay independently of the delay condition.

CRediT authorship contribution statement

N. Menghi: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Formal analysis, Conceptualization. **G. Melega:** Validation, Project administration, Investigation, Data curation. **A. Lidstrom:** Validation, Project administration, Investigation, Data curation. **L. Renoult:** Writing – review & editing, Conceptualization. **W. Penny:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis, Conceptualization.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.nlm.2025.108052.

Data availability

Data will be made available on request.

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